Oscillatory traveling waves reveal predictive coding abnormalities in schizophrenia

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Abstract (240/250)

In recent years, increasing interest has been in describing the computational mechanisms underlying psychiatric disorders. Diverse hypotheses aim at characterizing cognitive and perceptual alterations in schizophrenia and its major symptoms. One hypothesis, grounded in the Bayesian predictive coding framework, proposes that schizophrenia patients have alterations in encoding prior beliefs about the environment, resulting in abnormal sensory inference that may underlie some core aspects of this psychopathology. Here, we test this hypothesis from a neurophysiological perspective, leveraging recent work identifying oscillatory traveling waves as neural signatures of predictive coding. By analyzing one of the largest EEG datasets, comprising 146 schizophrenia patients and 96 age-matched healthy controls, we found that schizophrenia patients have stronger top-down alpha-band traveling waves compared to healthy controls during resting state, thereby reflecting an increased flow of prior information from higher-level into sensory brain areas. EEG traveling waves during resting state were strongly correlated to those observed during a visual backward masking task, showing that schizophrenia patients have an inherent impairment in the flow of prior signals into sensory areas that spans many functioning domains. Importantly, the present results yield a novel spatial-based characterization of oscillatory dynamics in schizophrenia, considering brain rhythms as traveling waves and providing a unique framework to study the different components involved in a predictive coding scheme. Altogether, our findings significantly advance our understanding of the mechanisms involved in fundamental pathophysiological aspects of schizophrenia, promoting a more comprehensive and hypothesis-driven approach to psychiatric disorders.

Keywords: Predictive Coding, Schizophrenia, Traveling Waves, Resting-state, Psychiatry

Significance

We provide novel evidence favoring the Bayesian predictive coding interpretation of schizophrenia. Taking advantage of computational and experimental works that characterized the electrophysiological correlates of predictive processes, we investigate the pattern of oscillatory traveling waves in a large EEG dataset of 146 schizophrenia patients and 96 age-matched healthy controls. Our results reveal stronger top-down alpha-band traveling waves in schizophrenia patients, reflecting an alteration in the precision of their high-level priors.

Traveling waves observed during resting-state were strongly correlated to those observed during a visual backward masking task, suggesting that traveling waves probe a general mechanism of predictive processing. Impairments in this mechanism may underlie some of the major perceptual and cognitive alterations as well as the pronounced clinical symptoms of schizophrenia. The strong hypothesis-driven nature of our results accentuates the relevance of our findings.

Introduction

Schizophrenia is a severe mental disorder with a complex genetic and neurobiological profile that affects about one percent of the world's population (McCutcheon et al., 2020). Schizophrenia is characterized by a large range of psychotic symptoms as well as by strong impairments in mental functioning, including perception, cognition, and personality. Numerous hypotheses and mechanisms have been proposed to explain these abnormalities. One hypothesis is that schizophrenia patients dysfunctionally update their cognitive world model, usually described within the framework of Bayesian inference and predictive coding (Corlett et al., 2009; Krystal et al., 2017). According to this framework, perception combines incoming sensory evidence with prior information, i.e., beliefs about the world (figure 1A). Within this Bayesian framework, it was proposed that schizophrenia patients weigh the prior information more strongly than the sensory information, explaining symptoms such as hallucinations or delusions (Friston et al., 2016; Krystal et al., 2017). Experimental evidence for the hypothesis from behavioral studies is mixed, with supportive ones (Cassidy et al., 2018; Powers et al., 2017), others which found stronger reliance on sensory information in the patients (Stuke et al., 2019; Weilnhammer et al., 2020), and even studies which found intact processing (Choung et al., 2022; Kaliuzhna et al., 2019; Tibber et al., 2013).

Here, we tested the Bayesian hypothesis from a *neurophysiological* perspective. In recent work, it was shown that oscillatory alpha-band (8-12Hz) traveling waves are neural signatures of predictive coding (Alamia & VanRullen, 2019; Arnal & Giraud, 2012; Bastos et al., 2012, 2015; Friston, 2019; Michalareas et al., 2016). In these studies (Alamia & VanRullen, 2019; Pang et al., 2020), neural activity was measured along the central midline of electrodes (Oz-Fz) to determine how oscillations propagate as traveling waves from occipital to frontal areas (forward waves) or in the opposite direction (backward waves). Based on a model, implementing predictive coding under minimal assumptions (Alamia & VanRullen, 2019), the authors proposed that forward traveling waves encode sensory information and prediction-errors (i.e., the difference between top-down predictions and the actual activity), while backward waves carry the prior information (Rao & Ballard, 1999). Importantly, a pharmacological study provided additional evidence for the relationship between traveling waves and predictive coding using a serotonergic psychedelics drug (i.e., N, N-Dimethyltryptamine, DMT; Alamia et al., 2020). According to a recently proposed hypothesis (Carhart-Harris & Friston, 2019), psychedelics act on the high-level prior distributions in the brain, decreasing their precision (defined as the inverse of the variance, figure 1B). As a consequence, there is an increase in

forward waves carrying prediction-errors (figure 1B, left panel). The study confirmed this prediction, observing a decrease (increase) in the alpha-band top-down (bottom-up) traveling waves after the intake. Here, we used the very same analysis to test whether patients rely more on prior beliefs than on sensory evidence, i.e., whether alpha band backward waves are stronger in schizophrenia patients than in healthy controls, and whether forward waves, reflecting the prediction-errors, are lower (figure 1B). We analyze a large EEG dataset comprising 146 schizophrenia patients and 96 age-matched healthy controls.

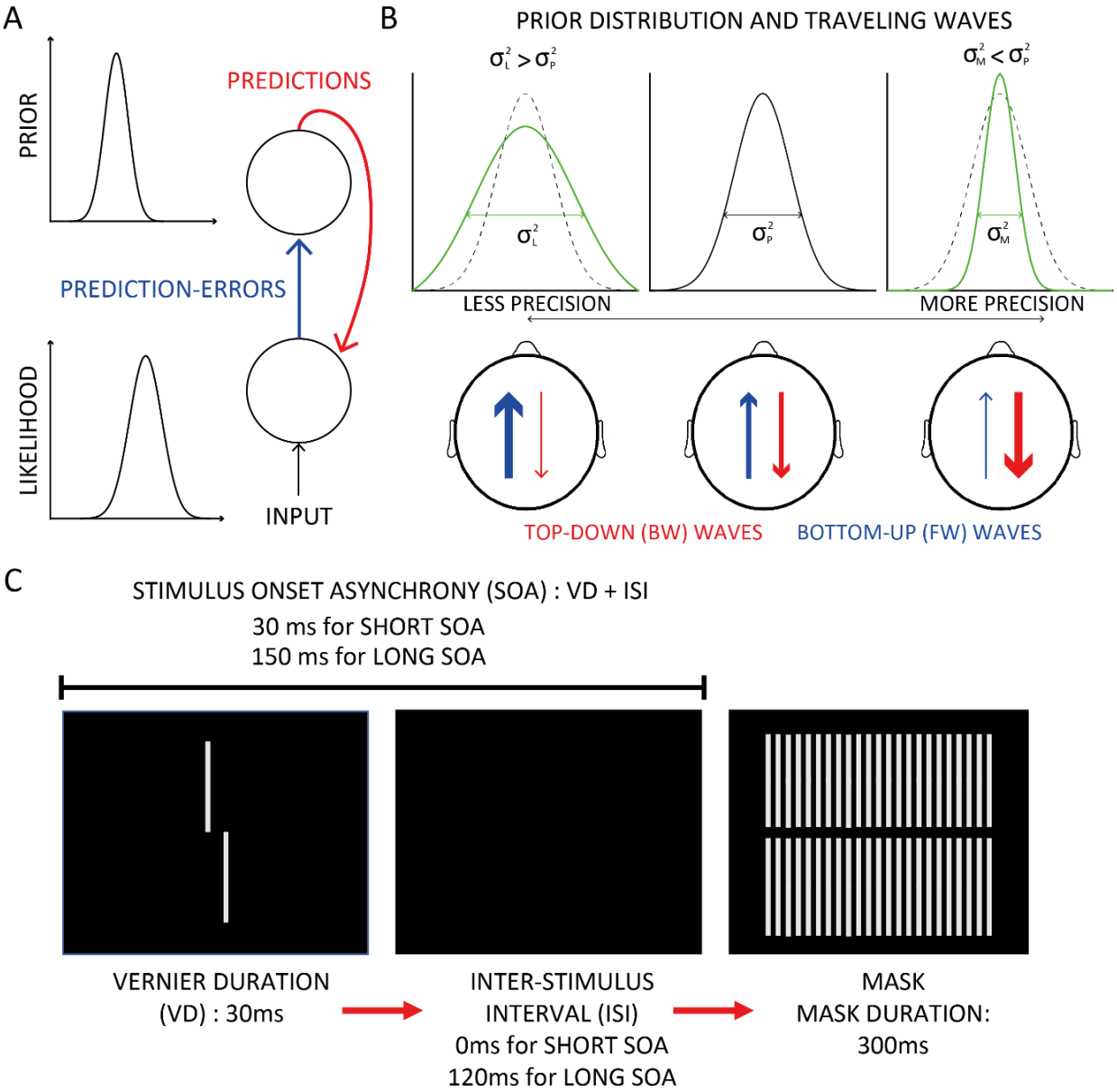

Figure 1 – Predictive coding and traveling waves. A) In the Bayesian predictive coding perspective, predictions are generated by prior distributions in higher brain regions, prediction-errors are computed to update the prior based on the sensory evidence (i.e., the likelihood). B) Considering backward (BW) and forward (FW) waves as proxies of predictions and prediction-errors, respectively (Alamia &

VanRullen, 2019), one would expect different patterns of traveling waves depending on the precision of the prior: more precise prior (rightmost panel) generate stronger predictions, and in turn stronger backward waves, whereas less precise prior information (leftmost pattern) generates inaccurate predictions, hence higher prediction-errors, reflected by stronger forward waves. C) In our experiment, the target consisted of a Vernier, i.e., two vertical lines slightly offset horizontally either to the left or right (as shown). Participants were instructed to indicate the offset direction. A grating mask was presented afterwards, making the discriminability of the offset spatially and temporally challenging.

Results

We re-analyzed EEG data from previous studies with resting state data (eyes closed; da Cruz et al., 2020; Gordillo et al., 2023) and a visual backward masking task (da Cruz, Shaqiri, et al., 2020; Garobbio et al., 2021). We quantified brain oscillations along the central electrodes' mid-line (from Oz to Fz, figure 2), as in our previous work (Alamia & VanRullen, 2019; Pang (庞兆阳) et al., 2020). We considered sliding time windows of 1 and 0.5 seconds from two different datasets, one eyes-closed resting state and one visual backward masking (VBM) task (see Methods and figure 2). First, for all time windows, we create 2D maps by stacking the signals from the seven electrodes, obtaining images with time and electrodes as axes (figure 2).

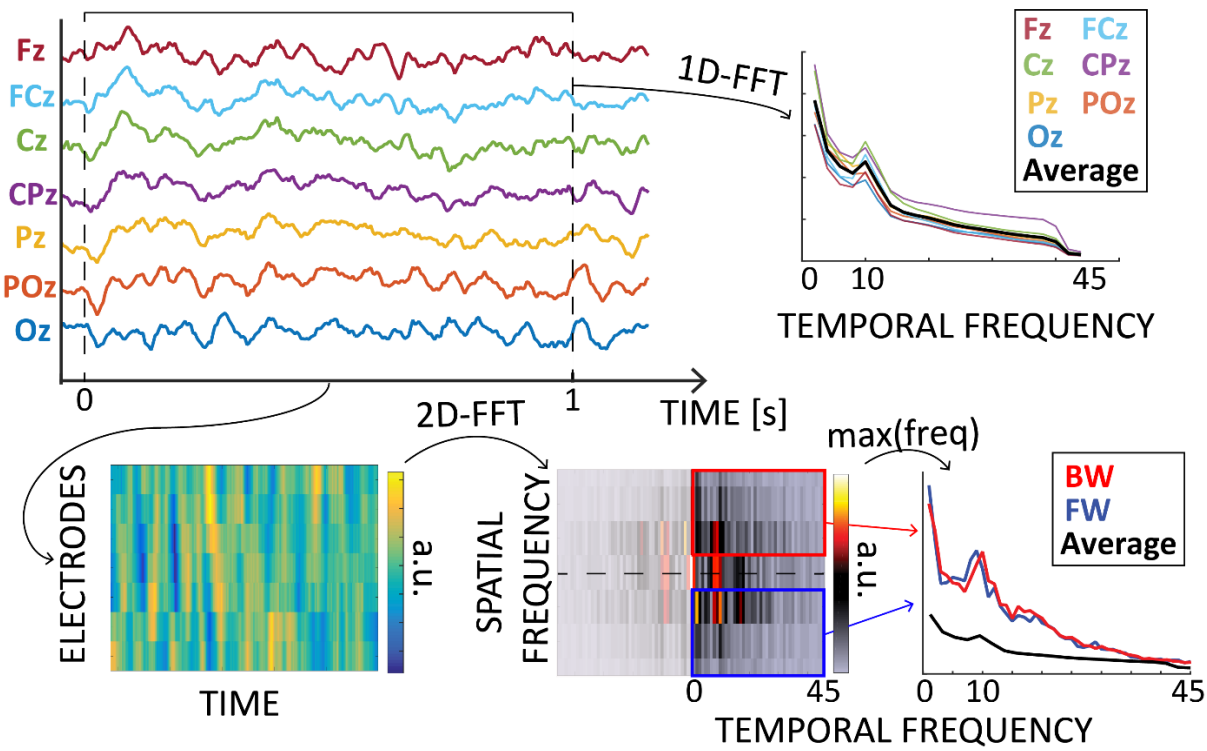

Figure 2 – Quantifying traveling waves. From a 0.5 or 1-second time window, we extract 2D maps by combining seven midline electrodes. We then compute 2D-FFT to evaluate forward (FW – in blue) and backward (BW – in red) waves, as quantified by the maximum values in the lower- and upper-right

quadrants, respectively. Lastly, we computed the waves amount in decibels by using the average 1D-FFT of each electrode as a baseline (see Methods).

For each of these images, we computed 2D Fast Fourier Transform (FFT) to quantify the amount of traveling waves propagating from occipital to frontal areas and vice versa (i.e., forward or backward, respectively). To determine an appropriate baseline (see Methods), we averaged each midline electrode 1D-FFT to obtain a baseline accounting for fluctuations in the overall power unrelated to the traveling waves (i.e., without the spatial information of the electrodes). The waves' amount is expressed as a log-ratio in decibels [dB] (see Methods).

Traveling waves during rest.

In both the patients (N=121) and the control group (N=75), we quantified the spectral power in five frequency bands (θ: 3Hz - 7Hz, α: 8Hz – 12 Hz, low β:13Hz – 22Hz, high β: 23Hz –30 Hz, and γ: 30Hz – 45Hz) along the midline electrodes (from Oz to Fz, see figure 2). First, we compared each electrode's spectral power between the two groups. For each frequency band, we performed Bayesian ANOVA, considering ELECTRODE and GROUP as factors (see Methods for details). As shown in figure 3A, we found a higher spectral power in the patients compared to the control group in the θ and α bands (GROUP factor $BF_{10}>>10^4$ in both frequency bands) but not in the beta- and gamma-bands. For all frequency bands, the ELECTRODE factor revealed a strong effect (all $BF_{10}>>10^{66}$). Next, we focused on the spatial component of brain oscillations by investigating differences in the spectra of traveling waves propagating forward (FW) and backward (BW). Figure 3B shows the spectra for both groups: as in our previous work (Alamia et al., 2023), in the control group, we found a typical spectral pattern with high backward waves in the α and low β (13Hz -22Hz) bands, and a flat profile in the forward waves (i.e., no difference between bands). We then compared the FW and BW spectra of the control group with those of the patients, considering the five frequency bands (θ, α, low and high β, and γ; figure 3B). We performed two-factor ANCOVAs, considering GROUP and BAND as factors and GENDER, AGE, and EDUCATION as covariates. For both FW and BW waves, we found a similar pattern of results: a very strong effect for the BAND factor ($BF_{10}>>10^{11}$ for both FW and BW waves) but mild to no effect in the GROUP factor (BW waves, $BF_{10}=7.519$; FW waves, $BF_{10}=0.514$); however, in both directions, we found a very robust effect of the GROUP x BAND interaction (for both FW and BW waves $BF_{10}>>400$), revealing significant differences between the two groups. Concerning the covariates, there are no effects of EDUCATION or GENDER (BW waves, $BF_{10}<0.4$; FW waves, $BF_{10}<0.8$), but a small effect of AGE for the FW

waves (BW waves, BF_{10}=1.968; FW waves, BF_{10}=4.684). We further analyzed these results by performing Bayesian ANOVAs for each frequency band separately, considering as factors GROUP and DIRECTION (either forward or backward).

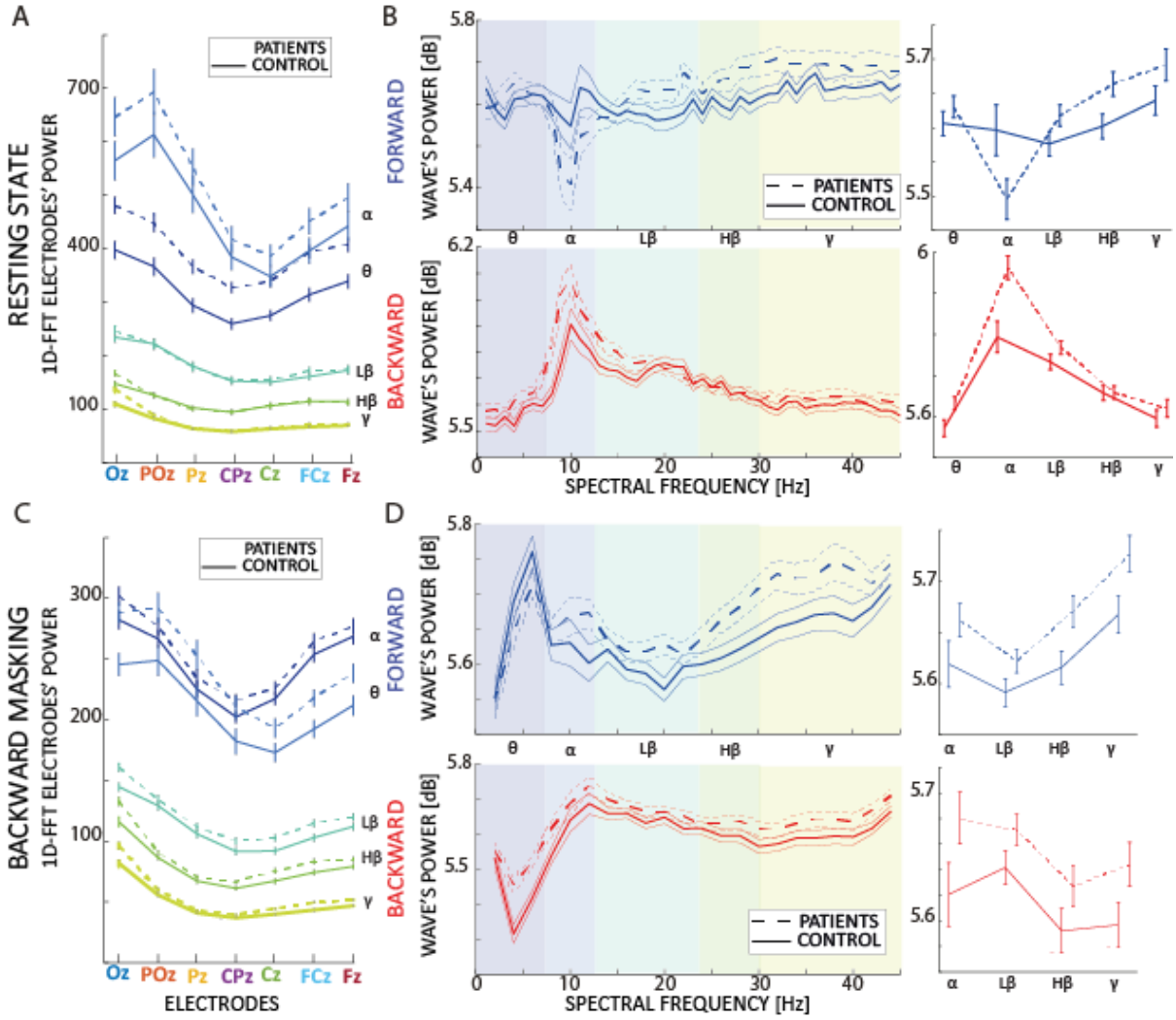

Figure 3 – Differences in traveling waves between patients and controls. A, C) Raw power for each spectral band in the midline electrodes (x-axis), for both the patients and control group in the two datasets. Each color represents a different frequency band. Error bars represent standard errors. B, D) The left panels illustrate the spectra for both forward (blue) and backward (red) waves for the two groups in both datasets; the right panels show the mean for each frequency band. Error bars represent standard errors.

Overall, the results show no difference between the groups (all frequency bands, $0.1<BF_{10}<1$), and a robust effect in the DIRECTION factor for θ, low β, and γ (all $BF_{10}>>10^7$). However, there was a strong interaction between GROUP and DIRECTION in the α band ($BF_{10}>>500$), which, in line with our previous analysis, reveals distinct oscillatory dynamics between the patient and the control group. Specifically, these results confirm the difference shown in figure 3B: the most substantial effect was observed in the alpha-band (as confirmed by a larger Bayes Factor),

where schizophrenia patients revealed an increase in backward waves and a decrease in forward waves.

Traveling waves for backward masking.

Previous results showed that the traveling wave pattern changes drastically between resting state EEG and visual stimulation (Pang (庞兆阳) et al., 2020). To test such differences in schizophrenia patients, we investigated another dataset in which the patient and control group performed a Visual Backward Masking (VBM) task (see Herzog et al., 2004 for details). In VBM, a briefly presented target is followed by a mask that interferes with the target processing (figure 1C). There were 4 conditions: *Vernier only*, *Long SOA*, *Short SOA*, and *Mask only* conditions. In the *Vernier only* condition, there was no mask, whereas in the *Long SOA*, and *Short SOA* conditions, the target Vernier was followed by a mask with either an SOA of 150 or 30 ms, respectively. The Mask only condition provides a control condition, where no target was presented.

As in the resting state analysis, we first assessed the spectral power in each electrode separately (figure 3C), however, given the shorter duration of the analyzed time-window (~300 ms excluding the baseline), we did not include the θ frequency band, as -in the 4Hz case- it barely comprises a full cycle. The Bayesian ANOVA, having ELECTRODE and GROUP as factors, revealed an overall higher power in the patient than in the control group in all frequency bands. As in the previous dataset, we also found a substantial effect of the ELECTRODE factor in all bands (all $BF_{10}>>10^{48}$). We then investigated the FW and BW traveling waves via two-factor ANCOVAs, with GROUP and BAND as primary factors and GENDER, AGE, and EDUCATION as covariates (figure 3D). Regarding the backward waves, we found a strong effect of BAND ($BF_{10}>10^{57}$) as well as GROUP ($BF_{10}>10^{3}$), but no evidence of the interaction ($BF_{10}=0.932$) or the covariates (all $0.4<BF_{10}<1.5$). These results suggest that patients have a higher amount of backward waves irrespective of the frequency band, corroborating the results of the resting state dataset. We found similar results in the FW waves, in which we observed a strong effect in the BAND factor ($BF_{10}>10^{10}$ in the FW waves, and $BF_{10}=10$ in the BW waves) as well as in the group factor ($BF_{10}=32$ and $BF_{10}=10$ in the BW and FW waves, respectively). As in the resting-state dataset, we performed Bayesian ANOVAs for each frequency band, with GROUP and DIRECTION as factors, and we report differences between FW and BW waves in β, and γ (all $BF_{10}>10^{4}$), but no interaction between the two factors in all frequency bands (all $BF_{10}<0.26$). Additionally, we investigated differences in FW and BW waves in each condition separately

(i.e., *Vernier only*, *Long SOA*, *Short SOA*, and *Mask only* conditions, see above for details). As shown in supplementary figure S1, we did not observe any difference between conditions, despite differences in the task and visual stimulation. Overall, these results suggest that forward waves, as measured in this work, do not reflect any specific processes related to the task, but may be rather involved in more global processes, such as task engagement or attention.

Correlation between the resting-state and the VBM dataset.

Out of the 144 patients and 96 control participants, 119 and 75, respectively, also belonged to the resting-state dataset, thus allowing us to reveal whether oscillatory traveling waves during rest are predictive of waves occurring during backward masking, reflecting general dynamics underlying predictive processes, which are not specific to the different tasks and/or experimental design. We correlated band by band the amount of forward and backward waves in both groups (figure 4), using Pearson correlations. Regarding α band traveling waves, we found a medium correlation between datasets in the control group for both FW and BW waves (FW: r=0.48, $BF_{10}>10^4$; BW: r=0.46, $BF_{10}>10^3$), and in the patient group for FW but not BW waves (FW: r=0.32, BF_{10}=19.27; BW: r=0.20, BF_{10}=0.85), possibly suggesting a differential involvement of BW α band oscillations during resting-state and visual perception in schizophrenia patients. Lastly, all other higher frequency bands (i.e., low β, high β and γ) reveal a positive correlation between datasets in both FW and BW waves in the control group (low β: FW: r=0.52, $BF_{10}>10^5$; BW: r =0.31, BF_{10}=5.35; high β: FW: r=0.57, $BF_{10}>10^6$; BW: r=0.55, $BF_{10}>10^5$; γ: FW: r=0.75, $BF_{10}>10^{12}$; BW: r=0.73, $BF_{10}>10^{11}$) and in the patient one (low β: FW: r=0.35, BF_{10}=73.07; BW: r=0.35, BF_{10}>55.12; high β: FW: r=0.42, $BF_{10}>10^3$; BW: r=0.21, $BF_{10}>10^3$; γ: FW: r=0.52, $BF_{10}>10^6$; BW: r=0.35, BF_{10}>73.8).

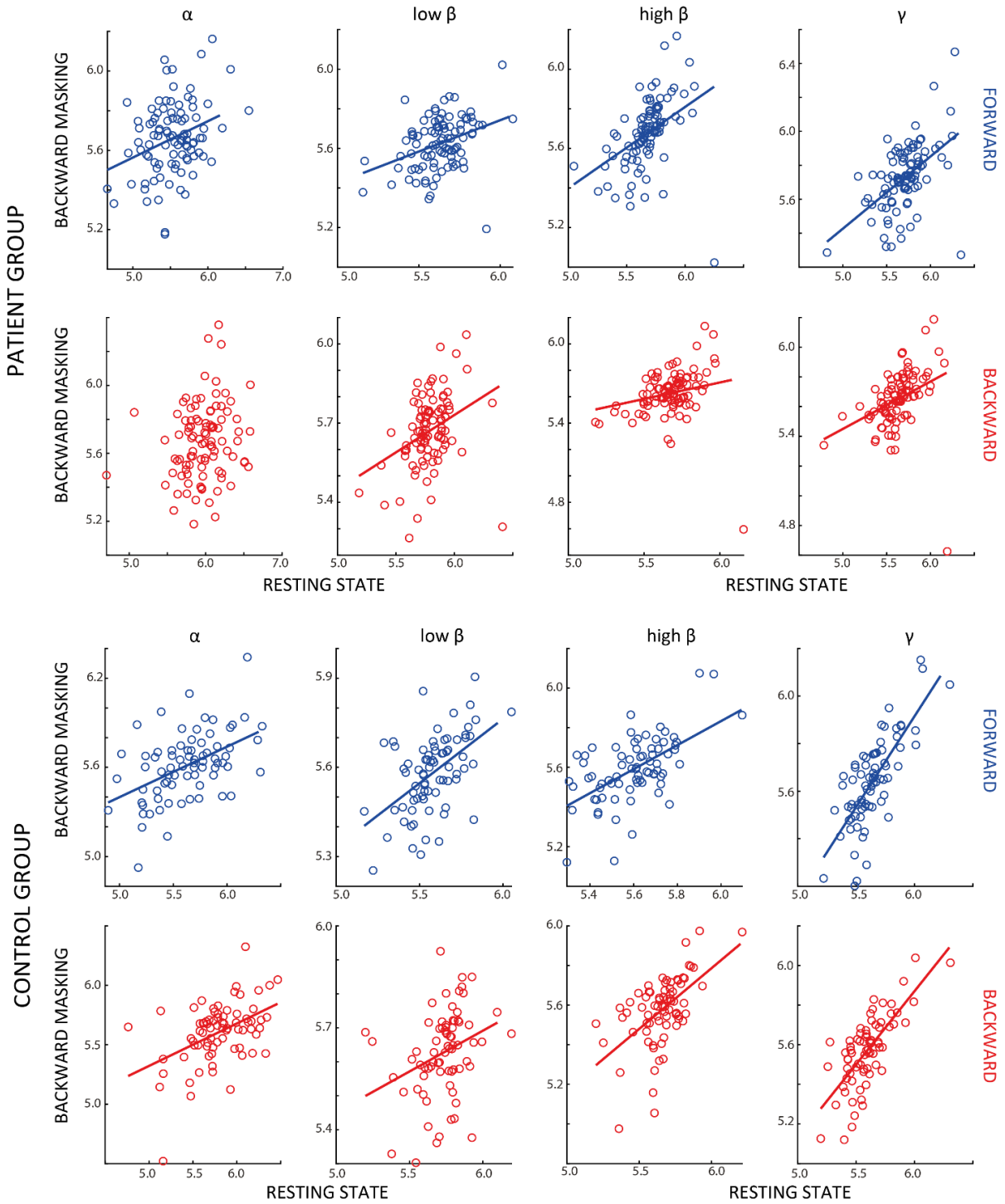

Figure 4 – Correlations between datasets. Each subplot shows the correlation between traveling waves in the two datasets (resting state vs. VBM task). Columns represent different frequency bands, red and blue plots indicate backward and forward waves, respectively. The presence of the fitted line indicates significant (Pearson) correlations (see results for details).

Testing the effects of medication and symptoms profile on traveling waves.

To exclude potential confounds due to medication intake and to investigate whether traveling waves are associated to psychopathology in the schizophrenia patients, we correlated the amount of forward and backward waves in each frequency band with the Chlorpromazine

(CPZ) equivalent dose that each patient received during the time of the recordings and with the scores in the negative and positive symptoms assessment (SANS and SAPS, respectively). All Pearson correlations in both datasets and for all frequency bands provided evidence in favor of the null hypothesis, that is, a lack of correlation between the amount of waves and CPZ-equivalents (resting state dataset: for both FW and BW waves in all frequency band $-0.1<r<0.1$, $BF_{10}<0.19$; VBM dataset: for both FW and BW waves in all frequency band $-0.14<r<0.1$, $BF_{10}<0.22$). Second, we performed a correlation between FW and BW waves and the SANS and SAPS scores (see Methods). We did not find evidence for correlations between traveling waves and SANS or SAPS scores (for both FW and BW waves in all frequency bands, $-0.13<r<0.13$, $BF_{10}<0.23$). We obtained similar results in the VBM dataset, in which we did not find any correlation in most frequency bands ($-0.15<r<0.15$, $BF_{10}<0.3$), except for a small correlation between SAPS and BW waves in the low β ($r=0.24$, $BF_{10}=3.1$), high β bands ($r=0.26$, $BF_{10}=5.16$), and in the γ band ($r=0.26$, $BF_{10}=4.58$); and between SAPS and FW waves in the γ band ($r=0.27$, $BF_{10}=7.404$).

Discussion

Analyzing one of the largest datasets of EEG recordings in schizophrenia patients and healthy controls (da Cruz, Favrod, et al., 2020; da Cruz, Shaqiri, et al., 2020; Garobbio et al., 2021; Gordillo et al., 2023), we found direct evidence for a dysfunctional updating of beliefs about the world in schizophrenia patients (Fletcher & Frith, 2009). Previous studies have shown indirect evidence in favor of this interpretation, which is usually described within the framework of Bayesian inference and predictive coding (Corlett et al., 2009; Krystal et al., 2017), for example, by comparing patients and controls in conditioning paradigms with different levels of expectations (Ellson, 1941; Kafadar et al., 2022; Kot & Serper, 2002). In our study, we directly quantified abnormalities in oscillatory traveling waves, which reflect the flow of information in predictive processes (Alamia et al., 2020; Alamia & VanRullen, 2019). Unlike previous work, our analysis allowed us to visualize and disentangle the different actors involved in the predictive coding process, and eventually compare predictions, flowing from higher to lower cortical areas, and prediction-errors, propagating in the opposite bottom-up direction in schizophrenia patients and healthy controls. Our results reveal a substantial increase in top-down and a decrease in bottom-up alpha-band traveling waves in schizophrenia patients compared to healthy participants in both resting state and visual backward masking, demonstrating that schizophrenia patients have more precise priors (i.e., smaller variability)

than healthy participants (Corlett et al., 2019; Friston, 2005; Powers et al., 2017). Importantly, these findings describe not only the temporal but also the spatial component of brain rhythms, supporting the key idea that oscillatory dynamics are best understood when interpreted as traveling waves propagating across cortical regions, coordinating and synchronizing different brain regions (Alexander et al., 2009; Muller et al., 2018).

Our results may reconcile previously contradictory findings. Some authors proposed that positive symptoms in schizophrenia relate to abnormalities in prior expectations (Wacongne, 2016; Weilnhammer et al., 2020); on the other hand, other authors argued against this interpretation, based on indirect experimental findings, such as intact illusion perception and intact contextual processing (Choung et al., 2022; Grzeczkowski et al., 2018; Lhotka et al., 2023). To reconcile these contradicting findings, a more nuanced framework was proposed to account, separating priors in the lower areas from those in higher ones (Corlett et al., 2019; Sterzer et al., 2018). For example, visual illusions may rely on relatively lower-level priors, which affect visual perception specifically, whereas schizophrenia patients may have impairments in higher-level priors, involved in higher-order functions. Accordingly, schizophrenia patients proved to be more sensitive than controls to illusions involving higher-order processing, such as temporal expectations in the triple flash illusion (Norton et al., 2008), than simpler visual illusions. Crucially, our results are in line with this hypothesis. In particular, we measured traveling waves during rest and during a visual backward masking task, in which neither predictions nor sensory expectations play any substantial role (especially in resting state), suggesting that alpha-band traveling waves do not reflect specific perceptual features of the task, but rather broader brain states. This conclusion is further corroborated by the lack of difference between distinct conditions in the visual backward masking task (fig. S1).

Neural oscillations have long been studied in schizophrenia research and have been proposed to play a crucial role in coordinating neural activity, and aberrancies in their strength and synchronization may be a core pathophysiological mechanism of schizophrenia (Uhlhaas & Singer, 2006, 2010). Our findings are consistent with previous studies, in which differences between schizophrenia patients and healthy controls have been observed in several frequency bands during resting-state (Gordillo et al., 2023; Newson & Thiagarajan, 2019) and different tasks or experimental conditions (Hirano & Uhlhaas, 2021; Javitt et al., 2018; Roach & Mathalon, 2008). For example, during resting-state, schizophrenia patients show increased activity in the delta, theta and beta bands (Venables et al., 2009), whereas activity in the alpha and gamma bands is strongly decreased, compared to healthy controls (Knyazeva et al., 2008; Uhlhaas & Singer, 2013). Similarly, during visual processing, activity in the delta, theta and

gamma bands has been shown to be reduced in schizophrenia patients (Martínez et al., 2018; Uhlhaas et al., 2006). Accordingly, our results reveal consistent differences between schizophrenia patients and healthy participants in a broad-band fashion but with a more substantial effect in the alpha-band, consistent with our hypothesis. As in our work, previous studies also related brain oscillations to predictive coding, associating prediction and prediction-error to different frequency bands based on consistent experimental evidence (Bastos et al., 2012, 2015; Michalareas et al., 2016; Vezoli et al., 2021). Specifically, gamma oscillations (>30Hz) reflect local cortical processes, and besides characterizing a wide range of cognitive functions (Lundqvist et al., 2016; Zhang et al., 2012), they proved to match reliably sensory expectations and prediction errors, corroborated by the fact that the regular repetition and the unexpected omission of a stimulus respectively decrease and increase gamma oscillations' activity (Fujioka et al., 2009; Iversen et al., 2009). In agreement with our interpretation, alpha and beta band oscillations (~8-30Hz) have been related to top-down activity, carrying predictions from higher to lower brain regions (Haegens et al., 2011; Samaha et al., 2015; van Pelt et al., 2016). In our results, the relationship between top-down traveling waves and prior belief is further corroborated by the positive correlation between backward waves in the beta and gamma bands, and positive symptoms assessment (SAPS), which quantifies the symptoms related to hallucinations, delusions, and aberrancies in perception. Importantly, our study is the first one to consider oscillations as traveling waves propagating through the cortex in a forward and backward manner, thus, taking into account not only the temporal but also the spatial dimension of oscillations. It is this aspect that allowed us to reconcile the mixed findings about Bayesian predictions in schizophrenia.

All in all, our findings demonstrate that schizophrenia patients have stronger priors, which elicit stronger alpha-band oscillations, leading to a dysfunctional updating of their cognitive world model. Our results provide direct and convincing evidence in favor of an abnormality in high-level prior in schizophrenia patients.

Methods

Participants. We present resting-state and evoked EEG data collected from two groups of participants: schizophrenia patients (N=146) and healthy controls (N=96). Resting-state EEG data were recorded for 121 schizophrenia patients and 75 healthy controls. Visual backward masking (VBM) EEG data were recorded from 144 schizophrenia patients and 96 healthy

controls, with 119 schizophrenia patients and 75 healthy controls also having resting-state recordings. Previous studies have already utilized the resting-state data for 121 schizophrenia patients and 75 healthy controls (Gordillo et al., 2023), as well as the VBM EEG data for 121 schizophrenia patients and 94 healthy controls (Garobbio et al., 2021).

Schizophrenia patients were recruited from the Tbilisi Mental Health Hospital or the psycho-social rehabilitation center. Among the patients, 49 were inpatients, while 97 were outpatients. Diagnostic assessment for patients was determined using the Diagnostic and Statistical Manual of Mental Disorders Fourth Edition (DSM-IV) through interviews, information from staff, and examination of patients' records. The severity of the patient's symptoms was assessed by an experienced psychiatrist using the Scale for the Assessment of Negative Symptoms (SANS) and the Scale for the Assessment of Positive Symptoms (SAPS). Out of the 144 patients, 131 were receiving neuroleptic medication. The equivalent doses of Chlorpromazine (CPZ) are provided in Table 1.

Controls were selected from the general population in Tbilisi, aiming to closely match the demographics of the patient group. All control participants had no psychiatric axis I disorders and no family history of psychosis. Exclusion criteria included alcohol or drug abuse, severe neurological incidents or diagnoses, developmental disorders such as autism spectrum disorder or intellectual disability, or other significant somatic illnesses affecting mental functioning. These criteria were assessed through interviews conducted by certified psychiatrists. Detailed characteristics of the groups are presented in Table 1.

Before participating in the study, all individuals provided informed consent and were informed of their right to withdraw from the study at any time. The study procedures were conducted in accordance with the Declaration of Helsinki (except for preregistration) and were approved by the Ethical Committee of the Institute of Postgraduate Medical Education and Continuous Professional Development in Georgia (protocol number: 09/07; title: "Genetic polymorphisms and early information processing in schizophrenia").

Table 1.

	VBM patients	VBM controls	Statistics	RS patients	RS controls	Statistics
Gender (M/F)	115/29	49/47	$X^2(1)=22.108$, $P<0.001$[a]	22/99	39/36	$X^2(1)=24.702$, $P<0.001$[a]

Age (years)	35.5±9.1	35.0±8.3	t(238)=-0.393, P=0.695[b]	35.8±9.2	35.1±7.7	t(194)=-0.519, P=0.604[b]
Education (years)	13.2±2.6	15.2±2.9	t(238)=-5.432, P<0.001[b]	13.3±2.6	15.1±2.9	t(194)=4.418, P<0.001[b]
Handedness (L/R)	7/137	6/90	X^2(1)=0.217, P=0.641[a]	6/115	4/71	X^2(1)=0.013, P=0.908[a]
Illness duration (years)	10.7±8.5			10.8±8.7		
SANS	10.1±5.2			10.1±5.2		
SAPS	8.7±3.2			8.6±3.2		
CPZ equivalent	578.3±391.6			561.1±389.4		
Visual acuity	1.4±0.4	1.6±0.4	t(238)=-3.388, P<0.001[b]	1.4±0.4	1.6±0.4	t(194)=2.969, P=0.003[b]
Vernier duration*	20 [20, 50]	20[20, 20]	X^2(1)=37.949, P<0.001[c]	20 [20, 52.5]	20[20, 20]	X^2(1)=28.25, P<0.001[c]

Note: SANS, Scale for the Assessment of Negative Symptoms; SAPS, Scale for the Assessment of Positive Symptoms; CPZ, Chlorpromazine equivalents

[a] Pearson's chi-squared test

[b] Two-sided independent samples t-test

[c] Mood's median test

*Median [25th percentile, 75th percentile]; Vernier duration value is missing for one patient in both datasets

Experimental procedure.

Visual backward masking:

Stimuli. The stimuli consisted of two vertical line segments of 10' (arc-minutes) length with a gap of 1'. The lower bar was slightly offset either to the left or right compared to the

upper bar. The offset was fixed at about 1.2'. The mask was composed of 25 verniers without offset separated by 3.33'.

Apparatus. The stimuli were displayed on a cathode ray tube screen (Siemens Fujitsu P796-1) with a refresh rate of 100 Hz. The screen resolution was 1024 x 768 pixels. Participants were seated at 3.5m from the monitor in a dimly lit room. A pixel comprised about 18" (arc-seconds). Stimuli were white. The luminance was 100 cd/m^2 (measured with a Gretag Macbeth Eye-One Display 2 colorimeter) on a black background of < 1 cd/m^2.

Adaptive procedure. Further details of the paradigm can be found in a previous study (Herzog et al., 2004). We determined the Vernier Discrimination Threshold (VD) required for participants to achieve 75% of correct responses in identifying a vernier offset of 0.6'. Participants were required to achieve a VD shorter than 100 milliseconds. The vernier stimulus, with the individualized VD for each participant and an offset of 1.2', was presented, followed by an interstimulus interval and a mask lasting 300 milliseconds. Using a staircase procedure, we adaptively determined the target-mask stimulus onset asynchrony (SOA), calculated as the sum of VD and interstimulus interval (ISI), to achieve a performance level of 75% correct responses. This was done using Parametric Estimation by Sequential Testing (PEST). Each participant completed the test twice, and the results of the first and second tests were averaged and are presented in Table 1.

EEG experiment: ERP latencies and amplitudes vary with VD. Hence, for the EEG experiment, we maintained VDs and SOAs constant thereby using the same stimuli for all observers. We set the VD to 30 milliseconds, which corresponds to the average VD observed in previous studies involving patients (Chkonia et al., 2010; Herzog et al., 2004). Our experiment encompassed four distinct stimulus conditions (Favrod et al., 2017, 2019; Plomp et al., 2013). In the *Vernier Only* condition, only the target vernier stimulus was presented. The *Long SOA* condition involved the presentation of the mask following the target vernier, with an SOA of 150 milliseconds. In contrast, the *Short SOA* condition featured the immediate presentation of the mask after the target vernier, resulting in an SOA of 30 milliseconds. The selection of SOAs for the *Long SOA* and *Short SOA* conditions was based on the mean SOAs observed in previous studies involving both schizophrenia patients and controls (Chkonia et al., 2010; Favrod et al., 2018; Herzog et al., 2004; Plomp et al., 2013). To provide a control condition, we included the Mask Only condition, wherein only the mask stimulus was presented. In this particular case, accuracy was determined by comparing the left/right offset response to a randomly chosen hypothetical offset.

Resting-state: Resting-state EEG data were recorded for 5min. Participants were seated in a dimly lit room and were instructed to close their eyes and relax during the recording.

EEG recording and Preprocessing. EEG was recorded using a BioSemi Active 2 system with 64 Ag-AgCl sintered active electrodes, referenced to the common mode sense electrode. The sampling rate was 2048 Hz. Offline data were downsampled to 512 Hz and preprocessed using an automatic preprocessing pipeline (da Cruz et al., 2018). For resting-state EEG data, the preprocessing included the following steps: high-pass filtering at 1 Hz; power line noise removal (using CleanLine; www.nitrc.org/projects/cleanline); re-referencing to the bi-weight estimate of the average of all electrodes; removal and 3D spline interpolation of bad electrodes; removal of bad epochs; independent component analysis (ICA) to remove artifacts related to eye-movements, muscle activity, and bad electrodes, and removal of epochs with artifacts (1s epochs). For VBM EEG data, the preprocessing was similar to the resting-state data with the difference that a band-pass filtering between 1 and 40 Hz was performed instead of high-pass filtering at 1 Hz. VBM EEG data from 2 patients (both present in the resting-state dataset) and 2 healthy controls (1 present in the resting-state dataset) were discarded due to excessive EEG artifacts.

Traveling wave analysis. As in our previous studies (Alamia et al., 2020; Pang (庞兆阳) et al., 2020) we quantified traveling waves' propagation along seven midline electrodes, running from occipital to frontal regions (Oz, POz, Pz, CPz, Cz, FCz, Fz, as shown in figure 1). After segmenting the signal in a 1-second time window, we stacked the signals from the seven electrodes to create 2D maps, with time and electrodes as axes. From each map, we compute 2D-FFT transformation: importantly, the power in the lower and upper quadrants quantifies the amount of forward (FW - from occipital to frontal electrodes) and backward (BW - from frontal to occipital) waves, respectively (see figure 1). For each frequency in the 2-45Hz range, we considered the maximum values in both the upper and lower quadrant, obtaining a spectrum for both *BW* and *FW* waves, respectively. We then needed to determine a baseline to account for fluctuations in the overall power unrelated to the traveling waves. For this reason, we computed the *average* 1D-FFT of each midline electrode, which provides a baseline accounting for the spectral power unrelated to the traveling waves (i.e., without the spatial information obtained by combining the electrodes). We finally obtained the waves' amount in decibels [dB] as:

$$FW\ [dB] = 10 * log_{10}\left(\frac{FW}{average}\right); \quad BW\ [dB] = 10 * log_{10}\left(\frac{BW}{average}\right).$$

This value quantifies the total waves compared to the null distribution, thus being informative when contrasted against zero. It is important, however, to notice that this is a surface-level analysis, and it is not informative about the underlying sources. When interpreting these traveling waves results, it is also important to consider issues related to long-range connections and distortions due to scalp interference (Alexander et al., 2019; Nunez, 1974). In particular, when considering traveling waves analysis with non-invasive surface recordings (such as EEG), it is crucial to consider distortions and interference between coincident waves and limitations due to the electrode configurations (Alexander et al., 2019; Nunez, 1974, 2000). Specifically, it's possible to detect only waves shorter than the spatial length of the sensor array and waves longer than twice the distance between electrodes (due to the Nyquist criterion in space). In addition, different cortical processes may generate a similar pattern of traveling waves visible via surface recordings (Alamia & VanRullen, 2023), thus limiting the interpretation of possible underlying sources.

Statistical analyses. We analyzed frequency-band averaged traveling waves by means of Bayesian ANOVAs. In all analyses, we computed Bayes Factors (BF) as the ratio between the models testing the alternative against the null hypothesis. All BFs are denoted as BF_{10} throughout the paper. In practice, BFs provide substantial (BF>~5) or strong (BF>~10) evidence in favor of the alternative hypothesis, and low BF (BF<~0.5) suggests a lack of effect (Masson, 2011). In each dataset, we performed a Bayesian ANOVA on each electrode spectral power considering ELECTRODE (from Oz to Fz along the midline) and GROUP (patients and control) as fixed factors and SUBJECT as the random term. We also performed an ANCOVA considering GENDER, AGE, and EDUCATION as covariates, GROUP and BAND as fixed terms, and SUBJECT as random terms. Lastly, all Bayesian correlations were computed considering both Pearson and Kendall, but we reported for simplicity only Bayes Factor for the Pearson *r*, (similar results were obtained considering Kendall correlations). We performed all analyses in JASP (Love et al., 2019), considering default uniform prior distributions.

Acknowledgment

This project was funded by the European Union under the European Union's Horizon 2020 research and innovation program (grant agreements No. 101075930 to Andrea Alamia) and the National Centre of Competence in Research (NCCR) Synapsy financed by the Swiss National Science Foundation under grant 51NF40-185897. Views and opinions expressed are however

those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council (ERC). Neither the European Union nor the granting authority can be held responsible for them

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Supplementary figure S1

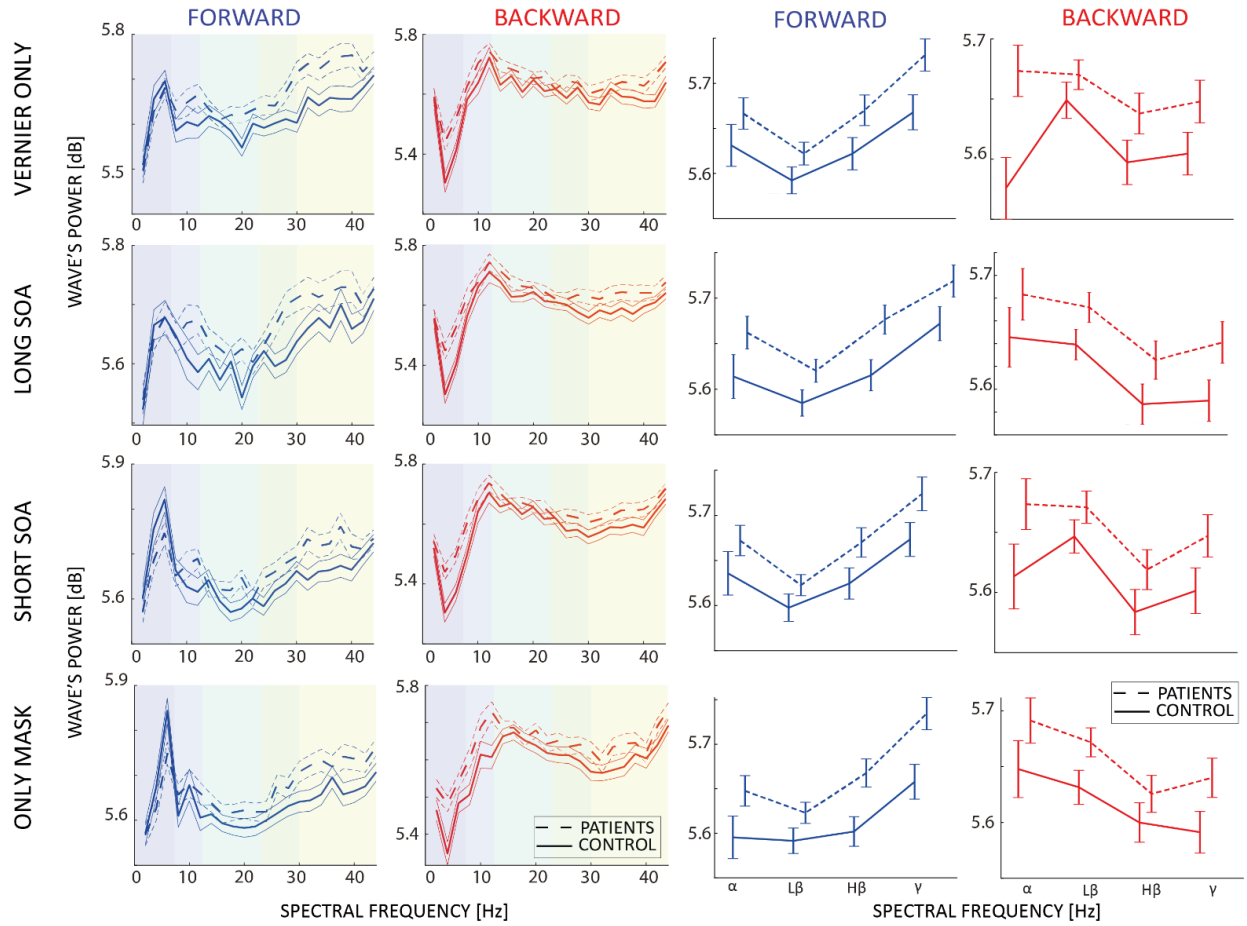

Figure S1 – Differences in traveling waves between patients and control in the visual dataset task. Each row represents a different condition. As in the main figures, the left panels show the spectra for both forward (blue) and backward (red) waves for the two groups in both datasets; the right panels show the mean for each frequency bands. Error bars represent standard errors.