



Abnormalities in both stimulus-induced and baseline MEG alpha oscillations in the auditory cortex of children with Autism Spectrum Disorder

Vardan Arutiunian¹ · Giorgio Arcara³ · Irina Buyanova^{2,10} · Makar Fedorov⁴ · Elizaveta Davydova^{5,8} · Darya Pereverzeva⁵ · Alexander Sorokin^{5,6} · Svetlana Tyushkevich⁵ · Uliana Mamokhina⁵ · Kamilla Danilina^{5,9} · Olga Dragoy^{2,7}

Received: 8 July 2023 / Accepted: 22 April 2024 / Published online: 29 April 2024
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2024

Abstract

The neurobiology of Autism Spectrum Disorder (ASD) is hypothetically related to the imbalance between neural excitation (E) and inhibition (I). Different studies have revealed that alpha-band (8–12 Hz) activity in magneto- and electroencephalography (MEG and EEG) may reflect E and I processes and, thus, can be of particular interest in ASD research. Previous findings indicated alterations in event-related and baseline alpha activity in different cortical systems in individuals with ASD, and these abnormalities were associated with core and co-occurring conditions of ASD. However, the knowledge on auditory alpha oscillations in this population is limited. This MEG study investigated stimulus-induced (Event-Related Desynchronization, ERD) and baseline alpha-band activity (both periodic and aperiodic) in the auditory cortex and also the relationships between these neural activities and behavioral measures of children with ASD. Ninety amplitude-modulated tones were presented to two groups of children: 20 children with ASD (5 girls, $M_{\text{age}} = 10.03$, $SD = 1.7$) and 20 typically developing controls (9 girls, $M_{\text{age}} = 9.11$, $SD = 1.3$). Children with ASD had a bilateral reduction of alpha-band ERD, reduced baseline aperiodic-adjusted alpha power, and flattened aperiodic exponent in comparison to TD children. Moreover, lower raw baseline alpha power and aperiodic offset in the language-dominant left auditory cortex were associated with better language skills of children with ASD measured in formal assessment. The findings highlighted the alterations of E / I balance metrics in response to basic auditory stimuli in children with ASD and also provided evidence for the contribution of low-level processing to language difficulties in ASD.

Keywords Autism Spectrum Disorder · Auditory cortex · Event-related desynchronization (ERD) · Excitation (E) / inhibition (I) balance · Language abilities · Periodic and aperiodic activity

✉ Vardan Arutiunian
vardan.arutyunyan89@gmail.com

¹ Center for Child Health, Behavior and Development, Seattle Children’s Research Institute, 1920 Terry Ave, Seattle, WA 98101, United States of America

² Center for Language and Brain, HSE University, Moscow, Russia

³ IRCCS San Camillo Hospital, Venice, Italy

⁴ Center for Language and Brain, HSE University, Nizhny Novgorod, Russia

⁵ Federal Resource Center for ASD, Moscow State University of Psychology and Education, Moscow, Russia

⁶ Haskins Laboratories, New Haven, CT, United States of America

⁷ Institute of Linguistics, Russian Academy of Sciences, Moscow, Russia

⁸ Chair of Differential Psychology and Psychophysiology, Moscow State University of Psychology and Education, Moscow, Russia

⁹ Scientific Research and Practical Center of Pediatric Psychoneurology, Moscow, Russia

¹⁰ University of Otago, Dunedin, New Zealand

Introduction

Stimulus-induced and resting-state / pre-stimulus alpha-band (8–12 Hz) neural activity in magneto- and electroencephalography (MEG and EEG) is related to a variety of perceptual and cognitive processes and abilities, including visual spatial orienting (Doesburg et al. 2016; Hong et al. 2015), working memory (Bonfond and Jensen 2012; Zheng et al. 2021), attention (Cona et al. 2020; Händel et al. 2011; Hanslmayr et al. 2011), filtering of irrelevant information (Payne et al. 2013), etc. In the sensory systems, event-related alpha-band desynchronization (ERD) is associated with the involvement of a neural tissue in stimulus-induced information processing (Bastarrika-Iriarte and Gaudes-Caballero 2019; Bastiaansen et al. 2001; Weisz et al. 2011), whereas synchronization in the alpha-band reflects the suppression or filtering external stimuli (Klimesch 2012; Klimesch et al. 2007). At the same time, resting state / baseline or pre-stimulus alpha power indicates the extent of cortical excitability, i.e., the lower power is related to the higher level of excitation of the cortical network (Mathewson et al. 2011; Thies et al. 2018). Summarizing, alpha oscillations are associated with neural excitability and inhibition and in MEG / EEG can be a non-invasive measure of the activation level in the brain (Bazanov and Vernon 2014; Bergmann et al. 2019; Sauseng et al. 2009).

According to recent studies, the neurobiology of Autism Spectrum Disorder (ASD) is hypothetically related to the imbalance between neural excitation (E) and inhibition (I) (Edgar et al. 2016; Levin and Nelson 2015; Rubenstein and Merzenich 2003; Seymour et al. 2020; Sohal and Rubenstein 2019; Tang et al. 2021; Yizhar et al. 2011) and, thus, investigation of alpha oscillations may be of particular interest in this population. ASD is a neurodevelopmental disorder characterized by the deficits in social interaction / communication and the presence of repetitive / restricted behavior (American Psychiatric Association 2013). Along with the core symptoms, children with ASD may have co-occurring intellectual disability (Polyak et al. 2015), language impairment (Kjelgaard and Tager-Flusberg 2001), attention deficit (Matson et al. 2013), reduced working memory (Habib et al. 2019), etc. Numerous studies have revealed that dysregulated stimulus-induced and resting-state / baseline alpha-band activity is reflected in core and co-occurring conditions of ASD (Dickinson et al. 2018; Larrain-Valenzuela et al. 2017; Keehn et al. 2017).

Research in alpha-band ERD has shown an abnormal suppression of the alpha power in different sensory systems and during different tasks in children with ASD (Cañigual et al. 2021; Ewen et al. 2016; Murphy et al. 2021). For example, Keehn et al. (2017), using an attentional capture task, demonstrated that children with ASD exhibited a

significantly lower alpha desynchronization level in different cortical regions compared to age- and non-verbal IQ-matched typically developing (TD) controls. In the visual system, the altered alpha-band ERD was also observed in individuals with ASD and the amplitude of ERD correlated with the severity of autistic symptoms (Martínez et al. 2019). In the auditory cortex, Bloy et al. (2019) showed that the greater ERD was associated with better language abilities of children with ASD, however, no between-group difference in ERD has been observed.

Abnormalities in resting-state / baseline or pre-stimulus alpha-band activity were also detected in a variety of cortical regions in autistic individuals, but the findings are controversial and showed both lower and higher alpha power in this population depending on age and condition, such as eyes closed vs. open (e.g., Bellato et al. 2020; Cantor et al. 1986; Chan et al. 2007; Cornew et al. 2012; Dawson et al. 1995; Edgar et al. 2015b, 2019; Larrain-Valenzuela et al. 2017; Leno et al. 2018; Levin et al. 2017; Liang and Mody 2022; Mash et al. 2020; Mathewson et al. 2012; Murias et al. 2007; Neuhaus et al. 2021; Sheikhan et al. 2012; Shepard et al. 2018; Takarae et al. 2022; Tierney et al. 2012; Wang et al. 2013; Zhao et al. 2023). In general, reduced alpha power during rest is associated with increased neural activation (Chapeton et al. 2019; Jensen and Mazaheri 2010), pointing to a higher level of excitability in the cortical networks in ASD. Some authors proposed that the etiology of such neural profile in ASD can be related to abnormal functioning of gamma-aminobutyric acidergic (GABAergic) inhibitory system (see, Wang et al. 2013). These alterations in resting-state / baseline or pre-stimulus alpha activity were linked to the core and co-occurring conditions in ASD such as deficit in social functioning, intellectual delay, impairments in language and auditory processing, attention to details, etc. (e.g., Dickinson et al. 2018; Edgar et al. 2015a, 2019; Larrain-Valenzuela et al. 2017; Leno et al. 2021; Mathewson et al. 2012; Neuhaus et al. 2021). Remarkably, some studies showed that the relationship between resting-state alpha power and cognitive functioning of children with ASD depended on the children's age (e.g., Edgar et al. 2019). It is important to note that although resting-state and pre-stimulus alpha activity can reflect different phenomena, some authors consider them as a similar measure of the same state (e.g., Bai et al. 2016).

Summarizing, most previous studies revealed atypicality in alpha-band ERD and resting-state / baseline alpha power in ASD, which hypothetically can be related to the imbalance between E and I. This abnormal oscillatory functioning was reflected in core and co-occurring conditions of ASD. However, although a number of studies have focused on the alpha-band activity in ASD, most of them addressed visual, frontal or somatosensory systems, whereas the knowledge

on auditory alpha oscillations (both ERD and baseline) is limited (see Weisz et al. 2011). At the same time, given the functional importance of alpha-band neural activity in the basic auditory perception, its pathological state in the auditory cortex can be related to language abilities of children with ASD.

Previous studies with other paradigms have also shown that the low-level auditory perception is altered in ASD and can be associated with language and communication impairments in these children (e.g., Berman et al. 2016; Bloy et al. 2019; Matsuzaki et al. 2019; Roberts et al. 2008, 2010, 2011, 2019, 2021). For example, Roberts et al. (2011), using mismatch negativity paradigm in MEG (MMF), have shown that a delayed latency of this response was related to language abilities of children with ASD. In a group of minimally verbal autistic individuals, it has been revealed the delayed latencies of M50 and M100 components in comparison to verbal individuals with ASD (Roberts et al. 2019). Using 40 Hz Auditory Steady-State Response (ASSR) paradigm, Stroganova et al. (2020) have demonstrated the specific left-hemispheric deficit in sustained field (SF) in the ‘core auditory area’ in children with ASD and proposed a possible association between this response and pitch processing. A direct link between 40 Hz steady-state gamma response in the language-dominant left auditory cortex and the language abilities of children with ASD has been shown in Arutiunian et al. (2023b) study. A similar relationship between low-level gamma activity and language skills in autistic children was also revealed by Roberts et al. (2021). Therefore, previous studies have identified that the primary and secondary processing difficulties in the auditory cortex can be associated with language impairment in ASD.

The goal of this study was to investigate stimulus-induced alpha ERD and baseline alpha activity (both periodic and aperiodic components) in the auditory cortex of children with ASD, using MEG. *First*, we aimed to estimate the cortical sources of the sustained auditory response and to assess the stimulus-induced and baseline alpha activity in the same region. We expected that similar to the findings in other sensory systems, alpha-band ERD and baseline alpha activity would be altered in the auditory cortex of children with ASD. *Second*, the study addressed the relationships between alpha-band parameters and individual characteristics of children with ASD (language abilities, non-verbal IQ, the severity of autism, age). The novelty of the study is that it focused on the auditory alpha activity which is largely unexplored compared to the alpha-band activity in other cortical systems (Weisz et al. 2011). Moreover, the study addressed not only the raw baseline power in the auditory cortex but also periodic (oscillatory) and aperiodic (arrhythmic) components of a neural field that are associated with different neurobiological mechanisms (see Levin et al.

2020). This will help to highlight specific mechanisms that could be altered in children with ASD and related to their language functioning.

In the previous study with the same group of participants (Arutiunian et al. 2023a), we analyzed stimulus-induced auditory and visual alpha oscillations in children with ASD and their relationships with the severity of autistic traits. The present study aimed to reanalyze the data from the previous work and to present a comprehensive neural parameterization as well as association of different neural parameters with a number of phenotypic characteristics of children with ASD.

Methods

Participants

Forty children were included in this study: 20 children with ASD (5 female, age range 8.02–14.01 years, $M_{\text{age}} = 10.03$, $SD = 1.7$) and 20 TD children (9 female, age range 7.02–12.03 years, $M_{\text{age}} = 9.11$, $SD = 1.3$). All participants had normal hearing (based on the parental reports as well as the screening with Audiogramm version 4.6.1.3, Professional Audiometric System; Sennheiser HAD 280 audiometry headphones) and normal or corrected-to-normal vision (based on the parental reports).

Children with ASD met the criteria of the International Classification of Diseases – 10 (World Health Organization 2016), and 18 out of 20 children were additionally assessed with Autism Diagnosis Observation Schedule – Second Edition, ADOS-2 (Lord et al. 2012). Also, parents of both groups of children completed the Autism Spectrum Quotient: Children’s Version, AQ (Auyeung et al. 2008). Exclusion criteria for the ASD group were co-occurring neurological disorders (e.g., epilepsy) and the presence of known single-gene conditions (e.g., Fragile X syndrome). The information of medication status of children was not available.

The non-verbal IQ of children with ASD was measured with the Kaufman Assessment Battery for Children, NVI index (Kaufman and Kaufman 2004), or the Wechsler Intelligence Scale for Children – Third Edition, performance IQ score (Wechsler 1991); the non-verbal intelligence of TD children was assessed with the Raven’s Colored Progressive Matrices (Raven 2000). Language abilities were screened with the Russian Child Language Assessment Battery, RuCLAB (Arutiunian et al. 2022b); mean language score (MLS) was calculated for each child (Table 1). RuCLAB consists of 11 subtests assessing phonology, vocabulary, morphosyntax and discourse in both production and comprehension; MLS is a standard average score (from 0.0 to

Table 1 The demographic information, $M \pm SD$ (range)

Characteristics	Group		<i>t</i>	<i>p</i>
	ASD (<i>N</i> =20)	TD (<i>N</i> =20)		
Age in years	10.03 ± 1.7 (8.02–14.01)	09.11 ± 1.3 (7.02–12.03)	0.70	0.48
Mean language score	0.75 ± 0.23 (0.20–0.93)	0.95 ± 0.02 (0.91–0.99)	−4.04	<0.001***
AQ score ¹	83.6 ± 18.8 (45–120)	50.2 ± 14.2 (25–83)	6.23	<0.001***
Non-verbal IQ ²	85.4 ± 17.9 (41–118)	31.8 ± 2.7 (23–36)	–	–
ADOS, raw score				
Module 1 (<i>N</i> _{children} = 1)	12	NA	–	–
Module 2 (<i>N</i> _{children} = 5)	16.2 ± 4.96 (8–20)	NA	–	–
Module 3 (<i>N</i> _{children} = 12)	10.5 ± 1.98 (8–14)	NA	–	–
ADOS ³ , severity score				
Module 1 (<i>N</i> _{children} = 1)	6	NA	–	–
Module 2 (<i>N</i> _{children} = 5)	6.8 ± 1.6 (4–8)	NA	–	–
Module 3 (<i>N</i> _{children} = 12)	6.5 ± 1.0 (5–8)	NA	–	–

Note: we run *t*-tests to compare the characteristics of ASD and TD groups of children. The significance is labeled with * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

¹Autism Spectrum Quotient: Children's Version, AQ is a standardized questionnaire (parental report) that allows to quantify autistic traits in children. AQ score can range from 0 to 150 where the higher score reflects the higher presence / more severe autistic traits (Auyeung et al. 2008)

²Because non-verbal IQ was measured with different tools, we do not provide the comparison between groups. All TD children were within the normal range, according to Raven's Colored Progressive Matrices. We used cut-off values presented in the original publication for each age-group (i.e., 22 for 7–7.5-year-olds, 23 for 7.5–8-year-olds, etc.)

³Autism Diagnosis Observation Schedule – Second Edition (ADOS-2) is a standardized formal assessment of children that allows to quantify the severity of autistic symptoms as well as to confirm the diagnosis of ASD. ADOS severity score has a range of 0 to 10, with a score of ≥ 4 consistent with a diagnosis of ASD and the higher score reflects more severe autistic symptoms. ADOS consists of four Modules and a child is assessed by one of them depending on the level of his/her expressive communication (Gotham et al. 2009)

1.0) across all subtests. Additional information about each subtest as well as scoring is freely available online: (1) <https://osf.io/uaxrd> and (2) <https://osf.io/x8hty>.

The study was approved by the ethics committee of Moscow State University of Psychology and Education (for ASD group) and the HSE University Committee on Inter-university Surveys and Ethical Assessment of Empirical Research (for TD group) and was conducted according to the Declaration of Helsinki.

Materials and procedure

The stimuli were 40 Hz amplitude-modulated tones with 1000 ms duration. The presentation of stimuli ($N=90$) was binaural with 2000 ms inter-trial interval. The duration of the experiment was ~ 5 min. The experiment was programmed and run with the PsychoPy software (Peirce 2007). Stimuli were delivered via plastic ear tubes with foam tips inserted into the ear canals, and the intensity level was set at 83.7 dB sound pressure level. Prior the experiment, the children were instructed to sit as still as it is possible, listen to the sounds, and look at the fixation cross on the screen in front of them during MEG recording. During the experiment, lab assistant was monitoring if children pay attention to the task.

MEG acquisition and pre-processing

MEG was collected with a whole-head 306-channel MEG system (Vectorview, Elekta Neuromag) which consists of 204 orthogonal planar gradiometers and 102 magnetometers. The data were acquired in a sitting position in a magnetically shielded room. The head position in the MEG helmet was monitored every 4 ms during the recording via four head position indicator (HPI) coils which were digitized together with fiducial points with the 3D digitizer 'Fastrak' (Polhemus). To remove external interference signals and to compensate for head movements, we applied the temporal signal space separation (Taulu and Simola 2006) and the movement compensation approaches implemented in MaxFilter software. We used an electrooculogram (EOG) to detect the blinks (the electrodes were placed above and below the left eye) and horizontal eye movements (the electrodes were placed at the left and right outer canthi). An electrocardiography (ECG) was monitored with ECG electrodes to compensate for cardiac artifacts.

MEG was acquired at 1000 Hz sampling rate, band-pass filtered offline in the 0.1–330 Hz frequency range, and a notch filter of 50 Hz was applied. We used only gradiometers for the analysis because of the current debates over mixing both magnetometers and gradiometers, which have different levels of noise (see Seymour et al. 2020). Ocular and cardiac artifact removal was performed with EEGLAB's

(Delorme and Makeig 2004) Independent Component Analysis (ICA) implemented in Brainstorm (Tadel et al. 2011). Cleaned MEG data were segmented in 3000 ms epochs with 1500 ms before and after stimulus onset. The DC offset correction of from -100 ms to -2 ms was applied. Epochs were inspected visually and those affected by muscular artifacts (± 3000 fT) were rejected. The number of artifact-free epochs did not differ between groups of children: TD group, $M_{\text{number}} = 84$, $SD = 3.30$, range 77–87; ASD group, $M_{\text{number}} = 84$, $SD = 3.85$, range 75–87; $t(37.13) = 0.17$, $p = 0.86$.

MEG source analysis

To build individual brain models, we collected structural MRI data. T1 MRI scans were acquired with a 1.5 T Siemens Avanto scanner with the following parameters: repetition time = 1900 ms, echo time = 3.37 ms, flip angle = 15° , matrix size = $256 \times 256 \times 176$, voxel size = $1.0 \times 1.0 \times 1.0$ mm³. The segmentation of the individual MRIs and the reconstruction of cortical surface were performed with the FreeSurfer software (Dale et al. 1999). The surface was down-sampled to 15,000 vertices for each participant. The co-registration between MRI and MEG was performed with the Brainstorm toolbox based on the six reference points (left and right pre-auricular points, nasion, anterior and posterior commissure, and interhemispheric point) and the additional digitized head points ($N \sim 150$).

T1 MRIs were obtained for all TD children and for 15 out of 20 children with ASD. For those children with ASD who were not able to lie still in the MRI scanner, we used the template anatomy ('MRI: ICBM152') applying the special warping procedure implemented in Brainstorm. This algorithm allowed to build a pseudo-individual brain based on the head points digitized before the MEG data collection and represented the real head shape of each child.

To compute the individual head models, we used the 'Overlapping spheres' method (Huang et al. 1999). The inverse problem was solved with the depth-weighted linear L2-minimum norm estimate method (Lin et al. 2006), with the dipole orientation constrained to be normal to the cortical surface. A common imaging kernel was computed and then applied to obtain single epoch cortical reconstructions. A noise covariance was estimated from a 2 min empty room recording, taken after each participant's recording session. To provide a between-subject comparison, the individual MNEs were projected to the 'MRI: ICBM152' template brain.

To estimate the cortical sources of the sustained auditory potential, we selected the regions of interest (ROIs) that corresponded to the 'core auditory area' (primary auditory cortex and the vicinity of this region) in both hemispheres: transverse temporal gyrus, transverse temporal sulcus,

planum temporale of the superior temporal gyrus, lateral superior temporal gyrus, superior temporal sulcus, planum polar of the superior temporal gyrus, and inferior part of the circular sulcus of the insula based on the Destrieux parcellation cortical atlas (Destrieux et al. 2010).

Time-frequency (TF) analysis at the source level was performed with the Morlet wavelets (central frequency = 10 Hz, time resolution = 0.5 s) and the power was calculated. TF maps were normalized with an Event-Related Synchronization/Desynchronization approach considering the time window between -500 ms and -200 ms as a baseline. The normalized power was averaged in the standard alpha-band frequency range (8–12 Hz) in the interval from 200 ms to 1000 ms after stimulus onset. We chose this time window based on the previous study (Arutiunian et al. 2022a) which demonstrated that sustained auditory potential on the amplitude-modulated tones is evoked at around 200 ms and stays stable during auditory presentation. To localize the cortical sources of auditory alpha desynchronization, we estimated MNI coordinates of 30 vertices with the highest alpha power decrease values in the defined ROIs (15 vertices per hemisphere), and for the further analysis, extracted power averaged over these 15 vertices in the time interval between 200 ms and 1000 ms in each hemisphere for each child. This approach was successfully used previously because it accounts for the inter-individual variability of auditory response in the 'core auditory area' (defined ROIs) which contributes to a more precise source estimation (Arutiunian et al. 2022a; Stroganova et al. 2020).

The analysis of the baseline alpha activity was performed in the same ROIs defined for the auditory alpha desynchronization. Power spectral density (PSD) was calculated in the -1400 ms and -100 ms pre-stimulus time interval, and PSDs were normalized using Log₁₀. The normalized PSDs were averaged in frequency (8–12 Hz) and in the time window from -1400 ms to -100 ms. Also, to model the periodic and aperiodic components of power spectrum (Donoghue et al. 2020), we used the *specparam* toolbox (Ostlund et al. 2022) in Python v3.10 with the following settings: *peak_width_limit* = [1.5, 14], *n_peaks* = 2, *peak_height* = 0.10, and *frequency_range* = [1, 35]. For each child, the model provided two parameters (aperiodic offset and aperiodic exponent) to describe the aperiodic $1/f$ signal. Additionally, to determine an aperiodic-adjusted alpha power, the aperiodic signal from the model was subtracted from the raw power spectrum, resulting in a flattened spectrum. For the statistical analysis, raw and aperiodic-adjusted power were calculated for alpha-band frequency range, whereas aperiodic offset and aperiodic exponent were calculated for the broader range (1–35 Hz).

Statistical analysis

First, for between-group comparisons of stimulus-induced neural activities (alpha ERD), we applied linear mixed-effects models including a main effect of hemisphere, the effect of group (ASD vs. TD) nested within the left and right hemispheres as fixed effects, baseline power as a covariate, and participants as a random intercept. The structure of the models was as follows: $lmer(neural_activity \sim 1 + baseline\ power + Hemisphere / Group + (1 | ID), data = data, control = lmerControl(optimizer = "bobyqa"))$. For the baseline neural activity (baseline alpha power, aperiodic-adjusted alpha power, aperiodic offset, and aperiodic exponent), we used linear mixed-effects models with main effects of hemisphere, group, and hemisphere \times group interaction as fixed effects, and participants as a random intercept, as follows: $lmer(neural_activity \sim 1 + Hemisphere * Group + (1 | ID), data = data, control = lmerControl(optimizer = "bobyqa"))$. Second, to analyze the association between alpha-band ERD and baseline oscillatory alpha activity (aperiodic-adjusted alpha power), we used linear mixed-effects models including a main effect of hemisphere, main effect of group, and the effect of baseline alpha activity nested within the left and right hemispheres as fixed effects, and participants as a random intercept, according to the formula: $lmer(alpha_ERD \sim 1 + Hemisphere / alpha_baseline + Group + (1 | ID), data = data, control = lmerControl(optimizer = "bobyqa"))$. Finally, the relationships between neural activities and the behavioral measures of children with ASD were assessed with the Spearman's correlation analysis (as some of the variables were not normally distributed based on the Shapiro–Wilk test in R) and mediation models. The correction for multiple comparisons was used where it was needed (see details further).

All models were estimated in R (R Core Team 2019) with the *lme4* (Bates et al. 2015), *sem* (Fox 2006), *lavaan* (Rosseel 2012), and *Hmisc* (Harrell 2023) packages. The data were plotted with *ggplot2* package (Wickham 2016), and the figures for neural responses were created using Brainstorm and python data visualization library *matplotlib* (Hunter 2007).

Results

Sample description

We compared children with and without ASD in different domains of functioning (the severity of autistic traits and language abilities). The ASD group had a significantly higher presence of autistic symptoms compared to the TD group: $M_{ASD} = 83.6$ ($SD = 18.8$) vs. $M_{TD} = 50.2$ ($SD = 14.2$),

$t(35.4) = 6.23, p < 0.001$. There was also a significant difference in language abilities, indicating the lower scores in children with ASD: $M_{ASD} = 0.75$ ($SD = 0.23$) vs. $M_{TD} = 0.95$ ($SD = 0.02$), $t(19.37) = -4.04, p < 0.001$ (see Table 1). The ASD group was a highly heterogeneous in the cognitive level, including children both with intellectual disability (e.g., IQ = 41) and with a normal non-verbal cognition (e.g., IQ = 118).

Stimulus-induced alpha power decrease

The source estimation of alpha-band ERD in the auditory cortex showed that the highest values of alpha desynchronization were in the primary auditory cortex (A1) and adjacent regions of the superior temporal gyrus in both hemispheres in children with and without ASD (see the time-courses of the estimated sources in both hemispheres, Fig. 1). Between-group comparisons revealed a larger ERD in the TD group in comparison to the ASD group (even when accounting for the baseline power (averaged in -500 to -200 ms time interval) which can be different in two groups, see further), evident in the magnitude of the alpha power suppression: *left auditory ROI*, $M_{ASD} = -16.54$ ($SD = 8.79$) vs. $M_{TD} = -23.26$ ($SD = 8.00$), $\beta = -6.66$, $SE = 2.82$, $t = -2.36$, $p = 0.02$; *right auditory ROI*, $M_{ASD} = -14.89$ ($SD = 8.44$) vs. $M_{TD} = -21.10$ ($SD = 10.29$), $\beta = -6.38$, $SE = 2.83$, $t = -2.26$, $p = 0.03$ (Table 2; Fig. 2).

Baseline periodic and aperiodic neural activity

To investigate baseline alpha-band activity in both groups of children, we calculated PSD in the pre-stimulus time interval from -1400 ms to -100 ms in the same ROIs as were estimated for the stimulus-induced auditory alpha oscillations.

Baseline raw alpha power did not differ between groups of children: main effect of hemisphere, $\beta = -0.00$, $SE = 0.03$, $t = -0.03$, $p = 0.97$, main effect of group, $\beta = 0.04$, $SE = 0.09$, $t = 0.46$, $p = 0.69$, and hemisphere \times group interaction, $\beta = 0.03$, $SE = 0.04$, $t = 0.69$, $p = 0.49$ (Table 3; Fig. 3).

To determine differences in the aperiodic and oscillatory power spectrum components in the alpha-band frequency range, we used parameterization algorithm (Ostlund et al. 2022), estimating aperiodic $1/f$ and periodic / oscillatory components of the power spectrum. To obtain the aperiodic-adjusted alpha power, the aperiodic signal was subtracted from the raw power spectrum, resulting in a flattened spectrum. For the aperiodic-adjusted alpha power, the results revealed a significant main effect of group, $\beta = 0.10$, $SE = 0.05$, $t = 1.99$, $p = 0.05$, but no main effect of hemisphere, $\beta = 0.02$, $SE = 0.01$, $t = 1.57$, $p = 0.12$, or hemisphere \times group interaction, $\beta = 0.02$, $SE = 0.06$, $t = 1.48$, $p = 0.15$ (see Table 3; Fig. 3).

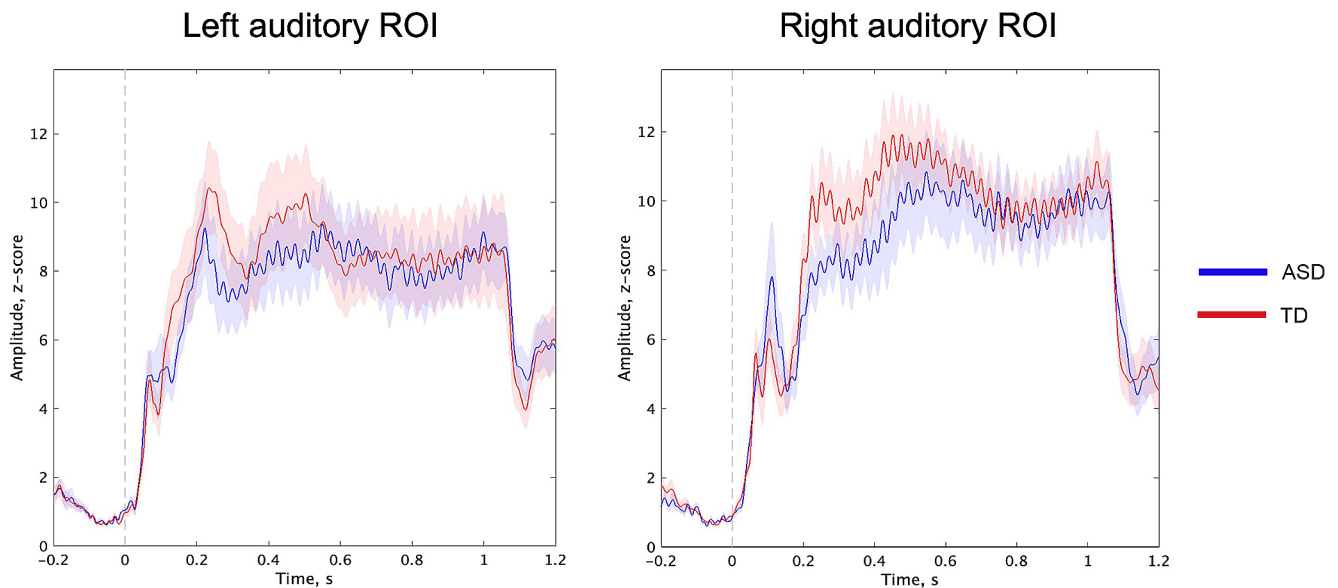


Fig. 1 The grand average time-courses of the estimated sources in the left and right auditory ROIs in children with and without ASD (amplitude, z-score)

Table 2 Between-group difference in stimulus-induced auditory alpha power decrease in children with and without ASD.

Predictors	Stimulus-induced alpha power decrease			
	Estimate	Standard error	<i>t</i>	<i>p</i>
(Intercept)	−56.62	54.60	−1.04	0.303
Hemisphere (Left)	−0.95	0.84	−1.13	0.26
Baseline power	−1.87	2.49	−0.75	0.46
Hemisphere (Left): TD group	−6.66	2.82	−2.36	0.02*
Hemisphere (Right): TD group	−6.38	2.83	−2.26	0.03*
Random Effects				
σ^2	26.92			
$\tau_{00 \text{ ID}}$	52.57			
ICC	0.66			
N_{ID}	40			
Observations	80			
Marginal R^2 / Conditional R^2	0.131 / 0.706			

Aperiodic exponent was also different between groups of children, main effect of group, $\beta=0.08$, $SE=0.04$, $t=2.06$, $p=0.04$, but there was no main effect of hemisphere, $\beta=0.01$, $SE=0.02$, $t=0.71$, $p=0.48$, and hemisphere \times group interaction, $\beta=0.01$, $SE=0.02$, $t=0.52$, $p=0.60$. No significant effects were observed for aperiodic offset, main effect of hemisphere, $\beta=-0.01$, $SE=0.03$, $t=-0.27$, $p=0.79$, main effect of group, $\beta=0.01$, $SE=0.08$, $t=0.09$, $p=0.93$, and hemisphere \times group interaction, $\beta=0.01$, $SE=0.05$, $t=0.25$, $p=0.81$ (see Table 3; Fig. 3).

The relationships between stimulus-induced and baseline alpha activity

The analysis revealed significant relationships between neural responses, indicating that the higher alpha-band ERD

was associated with the higher baseline aperiodic-adjusted alpha power in both hemispheres, however, no main effects were identified (Table 4; Fig. 4).

Brain-behavior correlations in children with ASD

First, to investigate the relationships between neural activity and behavioral measures (non-verbal IQ, language abilities, children's age, the severity of autism) in children with ASD, we used Spearman's correlation analysis. We applied a Bonferroni correction for the total number of correlations ($N=50$), so that the predictors were significant at the $\alpha=0.001$ level.

The results demonstrated two statistically significant correlations, i.e., between baseline alpha power / aperiodic offset in the language-dominant left auditory cortex

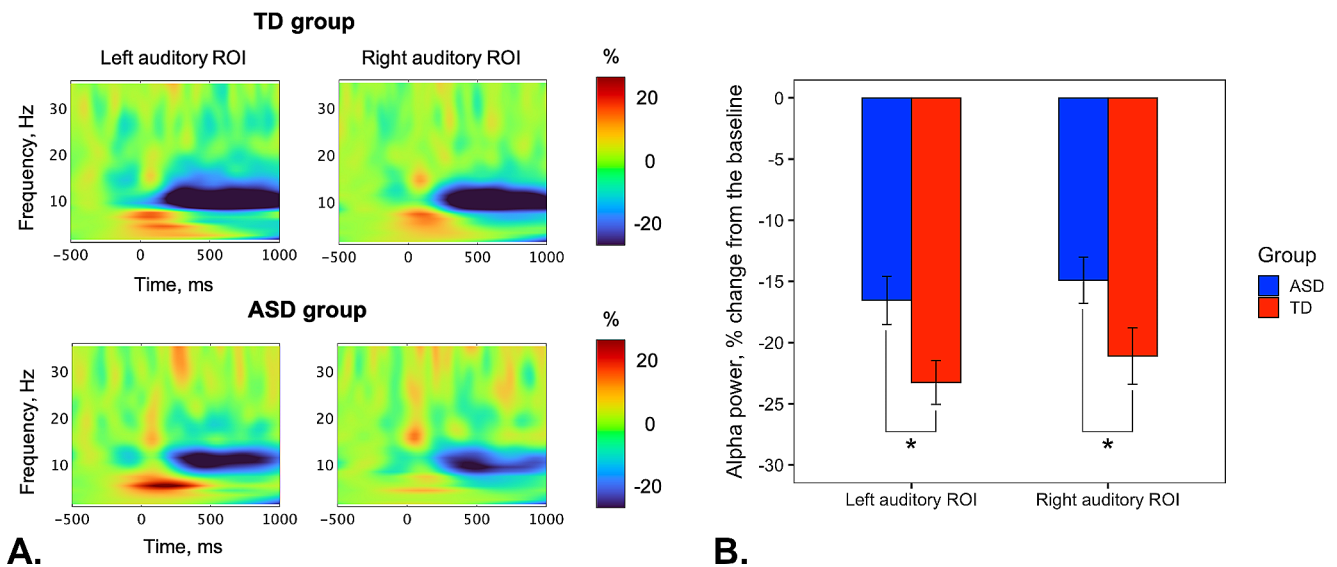


Fig. 2 The comparison of stimulus-induced alpha-band Event-Related Desynchronization (ERD) between children with and without ASD: **(A)** Time-frequency maps for the left and right auditory ROIs (normal-

ized power, % change from the baseline); **(B)** Between-group differences in alpha-band ERD (the significance is labeled as *)

and language abilities of children with ASD, $r = -0.71$, $p = 0.0003$ and $r = -0.77$, $p < 0.0001$ (Fig. 5; Table 5). This indicated that the lower power and lower offset were associated with better language skills.

Second, as previous studies have shown that non-verbal IQ was frequently associated with language skills of children with ASD, we provided an additional mediation modeling to assess whether non-verbal IQ plays a mediation role in the relationship between baseline alpha power / aperiodic offset in the left auditory cortex and language skills in the ASD group. The model assesses the direct effect between brain responses and language skills of children with ASD as well as a mediation role of non-verbal IQ in these relationships. The results of mediation modeling are presented in Table 6.

The results indicated the significant associations between language skills and both non-verbal IQ and brain responses. However, there is no significant direct relationship between non-verbal IQ and baseline alpha power / aperiodic offset as well as indirect mediation effect of non-verbal IQ.

Finally, we provided Spearman's correlation analysis between measures of alpha-band neural activity (alpha ERD, baseline alpha power, and aperiodic-adjusted alpha power) and AQ subscores related to attention, i.e., *attention to details* and *attention switching* domains (as the previous studies have reported that alpha power can be associated with the engagement of attention in the task). The analysis revealed no significant effects in any hemisphere for both AQ domains: *attention to details*, alpha ERD (right), $r = -0.13$, $p = 0.58$, alpha ERD (left), $r = -0.00$, $p = 0.97$; baseline alpha power (right), $r = -0.11$, $p = 0.64$, baseline

alpha power (left), $r = -0.33$, $p = 0.14$; aperiodic-adjusted alpha power (right), $r = 0.02$, $p = 0.92$, aperiodic-adjusted alpha power (left), $r = 0.25$, $p = 0.29$; *attention switching*, alpha ERD (right), $r = -0.09$, $p = 0.71$, alpha ERD (left), $r = 0.08$, $p = 0.75$; baseline alpha power (right), $r = -0.21$, $p = 0.36$, baseline alpha power (left), $r = -0.30$, $p = 0.19$; aperiodic-adjusted alpha power (right), $r = -0.22$, $p = 0.35$, aperiodic-adjusted alpha power (left), $r = -0.07$, $p = 0.74$.

Discussion

In this MEG study, we focused on the stimulus-induced alpha-band ERD and the baseline alpha activity (both periodic and aperiodic) in the auditory cortex of primary-school-aged children with ASD. Additionally, we aimed to investigate the relationships between these neural activities and behavioral measures in children with ASD. In general, we revealed abnormalities in both stimulus-induced and baseline neural activity in ASD and also the associations between the lower baseline alpha power and aperiodic offset in the left auditory cortex and the higher language scores of children with ASD.

MEG localization analysis demonstrated that the cortical sources of alpha-band ERD were in the primary auditory cortex (A1) and its vicinity in both hemispheres in children with and without ASD. This corresponded to the previous findings, which showed the sources of sustained auditory response to be in the A1 and adjacent regions (Arutiunian et al. 2022a; Pellegrino et al. 2019; Stroganova et al. 2020).

Table 3 Between-group differences in the baseline alpha-band activity in children with and without ASD.

Predictors	Baseline alpha power			Aperiodic-adjusted alpha power			Aperiodic offset			Aperiodic exponent					
	Est.	SE	t	Est.	SE	t	Est.	SE	t	Est.	SE	t	P		
(Intercept)	-22.07	0.06	-339.83	0.14	0.04	3.80	<0.001***	-21.07	0.06	-360.77	<0.001***	1.13	0.03	41.38	<0.001***
Hemisphere (Left)	-0.00	0.03	-0.03	0.02	0.01	1.57	0.12	-0.01	0.03	-0.27	0.79	0.01	0.02	0.71	0.48
Group (TD)	0.04	0.09	0.46	0.10	0.05	1.99	0.05*	0.01	0.08	0.09	0.93	0.08	0.04	2.06	0.04*
Hemisphere × group	0.03	0.04	0.69	0.02	0.06	1.48	0.15	0.01	0.05	0.25	0.81	0.01	0.02	0.52	0.60
Random Effects															
σ^2	0.04			0.01				0.04				0.01			
τ_{00} ID	0.06			0.02				0.05				0.01			
ICC	0.00			0.00				0.51				0.46			
N ID	40			40				40				40			
Observations	80			80				80				80			
Marginal R ² / Conditional R ²	0.009 / 0.619			0.118 / 0.812				0.001 / 0.514			0.088 / 0.505				

As we hypothesized, between-group comparisons revealed a bilateral reduction of alpha-band ERD in children with ASD, indicating that the suppression of alpha power in the auditory cortex was higher in the TD group. Our findings are in line with some of the previous studies that demonstrated abnormal alpha-band ERD in different cortical systems in ASD (Cañigüeral et al. 2021; Ewen et al. 2016; Keehn et al. 2017; Martínez et al. 2019). However, it is important to note that these abnormalities may have different directions: for instance, Martínez et al. (2019) have shown the elevated alpha ERD in the visual cortex whereas we observed a reduced alpha ERD in the auditory cortex, pointing to a possible difference in the alterations of alpha ERD depending on sensory modality. See also Bloy et al. (2019) where no difference in alpha ERD in children with ASD has been reported. The baseline alpha-band oscillatory activity (aperiodic-adjusted power) also differed between groups of children, so as the ASD group had a lower power. As well, this corresponded to other findings, indicating that the power of resting-state / baseline or pre-stimulus alpha oscillations in different cortical areas was decreased in children with ASD (Chan et al. 2007; Neuhaus et al. 2021; Wang et al. 2013). It is important to highlight, however, that most studies addressed resting-state rather than pre-stimulus alpha power and although we consider them as the same phenomena (based on Bai et al. 2016), they can reflect different neurophysiological states. In general, abnormalities in both stimulus-induced alpha-band ERD and the baseline alpha oscillations in ASD can be hypothetically associated with the imbalance between E and I (Edgar et al. 2016; Levin and Nelson 2015; Rubenstein and Merzenich 2003; Seymour et al. 2020; Sohal and Rubenstein 2019; Tang et al. 2021; Yizhar et al. 2011); a lower stimulus-induced alpha-band suppression as well as a lower baseline alpha power are related to a higher level of excitability in the cortical networks in ASD (Chapeton et al. 2019; Jensen and Mazaheri 2010). In addition to these between-group differences, our sample of ASD participants had flattened aperiodic exponent (a measure of E / I balance) in comparison to TD controls with the evidence of increased E relative to I in the auditory cortex of children with ASD, which is consistent with the previous findings (see, for example, Levin et al. 2020; Manyukhina et al. 2022; Wilkinson and Nelson 2021).

Studies in both humans and animals have suggested that the extent of desynchronization of the neuronal activity in the alpha-band during information processing and perception is primarily related to the extent of the involvement of neural tissue in the activity (e.g., Bastarrika-Iriarte and Gaudes-Caballero 2019; Bastiaansen et al. 2001; Weisz et al. 2011); importantly, increased alpha-band synchronization during task may signify active suppression / filtering of

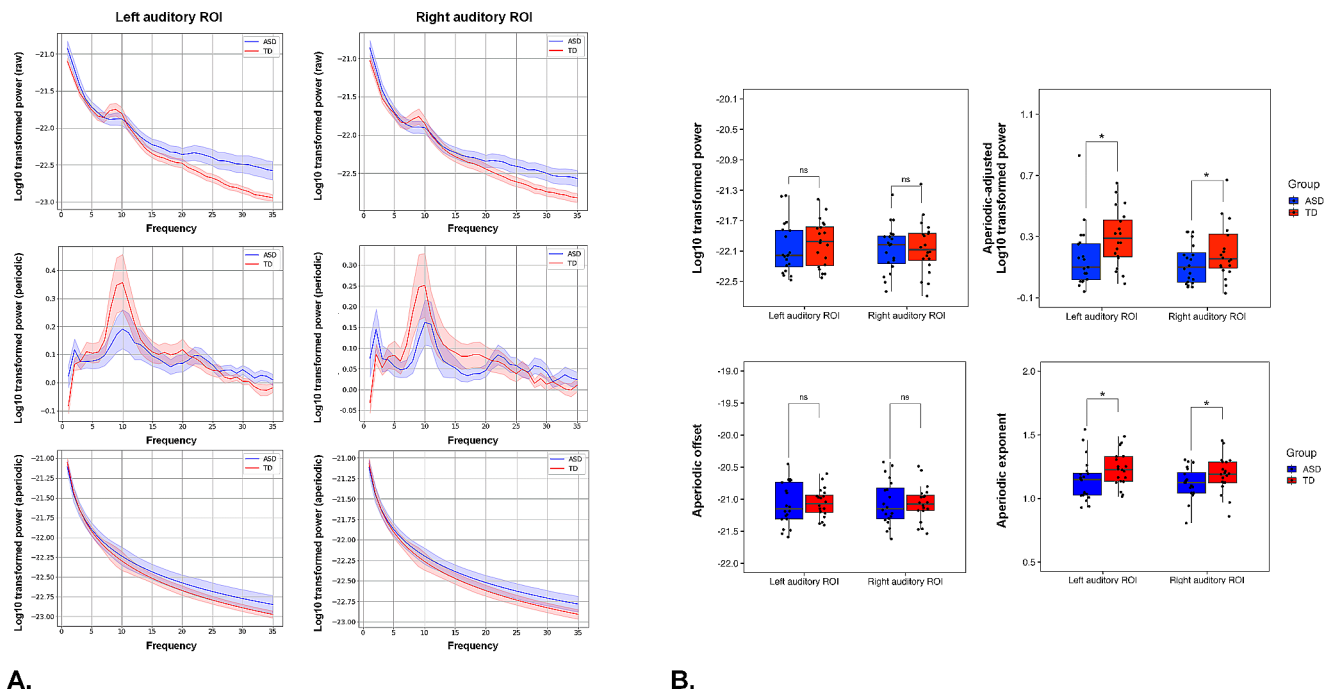


Fig. 3 The comparisons of baseline alpha-band activity between children with and without ASD: **(A)** Log10 transformed power for a raw spectrum (upper), periodic component of a spectrum (middle) and aperiodic component of a spectrum (lower); **(B)** Boxplots representing group differences in the metrics of the baseline neural activities (* = statistically significant difference, ns = non-significant)

Table 4 The relationships between alpha-band Event-Related Desynchronization and baseline aperiodic-adjusted alpha power

Predictors	Alpha-band Event-Related Desynchronization			
	Est.	SE	t	p
(Intercept)	-11.91	1.86	-6.41	< 0.001***
Hemisphere (Left)	-1.37	0.72	-1.91	0.06
Group	-3.71	2.44	-1.52	0.14
Hemisphere (Left): Aperiodic-adjusted baseline alpha	-20.98	5.63	-3.73	< 0.001***
Hemisphere (Right): Aperiodic-adjusted baseline alpha	-35.04	7.14	-4.90	< 0.001***
Random Effects				
σ^2	18.23			
$\tau_{00 ID}$	47.31			
ICC	0.72			
N_{ID}	40			
Observations	80			
Marginal R ² / Conditional R ²	0.340 / 0.817			

irrelevant information (see, e.g., Händel et al. 2011). Similarly, a higher level of synchronization of neuronal activity during a pre-stimulus / resting period in the same frequency range is associated with more rest condition of the cortical area (e.g., Klimesch et al. 2007). This means that altered neural activity in the alpha frequency band in the ASD group can be linked to the less involvement of the area to the processing / perception as well as ‘less resting’ condition of the neural tissue during rest. One of the possible functional explanations of lower alpha suppression and lower baseline alpha power in the auditory cortex of children with ASD is the involvement of attention to the task. Previous studies showed that when the attention is engaged in the perception

and processing of stimuli, the power of alpha (both ERD and resting) decreases (see Cona et al. 2020; Händel et al. 2011; Hanslmayr et al. 2011). Therefore, lower ERD in children with ASD can be associated with less involvement of attention to the task. Note, however, that our sample of children with ASD had not been screened for ADHD or attention problems, and we did not find significant relationships between neural metrics and attention skills (measured with AQ) in the ASD group.

The difference between raw and aperiodic-adjusted baseline alpha powers in the ASD group could shed some light on the specific neurobiological mechanisms that are impaired in our sample of participants. Raw power consists

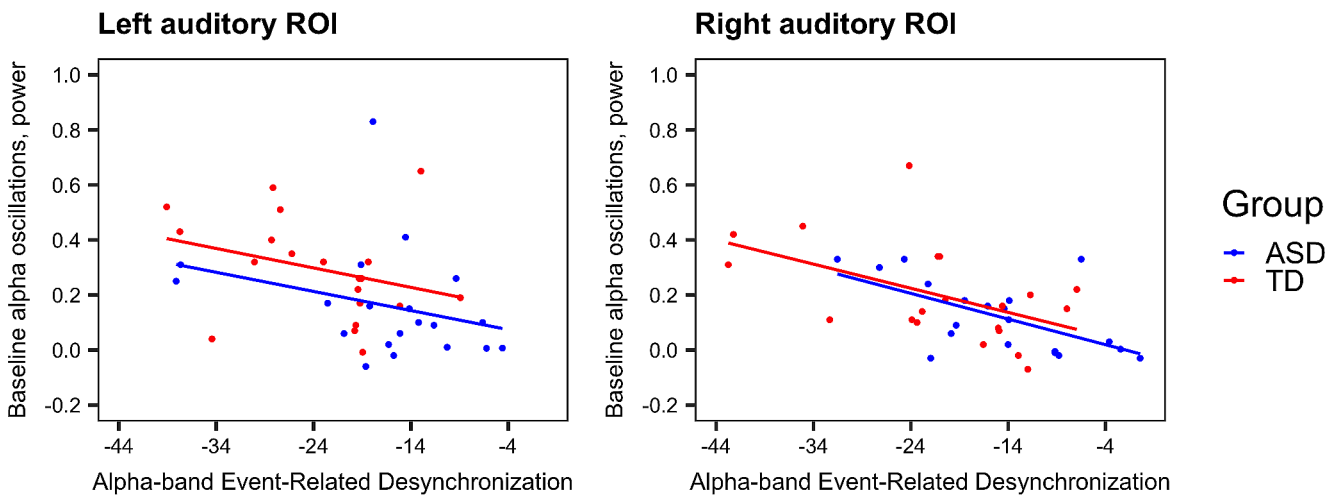


Fig. 4 The relationships between stimulus-induced Event-Related Desynchronization (ERD) in the alpha-band (% change from the baseline) and the aperiodic-adjusted baseline alpha activity (log10 transformed power) in children with and without ASD (the cases of negative power could be explained by the 1 / f subtraction)

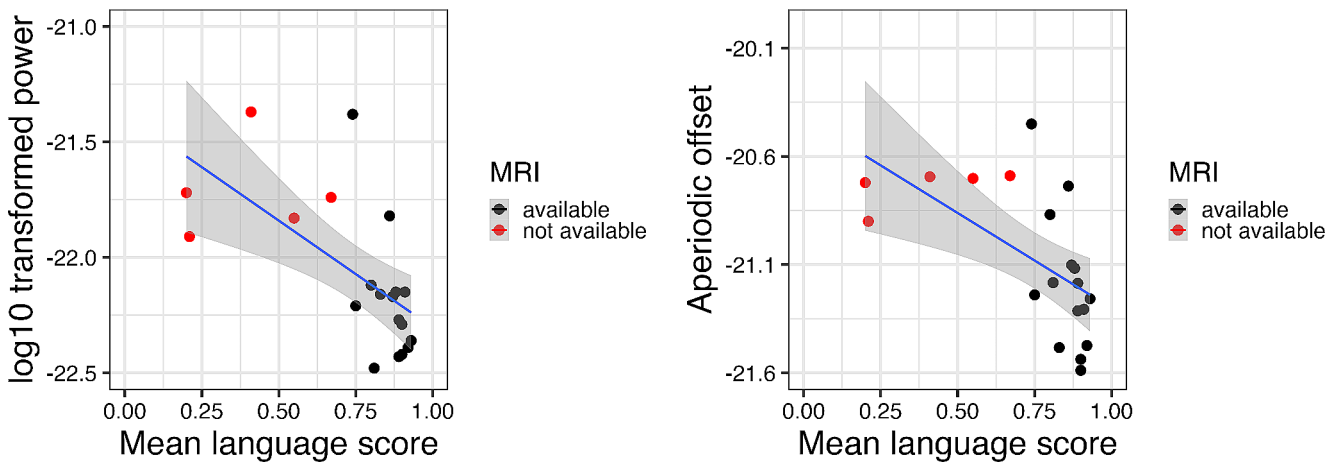


Fig. 5 The relationships between neural metrics in the left auditory cortex and language abilities of children with ASD

Table 5 The relationships between neural activities and behavioral measures in children with ASD (the results of Spearman’s correlation analysis)

Neural activity	Characteristics									
	AQ		IQ		Age		Language		ADOS	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
Left hemisphere										
Alpha desynchronization	-0.09	0.69	-0.19	0.40	-0.07	0.75	0.01	0.96	0.08	0.75
Baseline alpha power	0.05	0.81	-0.25	0.28	-0.06	0.80	-0.71	0.0003***	0.48	0.04
Aperiodic-adjusted alpha power	-0.21	0.37	-0.03	0.88	0.35	0.13	0.29	0.21	-0.14	0.58
Aperiodic offset	0.16	0.49	-0.10	0.66	-0.25	0.28	-0.77	< 0.0001***	0.51	0.03
Aperiodic exponent	-0.09	0.70	0.17	0.46	-0.16	0.49	0.17	0.46	0.19	0.45
Right hemisphere										
Alpha desynchronization	-0.05	0.81	-0.00	0.97	-0.13	0.57	-0.28	0.21	0.39	0.11
Baseline alpha power	0.11	0.65	-0.14	0.54	0.22	0.35	-0.44	0.05	-0.02	0.94
Aperiodic-adjusted alpha power	-0.33	0.15	-0.12	0.62	0.33	0.16	0.20	0.39	-0.29	0.24
Aperiodic offset	0.18	0.44	-0.08	0.72	0.14	0.54	-0.44	0.05	0.33	0.17
Aperiodic exponent	0.17	0.46	0.15	0.51	0.15	0.53	0.23	0.33	0.45	0.06

Predictors significant at $\alpha=0.05$ significance level are highlighted in bold. Predictors that retained their significance following the Bonferroni correction for the total number of correlations ($N=50$) are also labeled with *** (that is, significant at the $\alpha=0.001$ level)

Table 6 The output of the mediation models

Regressions	Estimate	SE	z-value	<i>P</i> (> z)	CI (lower)	CI (upper)
Baseline raw alpha power						
Nonverbal IQ ~ brain response (a1)	−15.102	11.620	−1.300	0.194	−37.878	7.674
Mean language score ~						
Nonverbal IQ (b1)	0.006	0.002	3.180	0.001**	0.002	0.010
Brain response (c)	−3.346	0.100	−3.446	0.001**	−0.543	−0.149
Variiances:						
Nonverbal IQ	282.393	89.300	3.162	0.002**	107.367	457.418
Mean language score	0.019	0.006	3.162	0.002**	0.007	0.032
Defined parameters:						
Indirect effect 1 (a1*b1)	−0.089	0.074	−1.203	0.229	−0.234	0.056
Aperiodic offset						
Nonverbal IQ ~ brain response (a1)	−10.471	11.737	−0.892	0.372	−33.475	12.534
Mean language score ~						
Nonverbal IQ (b1)	0.006	0.002	3.561	<0.001**	0.003	0.010
Brain response (c)	−3.337	0.097	−3.446	0.001**	−0.527	−0.146
Variiances:						
Nonverbal IQ	294.521	93.136	3.162	0.002**	111.978	477.063
Mean language score	0.019	0.006	3.162	0.002**	0.007	0.031
Defined parameters:						
Indirect effect 1 (a1*b1)	−0.068	0.078	−0.865	0.387	−0.221	0.086

of both oscillatory activity itself and aperiodic activity that refers to the arrhythmic component of neural field data (see He 2014). Neural oscillations (aperiodic-adjusted activity / rhythmic / periodic aspect of the spectra) registered with MEG / EEG reflect a synchronized activity of the large neuronal populations and a rhythmic fluctuation of excitability in neuronal ensembles associated with the dynamics of the circuits (e.g., Bauer et al. 2020; Gray et al. 1994). At the same time, aperiodic components hypothetically related to E / I balance and average firing rate (He 2014; Ostlund et al. 2022). This could mean that the abnormal auditory alpha-band activity that was observed in our sample of children with ASD was related to both rhythmic and arrhythmic (aperiodic exponent) components of MEG signal.

In our sample of participants, we found a relationship between alpha-band ERD and baseline alpha oscillations in both auditory cortices, indicating that the higher baseline aperiodic-adjusted alpha power was associated with better stimulus-induced alpha-band suppression. Similar results were shown by Keehn et al. (2017) in a mixed group of children with and without ASD. All these findings indicated that the pre-stimulus / baseline (or reference) alpha power is greatly associated with the stimulus-induced alpha-band suppression, interpreting the phenomenon in terms of more vs. less cortical excitability preceding a task performance / stimulus perception (e.g., Doppelmayr et al. 1998; Klimesch et al. 2006). Remarkably, although children with ASD had reduced alpha ERD and baseline aperiodic-adjusted alpha power, the pattern of relationship between them was similar to those as in TD children.

Our hypothesis that alpha-band neural activity in the auditory cortex would be related to the language abilities of children with ASD was partly confirmed. To the best of our knowledge, only one study has addressed the relationship between auditory alpha ERD and the language abilities of children with ASD (Bloy et al. 2019). The authors reported that the greater ERD was associated with better language skills. However, in our study, we did not find this relationship. Perhaps, the difference in results can be explained by the type of stimuli. Bloy et al. (2019) used high-order stimulus items (words and pseudowords), whereas we used low-level amplitude-modulated tones. Some studies demonstrated that the stimulus complexity influenced the extent of alpha-band ERD (Boiten et al. 1992; Sharma et al. 2019) and the difference of processing was found even between vowels and tones (Krause et al. 1995). Moreover, although the previous studies did not focus on the low-level auditory alpha-band activity and its relation to language in ASD, there is an evidence of the association between the low-level auditory perception and language skills in autistic individuals using other paradigms, such as presenting simple pure tones, phonemes, amplitude-modulated tones, click trains, and amplitude-modulated sweeps (e.g., Arutiunian et al. 2023b; Roberts et al. 2011, 2019, 2021; Stroganova et al. 2020). Thus, words / pseudowords used in (Bloy et al. 2019) were spectrally and semantically more complex than simple amplitude-modulated tones used in our study, and this can be one of the potential explanations for the difference between results.

However, we found that the raw baseline alpha power and aperiodic offset in the language-dominant left auditory cortex were negatively related to the language abilities of children with ASD, so that the lower power / aperiodic offset were associated with higher language skills. The link between baseline alpha power and language skills, at the first glance, demonstrates that more altered neural circuits in children with ASD (higher cortical excitability during rest) is related to better language skills and it is in contrast to most of the previous studies showed that higher E / I ratio was associated with worse phenotypic characteristics (e.g., see Bozzi et al. 2018; Nelson and Valakh 2015; Rivell and Mattson 2019; Sohal and Rubenstein 2019). However, this effect considered in the framework of the findings on aperiodic offset can be interpreted differently. Aperiodic offset is associated with a neuronal population spiking (Manning et al. 2009; Miller et al. 2014) and the blood oxygenated level dependent signal from functional MRI (Winawer et al. 2013); and to the best of our knowledge this is the first evidence of the relationship between this neural marker and language skills in children with ASD. Our results suggested that lower average firing rate (lower offset) and, thus, more rest condition of a neural tissue during rest is related to higher language scores. As there is no relationship between aperiodic-adjusted alpha power and language skills in the same brain area and a high correlation between raw baseline power and offset ($r=0.83$, $p<0.0001$), we hypothesize that the link between raw power and language skills is driven by the broadband shift of the spectrum rather than by the baseline alpha power itself. Our findings contributed to the previous evidence showing that not only stimulus-induced but also the baseline alpha oscillations in the auditory cortex can be related to language in ASD. Similarly to Bloy et al. (2019), we did not find any relationships between alpha-band neural activity and general cognitive functioning or the severity of autistic symptoms.

In conclusion, the study focused on largely unexplored alpha-band activity in the auditory cortex of children with ASD. We revealed both abnormal suppression of alpha power during sound perception and atypically low baseline aperiodic-adjusted alpha power as well as flattened aperiodic exponent in ASD. Moreover, the results revealed the association between the lower raw baseline alpha power and aperiodic offset in the language-dominant left auditory cortex and the better language scores of children with ASD. Future studies would benefit from addressing the changes in specifically the aperiodic offset in the auditory cortex and language skills of children with ASD during speech therapy. Moreover, as there is a difference in alpha-band ERD between complex and simple auditory stimuli, it is needed to use both types of stimuli in the same group of children. This will help to understand how different types of stimuli

influence alpha-band ERD and how this neural response is related to language in ASD.

Neural markers of excitation / inhibition balance: methodological considerations

Recent neurobiological studies in both humans and animals have proposed that E / I imbalance is considered as one of the core pathophysiological mechanisms in ASD (e.g., Levin and Nelson 2015; Sohal and Rubenstein 2019). Previous studies have identified a number of neural markers that reflect or are associated with E / I balance, such as gamma-band activity (Rubenstein and Merzenich 2003; Seymour et al. 2020), alpha-band activity (Weisz et al. 2011), and aperiodic exponent or 1 / f slope of arrhythmic component of the neural activity (Donoghue et al. 2020; Gao et al. 2017; Molina et al. 2020). In our study, we observed the alterations in both alpha-band neural activity and aperiodic exponent in children with ASD. These findings suggest that different metrics of E / I balance can complement each other as they reflect the same phenomena: all alterations in the neural activity in the ASD group (reduced alpha power suppression during sound perception, low baseline alpha power during rest, and flattened aperiodic exponent) are associated with increased E relative to I.

Limitations and future directions

The study has some limitations which should be mentioned. First, a sample size of participants is relatively small given a large age-range and imbalance in sex (25% and 45% of females in TD and ASD groups respectively). To generalize the findings, it is necessary to include larger sex-balanced sample sizes. Second, we used the constant inter-stimulus interval and, therefore, did not manipulate with that parameter; this, hypothetically, can cause adaptation to the stimulus presentation. To reduce that effect, future studies need to use different time intervals between stimuli. Third, we do not provide any measures of sensory processing. Future studies would benefit from addressing the relationships between sensory processing, auditory alpha-band activity and language abilities of children with ASD. Finally, we did not account for individual differences in hearing thresholds and loudness perception which can play a role in strengths of auditory response.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00429-024-02802-7>.

Acknowledgements We thank Roman Cheremin for providing access to the resources of the Center for Speech Pathology and Neurorehabilitation, Moscow, Russia. We also thank Olga Buiivolova and Natalia Deeva for their assistance with participant recruitment in the MRI part

of the study. Special thanks go to all children who enthusiastically participated in the study.

Author contributions VA: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing – Original Draft, Writing – Review & Editing, Project administration. GA: Methodology, Formal analysis, Writing – Review & Editing. IB: Investigation. MF: Data curation, Formal analysis. ED: Investigation. DP: Investigation. AS: Investigation. ST: Investigation. UM: Investigation. KD: Investigation. OD: Writing – Review & Editing, Resources. All authors read and approved the final manuscript.

Funding The study was supported by the Basic Research Program at the National Research University Higher School of Economics.

Data availability The datasets generated and analyzed during the current study are not publicly available as it is human data but are available from the corresponding author on reasonable request.

Declarations

Ethical approval The approval for this study was obtained from the HSE University Committee on Interuniversity Surveys and the Ethical Assessment of Empirical Research (for the TD group) and the local ethics committee of the Moscow State University of Psychology and Education (for the ASD group). The study was conducted in accordance with the Declaration of Helsinki.

Consent to participate A parent of each child signed a written consent form.

Conflict of interest The authors declare that the study was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Competing interests The authors declare no competing interests.

References

- American Psychiatric Association (2013) Diagnostic and statistical manual of mental disorders: DSM-5, 5th edn. American Psychiatric Publication, Washington, DC; London, p 947
- Arutiunian V, Arcara G, Buyanova I, Gomozova M, Dragoy O (2022a) The age-related changes in 40 hz auditory steady-state response and sustained event-related fields to the same amplitude-modulated tones in typically developing children: a magnetoencephalography (MEG) study. *Hum Brain Mapp* 43:5370–5383. <https://doi.org/10.1002/hbm.26013>
- Arutiunian V, Lopukhina A, Minnigulova A, Shlyakhova A, Davydova E, Pereverzeva D, Sorokin A, Tyushkevich S, Mamokhina U, Danilina K, Dragoy O (2022b) Language abilities of Russian primary-school-aged children with Autism Spectrum Disorder: evidence from Comprehensive Assessment. *J Autism Dev Disord* 52:584–599. <https://doi.org/10.1007/s10803-021-04967-0>
- Arutiunian V, Arcara G, Buyanova I, Buivolova O, Davydova E, Pereverzeva D, Sorokin A, Tyushkevich S, Mamokhina U, Danilina K, Dragoy O (2023a) Event-related desynchronization of MEG Alpha-Band oscillations during Simultaneous Presentation of Audio and Visual Stimuli in Children with Autism Spectrum Disorder. *Brain Sci* 13:1313. <https://doi.org/10.3390/brainsci13091313>
- Arutiunian V, Arcara G, Buyanova I, Davydova E, Pereverzeva D, Sorokin A, Tyushkevich S, Mamokhina U, Danilina K, Dragoy O (2023b) Neuromagnetic 40 hz auditory steady-state response in the left auditory cortex is related to language comprehension in children with Autism Spectrum Disorder. *Prog Neuropsychopharmacol Biol Psychiatry* 122:110690. <https://doi.org/10.1016/j.pnpbp.2022.110690>
- Auyeung B, Baron-Cohen S, Wheelwright S, Allison C (2008) The autism spectrum quotient: children's version (AQ-Child). *J Autism Dev Disord* 38:1230–1240. <https://doi.org/10.1007/s10803-007-0504-z>
- Bai Y, Nakao T, Xu J, Qin P, Chaves P, Heinzl A, Duncan N, Lane T, Yen N-S, Tsai S-Y, Northoff G (2016) Resting state glutamate predicts elevated pre-stimulus alpha during self-relatedness: a combined EEG-MRS study on rest-self overlap. *Soc Neurosci* 11:249–263. <https://doi.org/10.1080/17470919.2015.1072582>
- Bastarrika-Iriarte A, Gaudes-Caballero C (2019) Closing eyes during auditory memory retrieval modulates alpha rhythm but does not alter tau rhythm. *NeuroImage* 197:60–68. <https://doi.org/10.1016/j.neuroimage.2019.04.053>
- Bastiaansen MCM, Böcker KBE, Brunia CHM, de Munck JC, Spekreijse H (2001) Event-related desynchronization during anticipatory attention for an upcoming stimulus: a comparative EEG / MEG study. *Clin Neurophysiol* 112:393–403. [https://doi.org/10.1016/s1388-2457\(00\)00537-x](https://doi.org/10.1016/s1388-2457(00)00537-x)
- Bates D, Mächler M, Bolker BM, Walker SC (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bauer A-KR, Debener S, Nobre AC (2020) Synchronization of neural oscillations and cross-modal influences. *Trends Cogn Sci* 24:481–495. <https://doi.org/10.1016/j.tics.2020.03.003>
- Bazanova OM, Vernon D (2014) Interpreting EEG alpha activity. *Neurosci Biobehav Rev* 44:94–110. <https://doi.org/10.1016/j.neubiorev.2013.05.007>
- Bellato A, Arora I, Kochhar P, Hollis C, Groom MJ (2020) Atypical electrophysiological indices of eyes-open and eyes-closed resting-state in children and adolescents with ADHD and autism. *Brain Sci* 10:272. <https://doi.org/10.3390/brainsci10050272>
- Bergmann TO, Lieb A, Zrenner C, Ziemann U (2019) Pulsed facilitation of Corticospinal excitability by the Sensorimotor μ -Alpha rhythm. *J Neurosci* 39:10034–10043. <https://doi.org/10.1523/JNEUROSCI.1730-19.2019>
- Berman JI, Edgar JC, Blaskey L, Kuschner ES, Levy SE, Ku M, Dell J, Roberts TPL (2016) Multimodal Diffusion-MRI and MEG Assessment of Auditory and Language System Development in Autism Spectrum Disorder. *Front Neurosci* 10:30. <https://doi.org/10.3389/fnana.2016.00030>
- Bloy L, Shwayder K, Blaskey L, Roberts TPL, Embick D (2019) A Spectrotemporal Correlate of Language Impairment in Autism Spectrum Disorder. *J Autism Dev Disord* 49:3181–3190. <https://doi.org/10.1007/s10803-019-04040-x>
- Boiten F, Sergeant J, Geuze R (1992) Event-related desynchronization: the effects of energetic and computational demands. *Electroencephalogr Clin Neurophysiol* 82:302–309. [https://doi.org/10.1016/0013-4694\(92\)90110-4](https://doi.org/10.1016/0013-4694(92)90110-4)
- Bonnefond M, Jensen O (2012) Alpha oscillations serve to protect Working Memory maintenance against anticipated distracters. *Curr Biol* 22:1969–1974. <https://doi.org/10.1016/j.cub.2012.08.029>
- Bozzi Y, Provenzano G, Casarosa S (2018) Neurobiological bases of autism–epilepsy comorbidity: a focus on excitation/inhibition imbalance. *Eur J Neurosci* 47:534–548. <https://doi.org/10.1111/ejn.13595>
- Cañigueral R, Palmer J, Ashwood KL, Azadi B, Asherson P, Bolton PF, McLoughlin G, Tye C (2022) Alpha oscillatory activity during attentional control in children with Autism Spectrum disorder

- (ASD), Attention-Deficit/Hyperactivity disorder (ADHD), and ASD+ADHD. *J Child Psychol Psychiatry* 63:745–761. <https://doi.org/10.1111/jcpp.13514>
- Cantor DS, Thatcher RW, Hrybyk M, Kaye H (1986) Computerized EEG analyses of autistic children. *J Autism Dev Disord* 16:169–187. <https://doi.org/10.1007/BF01531728>
- Chan AS, Sze SL, Cheung M-C (2007) Quantitative electroencephalographic profiles for children with autistic spectrum disorder. *Neuropsychology* 21:74–81. <https://doi.org/10.1037/0894-4105.21.1.74>
- Chapeton JJ, Haque R, Wittig JH, Inati SK, Zaghoul KA (2019) Large-scale communication in the human brain is rhythmically modulated through alpha coherence. *Curr Biol* 29:2801–2811. <https://doi.org/10.1016/j.cub.2019.07.014>
- Cona G, Chiocci F, Tomasso SD, Pellegrino G, Piccione F, Bisiacchi P, Arcara G (2020) Theta and alpha oscillations as signatures of internal and external attention to delayed intentions: a magnetoencephalography (MEG) study. *NeuroImage* 205:116295. <https://doi.org/10.1016/j.neuroimage.2019.116295>
- R Core Team (2019) R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. URL: <https://www.R-project.org/>
- Cornew L, Roberts TPL, Blaskey L, Edgar JC (2012) Resting-state oscillatory activity in Autism Spectrum disorders. *J Autism Dev Disord* 42:1884–1894. <https://doi.org/10.1007/s10803-011-1431-6>
- Dale AM, Fischl B, Sereno MI (1999) Cortical surface-based analysis: I. Segmentation and surface reconstruction. *NeuroImage* 9:179–194. <https://doi.org/10.1006/nimg.1998.0395>
- Dawson G, Klinger LG, Panagiotides H, Lewy A, Castelleo P (1995) Subgroups of autistic children based on social behavior display distinct patterns of brain activity. *J Abnorm Child Psychol* 23:569–583. <https://doi.org/10.1007/BF01447662>
- Delorme A, Makeig S (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *J Neurosci Methods* 134:9–21. <https://doi.org/10.1016/j.jneumeth.2003.10.009>
- Destrieux C, Fischl B, Dale A, Hagren E (2010) Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature. *NeuroImage* 53:1–15. <https://doi.org/10.1016/j.neuroimage.2010.06.010>
- Dickinson A, DiStefano C, Senturk D, Jeste SS (2018) Peak alpha frequency is a neural marker of cognitive function across the autism spectrum. *Eur J Neurosci* 47:643–651. <https://doi.org/10.1111/ejn.13645>
- Doesburg SM, Bedo N, Ward LM (2016) Top-down alpha oscillatory network interactions during visuospatial attention orienting. *NeuroImage* 132:512–519. <https://doi.org/10.1016/j.neuroimage.2016.02.076>
- Donoghue T, Haller M, Peterson EJ, Varma P, Sebastian P, Gao R, Noto T, Lara AH, Wallis JD, Knight RT, Shestyk A, Voytek B (2020) Parameterizing neural power spectra into periodic and aperiodic components. *Nat Neurosci* 23:1655–1665. <https://doi.org/10.1038/s41593-020-00744-x>
- Doppelmayr MM, Klimesch W, Pachinger T, Ripper B (1998) The functional significance of Absolute Power with respect to event-related desynchronization. *Brain Topogr* 11:133–140. <https://doi.org/10.1023/A:1022206622348>
- Edgar JC, Khan SY, Blaskey L, Chow VY, Rey M, Gaetz W, Cannon KM, Monroe JF, Cornew L, Qasmieh S, Liu S, Welsh JP, Levy SE, Roberts TPL (2015a) Neuromagnetic oscillations predict evoked-response latency delays and Core Language deficits in Autism Spectrum disorders. *J Autism Dev Disord* 45:395–405. <https://doi.org/10.1007/s10803-013-1904-x>
- Edgar JC, Heiken K, Chen Y-H, Herrington JD, Chow V, Liu S, Bloy L, Huang M, Pandey J, Cannon KM, Qasmieh S, Levy SE, Schultz RT, Roberts TPL (2015b) Resting-state alpha in Autism Spectrum Disorder and Alpha associations with thalamic volume. *J Autism Dev Disord* 45:795–804. <https://doi.org/10.1007/s10803-014-2236-1>
- Edgar JC, Fisk 4th CL, Liu S, Pandey J, Herrington JD, Schultz RT, Roberts TPL (2016) Translating Adult Electrophysiology Findings to Younger Patient Populations: Difficulty Measuring 40-Hz Auditory Steady-State Response in Typically Developing Children and Children with Autism Spectrum Disorder. *Developmental Neuroscience* 38: 1–14. <https://doi.org/10.1159/000441943>
- Edgar JC, Dipiero M, McBride E, Green HL, Berman J, Ku M, Liu S, Blaskey L, Kuschner E, Airey M, Ross JL, Bloy L, Kim M, Koppers S, Gaetz W, Schultz RT, Roberts TPL (2019) Abnormal maturation of the resting-state peak alpha frequency in children with autism spectrum disorder. *Hum Brain Mapp* 40:3288–3298. <https://doi.org/10.1002/hbm.24598>
- Ewen JB, Lakshmanan BM, Pillai AS, McAuliffe D, Nettles C, Hallett M, Crone NE, Mostofsky SH (2016) Decreased modulation of EEG oscillations in high-functioning autism during a Motor Control Task. *Front Hum Neurosci* 10:198. <https://doi.org/10.3389/fnhum.2016.00198>
- Fox J (2006) Structural equation modeling with the sem package in R. *Structural equation modeling: a multidisciplinary journal* 13:465–486. https://doi.org/10.1207/s15328007sem1303_7
- Gao R, Peterson EJ, Voytek B (2017) Inferring synaptic excitation/inhibition balance from field potentials. *NeuroImage* 158:70–78. <https://doi.org/10.1016/j.neuroimage.2017.06.078>
- Gotham K, Pickles A, Lord C (2009) Standardizing ADOS scores for a measure of severity in Autism Spectrum disorders. *J Autism Dev Disord* 39:693–705. <https://doi.org/10.1007/s10803-008-0674-3>
- Gray CM (1994) Synchronous oscillations in neuronal systems: mechanisms and functions. *J Comput Neurosci* 1:11–38. <https://doi.org/10.1007/BF00962716>
- Habib A, Harris L, Pollick F, Melville C (2019) A meta-analysis of working memory in individuals with autism spectrum disorders. *PLoS ONE* 14:e0216198. <https://doi.org/10.1371/journal.pone.0216198>
- Händel BF, Haarmeier T, Jensen O (2011) Alpha oscillations correlate with the successful inhibition of unattended stimuli. *J Cogn Neurosci* 23:2494–2502. <https://doi.org/10.1162/jocn.2010.21557>
- Hanslmayr S, Gross J, Klimesch W, Shapiro KL (2011) The role of alpha oscillations in temporal attention. *Brain Res Rev* 67:331–343. <https://doi.org/10.1016/j.brainresrev.2011.04.002>
- Harrell JF (2023) Hmisc: Harrell Miscellaneous. R package version 5.1-2. <https://hbiostat.org/R/Hmisc/>
- He BJ (2014) Scale-free brain activity: past, present, and future. *Trends Cogn Sci* 18:480–487. <https://doi.org/10.1016/j.tics.2014.04.003>
- Hong X, Sun J, Bengson JJ, Mangun GR, Tong S (2015) Normal aging selectively diminishes alpha lateralization in visual spatial attention. *NeuroImage* 106:353–363. <https://doi.org/10.1016/j.neuroimage.2014.11.019>
- Huang MX, Mosher JC, Leahy RM (1999) A sensor-weighted overlapping-sphere head model and exhaustive head model comparison for MEG. *Phys Med Biol* 44:423–440. <https://doi.org/10.1088/0031-9155/44/2/010>
- Hunter JD (2007) Matplotlib: a 2D graphics environment. *Comput Sci Eng* 9:90–95. <https://doi.org/10.1109/MCSE.2007.55>
- Jensen O, Mazaheri A (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front Hum Neurosci* 4:186. <https://doi.org/10.3389/fnhum.2010.00186>
- Kaufman AS, Kaufman NL (2004) Kaufman Assessment Battery for Children, 2nd edn. American Guidance Service
- Keehn B, Westerfield M, Müller R-A, Townsend J (2017) Autism, attention, and alpha oscillations: an electrophysiological study of Attentional capture. *Biol Psychiatry: Cogn Neurosci Neuroimaging* 2:528–536. <https://doi.org/10.1016/j.bpsc.2017.06.006>

- Kjelgaard MM, Tager-Flusberg H (2001) An investigation of language impairment in autism: implications for genetic subgroups. *Lang Cogn Processes* 16:287–308. <https://doi.org/10.1080/01690960042000058>
- Klimesch W (2012) Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn Sci* 16:606–617. <https://doi.org/10.1016/j.tics.2012.10.007>
- Klimesch W, Doppelmayr M, Hanslmayr S (2006) Upper alpha ERD and absolute power: their meaning for memory performance. *Prog Brain Res* 159:151–165. [https://doi.org/10.1016/S0079-6123\(06\)59010-7](https://doi.org/10.1016/S0079-6123(06)59010-7)
- Klimesch W, Sauseng P, Hanslmayr S (2007) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res Rev* 53:63–88. <https://doi.org/10.1016/j.brainresrev.2006.06.003>
- Krause CM, Lang H, Laine M, Kuusisto M, Pörn B (1995) Cortical Processing of Vowels and tones as measured by event-related desynchronization. *Brain Topogr* 8:47–56. <https://doi.org/10.1007/BF01187669>
- Larrain-Valenzuela J, Zamorano F, Soto-Icaza P, Carrasco X, Herrera C, Daiber F, Aboitiz F, Billeke P (2017) Theta and Alpha Oscillation impairments in autistic spectrum disorder reflect Working Memory Deficit. *Sci Rep* 7:14328. <https://doi.org/10.1038/s41598-017-14744-8>
- Leno VC, Tomlinson SB, Chang S-AA, Naples AJ, McPartland J (2018) Resting-state alpha power is selectively associated with autistic traits reflecting behavioral rigidity. *Sci Rep* 8:11982. <https://doi.org/10.1038/s41598-018-30445-2>
- Leno VC, Pickles A, van Noordt S, Huberty S, Desjardins J, Webb SJ, Elsabbagh M, The BASIS Team (2021) 12-Month peak alpha frequency is a correlate but not a longitudinal predictor of non-verbal cognitive abilities in infants at low and high risk for autism spectrum disorder. *Dev Cogn Neurosci* 48:100938. <https://doi.org/10.1016/j.dcn.2021.100938>
- Levin AR, Nelson CA (2015) Inhibition-based biomarkers for Autism Spectrum Disorder. *Neurotherapeutics* 12:546–552. <https://doi.org/10.1007/s13311-015-0350-1>
- Levin AR, Varcin KJ, O’Leary HM, Tager-Flusberg H, Nelson CA (2017) EEG power at 3 months in infant at high familial risk for autism. *J Neurodevelopmental Disorder* 9:34. <https://doi.org/10.1186/s11689-017-9214-9>
- Levin AR, Naples AJ, Scheffler AW, Webb SJ, Shic F, Sugar CA, Murias M, Bernier RA, Chawarska K, Dawson G, Faja S, Jeste S, Nelson CA, McPartland JC, Sentürk D, the Autism Biomarkers Consortium for Clinical Trials (2020) Day-to-day test-retest reliability of EEG profiles in children with autism spectrum disorder and typical development. *Front Integr Neurosci* 14:21. <https://doi.org/10.3389/fnint.2020.00021>
- Liang S, Mody M (2022) Abnormal brain oscillations in Developmental disorders: application to resting state EEG and MEG in Autism Spectrum Disorder and Fragile X Syndrome. *Front Neuroimaging* 1:903191. <https://doi.org/10.3389/fnimg.2022.903191>
- Lin F-H, Witzel T, Ahlfors SP, Stufflebeam SM, Belliveau W, Hämäläinen MS (2006) Assessing and improving the spatial accuracy in MEG source localization by depth-weighted minimum-norm estimates. *NeuroImage* 31:160–171. <https://doi.org/10.1016/j.neuroimage.2005.11.054>
- Lord C, Rutter M, DiLavore PC, Risi S, Gotham K, Bishop SL (2012) *Autism Diagnostic Observation schedule*, 2nd edn. Western Psychological Services
- Manning JR, Jacobs J, Fried I, Kahana MJ (2009) Broadband shifts in local field potential power spectra are correlated with single-neuron spiking in humans. *J Neurosci* 29:13613–13620. <https://doi.org/10.1523/JNEUROSCI.2041-09.2009>
- Manyukhina VO, Prokofyev AO, Galuta IA, Goiaeva DE, Obukhova TS, Schneiderman JF, Altukhov DI, Stroganova TA, Orekhova EV (2022) Globally elevated excitation-inhibition ratio in children with autism spectrum disorder and below-average intelligence. *Mol Autism* 13:20. <https://doi.org/10.1186/s13229-022-00498-2>
- Martínez A, Tobe R, Dias EC, Ardekani BA, Veenstra-VanderWeele J, Patel G, Breland M, Lieval A, Silipo G, Javitt DC (2019) Differential patterns of visual sensory alteration underlying face emotion recognition impairment and motion perception deficits in Schizophrenia and Autism Spectrum Disorder. *Biol Psychiatry* 86:557–567. <https://doi.org/10.1016/j.biopsych.2019.05.016>
- Mash LE, Keehn B, Linke AC, Liu TT, Helm JL, Haist F, Townsend J, Müller RA (2020) Atypical relationships between spontaneous EEG and fMRI activity in autism. *Brain Connect* 10:18–28. <https://doi.org/10.1089/brain.2019.0693>
- Mathewson KE, Lleras A, Beck DM, Fabiani M, Ro T, Gratton G (2011) Pulsed out of awareness: EEG alpha oscillations represent a pulsed-inhibition of ongoing cortical processing. *Front Psychol* 2:99. <https://doi.org/10.3389/fpsyg.2011.00099>
- Mathewson KJ, Jetha MK, Drmic I, Bryson SE, Goldberg JO, Schmidt LA (2012) Regional EEG alpha power, coherence, and behavioral symptomatology in autism spectrum disorder. *Clin Neurophysiol* 123:1798–1809. <https://doi.org/10.1016/j.clinph.2012.02.061>
- Matson JL, Rieseke RD, Williams LW (2013) The relationship between autism spectrum disorders and attention-deficit/hyperactivity disorder: an overview. *Res Dev Disabil* 34:2475–2484. <https://doi.org/10.1016/j.ridd.2013.05.021>
- Matsuzaki J, Kuschner ES, Blaskey L, Bloy L, Kim M, Ku M, Edgar JC, Embick D, Roberts TPL (2019) Abnormal auditory mismatch fields are associated with communication impairment in both verbal and minimally verbal / nonverbal children who have autism spectrum disorder. *Autism Res* 12:1225–1235. <https://doi.org/10.1002/aur.2136>
- Miller KJ, Hermess D, Honey CJ, Hebb AO, Ramsey NF, Knight RT, Ojemann JG, Fetz EE (2012) Human Motor cortical activity is selectively phase-entrained on underlying rhythms. *PLoS Comput Biol* 8(9):e1002655. <https://doi.org/10.1371/journal.pcbi.1002655>
- Molina JL, Voytek B, Thomas ML, Joshi YB, Bhakta SG, Talledo JA, Swerdlow NR, Light GA (2020) Memantine effects on Electroencephalography measures of putative excitatory / inhibitory balance in Schizophrenia. *Biol Psychiatry: Cogn Neurosci Neuroimaging* 5:562–568. <https://doi.org/10.1016/j.bpsc.2020.02.004>
- Murias M, Webb SJ, Greenon J, Dawson G (2007) Resting state cortical connectivity reflected in EEG coherence in individuals with autism. *Biol Psychiatry* 62:270–273. <https://doi.org/10.1016/j.biopsych.2006.11.012>
- Murphy JW, Foxe JJ, Peters JB, Molholm S (2021) Susceptibility to distraction in Autism Spectrum Disorder: probing the Integrity of Oscillatory Alpha-Band suppression mechanisms. *Autism Res* 7:442–458. <https://doi.org/10.1002/aur.1374>
- Nelson SB, Valakh V (2015) Excitatory/Inhibitory Balance and Circuit Homeostasis in Autism Spectrum disorders. *Neuron* 87:684–698. <https://doi.org/10.1016/j.neuron.2015.07.033>
- Neuhaus E, Lowry SJ, Santhosh M, Kresse A, Edwards LA, Keller J, Libsack EJ, Kang VY, Naples A, Jack A, Jeste S, McPartland JC, Aylward E, Bernier R, Bookheimer S, Dapretto M, Van Horn JD, Pelphrey K, Webb S, ACE GENDAAR Network (2021) Resting state EEG in youth with ASD: age, sex, and relation to phenotype. *J Neurodevelopmental Disorders* 13:33. <https://doi.org/10.1186/s11689-021-09390-1>
- Ostlund B, Donoghue T, Anaya B, Gunther KE, Karalunas SL, Voytek B, Pérez-Edgar KE (2022) Spectral parameterization for studying neurodevelopment: how and why. *Dev Cogn Neurosci* 54:101073. <https://doi.org/10.1016/j.dcn.2022.101073>
- Payne L, Guillory S, Sekuler R (2013) Attention-modulated alpha-band oscillations protect against intrusion of irrelevant information. *J Cogn Neurosci* 25:1463–1476. https://doi.org/10.1162/jocn_a_00395

- Peirce JW (2007) PsychoPy – psychophysics software in Python. *J Neurosci Methods* 162:8–13. <https://doi.org/10.1016/j.jneumeth.2006.11.017>
- Pellegrino G, Arcara G, Di Pino G, Turco C, Maran M, Weis L, Piccione F, Siebner HR (2019) Transcranial direct current stimulation over the sensory-motor regions inhibits gamma synchrony. *Hum Brain Mapp* 40:2736–2746. <https://doi.org/10.1002/hbm.24556>
- Polyak A, Kubina RM, Girirajan S (2015) Comorbidity of intellectual disability confounds ascertainment of Autism: implications for genetic diagnosis. *Neuropsychiatric Genet* 168:600–608. <https://doi.org/10.1002/ajmg.b.32338>
- Raven J (2000) The raven's progressive matrices: change and stability over culture and time. *Cogn Psychol* 41:1–48. <https://doi.org/10.1006/cogp.1999.0735>
- Rivell A, Mattson MP (2019) Intergenerational metabolic syndrome and neuronal network hyperexcitability in Autism. *Trends Neurosci* 42:709–726. <https://doi.org/10.1016/j.tins.2019.08.006>
- Roberts TPL, Schmidt GL, Egeth M, Blaskey L, Rey MM, Edgar CJ, Levy SE (2008) Electrophysiological signatures: magnetoencephalographic studies of the neural correlates of language impairment in autism spectrum disorders. *Int J Psychophysiol* 68(2):149–160. <https://doi.org/10.1016/j.ijpsycho.2008.01.012>
- Roberts TPL, Khan SY, Rey M, Monroe JF, Cannon K, Blaskey L, Woldoff S, Qasmieh S, Gandal M, Schmidt GL, Zarnow DM, Levy SE, Edgar JC (2010) MEG detection of delayed auditory evoked responses in autism spectrum disorders: towards an imaging biomarker for autism. *Autism Res* 3:8–18. <https://doi.org/10.1002/aur.111>
- Roberts TPL, Cannon KM, Tavabi K, Blaskey L, Khan SY, Monroe JF, Qasmieh S, Levy SE, Edgar JC (2011) Auditory magnetic mismatch field latency: a Biomarker for Language Impairment in Autism. *Biol Psychiatry* 70:263–269. <https://doi.org/10.1016/j.biopsych.2011.01.015>
- Roberts TPL, Matsuzaki J, Blaskey L, Bloy L, Edgar CJ, Kim M, Ku M, Kuschner ES, Embick D (2019) Delayed M50/M100 evoked response component latency in minimally verbal / nonverbal children who have autism spectrum disorder. *Mol Autism* 10:34. <https://doi.org/10.1186/s13229-019-0283-3>
- Roberts TPL, Bloy L, Liu S, Ku M, Blaskey L, Jackel C (2021) Magnetoencephalography studies of the envelope following response during amplitude-modulated sweeps: diminished phase synchrony in Autism Spectrum Disorder. *Front Hum Neurosci* 15:787229. <https://doi.org/10.3389/fnhum.2021.787229>
- Rosseel Y (2012) Lavaan: an R Package for Structural equation modeling. *J Stat Softw* 48:1–36. <https://doi.org/10.18637/jss.v048.i02>
- Rubenstein JLR, Merzenich MM (2003) Model of autism: increased ratio of excitation / inhibition in key neural systems. *Genes Brain Behav* 2:255–267. <https://doi.org/10.1034/j.1601-183x.2003.00037.x>
- Sauseng P, Klimesch W, Gerloff C, Hummel FC (2009) Spontaneous locally restricted EEG alpha activity determines cortical excitability in the motor cortex. *Neuropsychologia* 47:284–288. <https://doi.org/10.1016/j.neuropsychologia.2008.07.021>
- Seymour RA, Rippon G, Gooding-Williams G, Sowman PF, Kessler K (2020) Reduced auditory steady state responses in autism spectrum disorder. *Mol Autism* 11:56. <https://doi.org/10.1186/s13229-020-00357-y>
- Sharma G, Daniel R, Chandra S, Singh R (2019) Effects of Complexity on Frontal Event Related Desynchronization in Mental Rotation Task. *Appl Psychophysiol Biofeedback* 44:235–245. <https://doi.org/10.1007/s10484-019-09436-0>
- Sheikhani A, Behnam H, Mohammadi MR, Noroozian M, Mohammadi M (2012) Detection of abnormalities for diagnosing of children with Autism Disorders Using of Quantitative Electroencephalography Analysis. *J Med Syst* 36:957–963. <https://doi.org/10.1007/s10916-010-9560-6>
- Shen G, Green HL, Franzen RE, Berman JI, Dipiero M, Mowad TG, Bloy L, Liu S, Airey M, Goldin S, Ku M, McBride E, Blaskey L, Kuschner ES, Kim M, Konka K, Roberts TPL, Edgar JC (2023) Resting-state activity in children: replicating and extending findings of early maturation of alpha rhythms in Autism Spectrum Disorder. *J Autism Dev Disord* 1–16. <https://doi.org/10.1007/s10803-023-05926-7>
- Shepard E, Tye C, Ashwood KL, Azadi B, Asherson P, Bolton PF, McLoughlin G (2018) Resting-state neurophysiological activity patterns in Young People with ASD, ADHD, and ASD+ADHD. *J Autism Dev Disord* 48:110–122. <https://doi.org/10.1007/s10803-017-3300-4>
- Sohal VS, Rubenstein JLR (2019) Excitation-inhibition balance as a framework for investigating mechanisms of neuropsychiatric disorders. *Mol Psychiatry* 24:1248–1257. <https://doi.org/10.1038/s41380-019-0426-0>
- Stroganova TA, Komarov KS, Syssoeva OV, Goiaeva DE, Obukhova TS, Ovsiannikova TM, Prokofyev AO, Orekhova EV (2020) Left hemispheric deficit in the sustained neuromagnetic response to periodic click trains in children with ASD. *Mol Autism* 11:100. <https://doi.org/10.1186/s13229-020-00408-4>
- Tadel F, Baillet S, Mosher JC, Pantazis D, Leahy RM (2011) Brainstorm: a user-friendly application for MEG / EEG analysis. *Comput Intell Neurosci* 2011:1–9. <https://doi.org/10.1155/2011/879716>
- Takarae Y, Zanesco A, Keehn B, Chukoskie L, Müller R-A, Townsend J (2022) EEG microstates suggest atypical resting-state network activity in high-functioning children and adolescents with autism spectrum development. *Dev Sci* 25:e13231. <https://doi.org/10.1111/desc.13231>
- Tang X, Jaenisch R, Sur M (2021) The role of GABAergic signalling in neurodevelopmental disorders. *Nat Rev Neurosci* 22:290–307. <https://doi.org/10.1038/s41583-021-00443-x>
- Taulu S, Simola J (2006) Spatiotemporal signal space separation method for rejecting nearby interference in MEG measurements. *Phys Med Biol* 51:1759–1768. <https://doi.org/10.1088/0031-9155/51/7/008>
- Thies M, Zrenner C, Ziemann U, Bergmann TO (2018) Sensorimotor Mu-alpha power is positively related to corticospinal excitability. *Brain Stimul* 11:1119–1122. <https://doi.org/10.1016/j.brs.2018.06.006>
- Tierney AL, Gabard-Durnam L, Vogel-Farley V, Tager-Flusberg H, Nelson CA (2012) Developmental trajectories of resting EEG power: an endophenotype of Autism Spectrum Disorder. *PLoS ONE* 7:e39127. <https://doi.org/10.1371/journal.pone.0039127>
- Wang J, Barstein J, Ethridge LE, Mosconi MW, Takarae Y, Sweeney J (2013) Resting state EEG abnormalities in autism spectrum disorders. *J Neurodevelopmental Disorders* 5:24. <https://doi.org/10.1186/1866-1955-5-24>
- Wechsler D (1991) The Wechsler Intelligence Scale for Children – Third Edition. The Psychological Corporation
- Weisz N, Hartmann T, Müller N, Lorenz I, Obleser J (2011) Alpha rhythms in audition: cognitive and clinical perspectives. *Front Psychol* 2:73. <https://doi.org/10.3389/fpsyg.2011.00073>
- Wickham H (2016) *Ggplot 2: elegant graphics for data analysis*. Springer, New York
- Wilkinson C, Nelson CA (2021) Increased aperiodic gamma power in young boys with fragile X syndrome is associated with better language ability. *Mol Autism* 12:17. <https://doi.org/10.1186/s13229-021-00425-x>
- Winawer J, Kay KN, Foster BL, Rauschecker AM, Parvizi J, Wandell AB (2013) Asynchronous Broadband signals are the principal source of the BOLD response in the human visual cortex. *Curr Biol* 23(13):1145–1153. <https://doi.org/10.1016/j.cub.2013.05.001>
- World Health Organization (2016) International Statistical Classification of Diseases and related health problems: ICD-10, 5th edn. pp.) WHO, p 1075

- Yizhar O, Fenno LE, Prigge M, Schneider F, Davidson TJ, O'Shea DJ, Sohal VS, Goshen I, Finkelstein J, Paz JT, Stehfest K, Fudim R, Ramakrishnan C, Huguenard JR, Hegemann P, Deisseroth K (2011) Neocortical excitation / inhibition balance in information processing and social dysfunction. *Nature* 477:171–178. <https://doi.org/10.1038/nature10360>
- Zhao Q, Luo Y, Mei X, Shao Z (2023) Resting-state EEG patterns of preschool-aged boys with autism spectrum disorder: a pilot study. *Appl Neuropsychology: Child* 1–8. <https://doi.org/10.1080/21622965.2023.2211702>
- Zheng Y, Liu XL, Hsieh L-T, Hurtado M, Wang Y, Niendam T, Carter CS, Ranganath C, Ragland JD (2021) Disrupted modulation of alpha and low Beta oscillations mediates temporal sequence memory deficits in people with Schizophrenia. *Biol Psychiatry: Cogn*

Neurosci Neuroimaging 6:1157–1164. <https://doi.org/10.1016/j.bpsc.2021.04.002>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.