International Journal of Psychophysiology 203 (2024) 112405

Contents lists available at ScienceDirect

International Journal of Psychophysiology

journal homepage: www.elsevier.com/locate/ijpsycho

Altered neural synchronization in response to 2 Hz amplitude-modulated tones in the auditory cortex of children with Autism Spectrum Disorder: An MEG study

Ilya Samoylov[a,*], Giorgio Arcara[b], Irina Buyanova[a,c], Elizaveta Davydova[d,e], Darya Pereverzeva[d], Alexander Sorokin[d,f], Svetlana Tyushkevich[d], Uliana Mamokhina[d], Kamilla Danilina[d,g], Olga Dragoy[a,h], Vardan Arutiunian[i]

[a] *Center for Language and Brain, HSE University, Moscow, Russia*
[b] *IRCCS San Camillo Hospital, Venice, Italy*
[c] *University of Otago, Dunedin, New Zealand*
[d] *Federal Resource Center for ASD, Moscow State University of Psychology and Education, Moscow, Russia*
[e] *Chair of Differential Psychology and Psychophysiology, Moscow State University of Psychology and Education, Moscow, Russia*
[f] *Haskins Laboratories, New Haven, CT, USA*
[g] *Scientific Research and Practical Center for Pediatric Psychoneurology, Moscow, Russia*
[h] *Institute of Linguistics, Russian Academy of Sciences, Moscow, Russia*
[i] *Center for Child Health, Behavior and Development, Seattle Children's Research Institute, Seattle, WA, USA*

ARTICLE INFO

Keywords:
Autism spectrum disorder (ASD)
Magnetoencephalography (MEG)
2 Hz auditory steady-state response (2 Hz ASSR)
Auditory delta oscillations
Amplitude-modulated tones

ABSTRACT

Objective: Some studies have hypothesized that atypical neural synchronization at the delta frequency band in the auditory cortex is associated with phonological and language skills in children with Autism Spectrum Disorder (ASD), but it is still poorly understood. This study investigated this neural activity and addressed the relationships between auditory response and behavioral measures of children with ASD.
Methods: We used magnetoencephalography and individual brain models to investigate 2 Hz Auditory Steady-State Response (ASSR) in 20 primary-school-aged children with ASD and 20 age-matched typically developing (TD) controls.
Results: First, we found a between-group difference in the localization of the auditory response, so as the topology of 2 Hz ASSR was more superior and posterior in TD children when comparing to children with ASD. Second, the power of 2 Hz ASSR was reduced in the ASD group. Finally, we observed a significant association between the amplitude of neural response and language skills in children with ASD.
Conclusions: The study provided the evidence of reduced neural response in children with ASD and its relation to language skills.
Significance: These findings may inform future interventions targeting auditory and language impairments in ASD population.

1. Introduction

Autism Spectrum Disorder (ASD) is a broad term used to describe a group of neurodevelopmental conditions that are characterized by difficulties in social interaction and communication, as well as stereotyped or repetitive behaviors (APA, 2013). These core symptoms are typically accompanied by co-occurring language impairments (Dunlop et al., 2016; Nadig and Shaw, 2012; Paul et al., 2005; Schelinski et al., 2022), but the neurophysiological mechanisms of these impairments remain understudied (Berman et al., 2016). Previous studies have shown that one of the neurophysiological mechanisms of language impairments in children with ASD is atypical processing of the basic features of auditory stimuli in the central auditory pathway and in the primary auditory cortex (Arutiunian et al., 2023; Demopoulos et al., 2017; Edgar et al., 2015; Gage et al., 2003; Matsuzaki et al., 2019; Roberts et al., 2014, 2010; Wolff et al., 2012). The temporal and spectral characteristics of a

---

[*] Corresponding author at: Center for Language and Brain, HSE University, 3 Krivokolenny pereulok, 101000 Moscow, Russia.
E-mail address: ivsamoylov@hse.ru (I. Samoylov).

https://doi.org/10.1016/j.ijpsycho.2024.112405
Received 31 March 2024; Received in revised form 13 May 2024; Accepted 17 July 2024

sound are specifically significant for auditory processing in these regions (Giraud et al., 2007; Luo and Poeppel, 2012). It is known that oscillatory activity in the brain and the time-frequency characteristics of auditory stimuli have to be synchronized in order to ensure effective spatiotemporal perception, and the ordering and processing of auditory input (Giraud and Poeppel, 2012; Nash-Kille and Sharma, 2014; Peelle and Davis, 2012). It is also important to note that a number of studies have underlined the distinctive role of cerebellum, which play a major role in rhythmic auditory motor synchronization (Hertrich et al., 2016; Schwartze and Kotz, 2016; Thaut et al., 2009) and, therefore, disruptions in specific cerebro-cerebellar loops in ASD might impede the functional and structural specialization of cortical regions involved in motor control, language, and social interaction (D'Mello and Stoodley, 2015; Mosconi et al., 2015).

One of the reliable paradigms to assess these low-level auditory processing and to register a neural response to auditory stimuli at a specific frequency is auditory steady-state response (ASSR) in electro- and/or magnetoencephalography (EEG and/or MEG) (Galambos et al., 1981; Kuwada et al., 1986; Picton et al., 1987; Rees et al., 1986; Stapells et al., 1988), where participants are presented with amplitude- or frequency-modulated tones or sequences of clicks. In response to that stimulation, afferent neurons in the primary auditory cortex synchronize their excitation patterns to the specific phase of these stimuli and generate phase-synchronized responses (Farahani et al., 2021; Picton et al., 2003; Poeppel and Teng, 2020; Thut et al., 2011). This method is based on a passive listening methodology that does not require any feedback from participants and it has high test-retest reliability (Legget et al., 2017; McFadden et al., 2014).

Previous EEG and MEG studies using ASSR in the ASD population have been focused mostly on the synchronization at the high frequency range, i.e., high beta and gamma, and the results are inconsistent with the evidence of reduced ASSR in ASD and no difference between children with and without ASD in this response (e.g., Ahlfors et al., 2023; Arutiunian et al., 2023; De Stefano et al., 2019; Edgar et al., 2016; Ono et al., 2020; Roberts et al., 2021; Seymour et al., 2020; Stroganova et al., 2020). Additionally, some of these studies have revealed an association between the synchronization at the high frequency range and language impairments in children with ASD (e.g., Arutiunian et al., 2023; Roberts et al., 2021). Although most studies in autism have been focused on high-frequency oscillations in relation to language skills, a number of studies have demonstrated a significance of the efficient low-frequency (delta) synchronization in the auditory cortex for the acquisition, perception, and production of language, as well as reading skills (Cogan and Poeppel, 2011; Di Liberto et al., 2018; Gross et al., 2013; Park et al., 2015; Peelle and Davis, 2012). Previous studies have shown that atypical low-frequency synchronization can lead to difficulties in word perception due to the altered processing of the prosodic features of speech, intonation features, and incorrect distribution of accents (Giraud and Poeppel, 2012; Molinaro et al., 2016; Nallet and Gervain, 2022; Peelle et al., 2012).

The association between low-frequency cortical activity and impaired language skills has also been confirmed in children with ASD (Jochaut et al., 2015; Wang et al., 2023). For example, in a recent EEG study by Wang et al. (2023), French-speaking children with ASD and age-matched typically developing (TD) controls were presented with four 2.5-minute cartoons in their native language, and children with ASD had reduced delta frequency power and delta-range speech tracking synchronization. The authors suggested that reduced delta activity during speech processing in ASD could be related to altered syntactic phrase fragmentation, which is supported by other studies indicating more difficulties with intonation processing in individuals with ASD (Haesen et al., 2011; Murphy and Benítez-Burraco, 2017).

On the other hand, the MEG study by Clumeck et al. (2014) reported no group difference between neural synchronization in the primary auditory cortex and speech stimuli at the delta frequency range between French-speaking children with and without ASD. The authors proposed that the neural activity at the delta frequency band during speech processing reflected a prelexical process of speech perception, and, therefore, it was related to low-level processes that may not be impaired in individuals with ASD. However, a recent meta-analysis has shown that there are only few studies addressing the synchronization at the delta frequency band in the auditory cortex of children with ASD, and the results are inconsistent (Palana et al., 2022). This makes such studies a priority, given the significant role of delta-band neural activity in the auditory cortex for language processing and the very limited number of studies with ASD individuals.

The aims of the present study were (1) to investigate the synchronization at the delta frequency band in the primary auditory cortex of children with ASD in comparison to age-matched TD controls at the source level in MEG, and (2) to examine the relationship between this brain response and behavioral measures of children with ASD (language skills, nonverbal IQ, and the severity of autistic traits). In this study, we utilized a passive pure tone listening paradigm at the delta frequency band in a population of elementary school-aged children with and without ASD. The advantage of this paradigm is that it allows us to examine auditory processing even in children with ASD who are minimally and/or completely nonverbal and those with severe intellectual disability (children with profound ASD).

2. Methods

2.1. Participants

MEG data were collected from 20 children with ASD (5 girls, age range 8.02–14.01 years, $M_{\text{age}} = 10.03$, SD = 1.7) and 20 TD children (9 girls, age range 7.02–12.03 years, $M_{\text{age}} = 9.11$, SD = 1.3) (Table 1). Children with ASD were recruited from the Federal Resource Center for Organization of Comprehensive Support to Children with Autism Spectrum Disorders (Moscow, Russia) and TD children were recruited from public schools in Moscow.

HSE University Committee on Interuniversity Surveys and 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) approved the study protocol following the Code of Ethics of the World Medical Association (Declaration of Helsinki) for

Table 1
The demographic information for ASD and TD groups of children.

Characteristics	ASD ($N = 20$)	TD ($N = 20$)	*t*	*p*
Age	10.03 ± 1.7	9.11 ± 1.3	0.7	0.48
Mean language score[1]	0.75 ± 0.23	0.95 ± 0.02	−4.04	**<0.001*****
AQ total	83.6 ± 18.8	50.2 ± 14.2	6.23	**<0.001*****
AQ social skills	15.9 ± 6.0	7.6 ± 3.0	5.5	**<0.001*****
AQ attention switching	16.2 ± 4.0	12.3 ± 3.0	3.39	**0.001****
AQ attention to details	14.9 ± 4.9	12.8 ± 4.9	1.37	0.17
AQ communication	21.1 ± 4.2	8.6 ± 4.7	8.94	**<0.001*****
AQ imagination	15.4 ± 6.4	8.9 ± 3.1	4.07	**<0.001*****
Non-verbal IQ: K-ABC or WISC III	85.4 ± 17.9	–	–	–
Non-verbal IQ: Raven's matrices	–	31.8 ± 2.7	–	–
ADOS raw				
Module 1 ($N = 1$)	12	NA	–	–
Module 2 ($N = 5$)	16.2 ± 4.96	NA	–	–
Module 3 ($N = 12$)	10.5 ± 1.98	NA	–	–

Note: [1]Mean language score (as well as language production and language comprehension scores) is a standard average score (from 0 to 1) across all subtests of the Russian Child Language Assessment Battery (see Arutiunian et al., 2022). We run *t*-tests to compare the characteristics of ASD and TD groups of children. The significance is labeled with $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$ and highlighted in bold.

experiments involving humans. All parents or legally authorized representatives of the children signed a written informed consent before the study.

2.2. Clinical and behavioral assessment

According to ICD-10, all participants in the ASD group were diagnosed with autism spectrum disorder, and 18 out of 20 children also were assessed by a licensed psychiatrist using Autism Diagnostic Observation Schedule - Second Edition (ADOS-2) (Lord et al., 2012). In addition, parents of children from both groups completed the Russian version of the Autism Spectrum Quotient: Children's Version, AQ (Auyeung et al., 2008). The non-verbal intelligence of TD children was assessed with Raven's Colored Progressive Matrices (Raven, 2000), and the non-verbal intelligence of children with ASD was measured with the Kaufman Assessment Battery for Children, K-ABC II (Kaufman and Kaufman, 2004), Wechsler Intelligence Scale for Children—Third Edition, WISC-III (1991), performance IQ score. Language skills of all participants were screened with the Russian Child Language Assessment Battery (RuCLAB), a standardized test for the assessment of phonology, vocabulary, morphosyntax, and discourse in both production and comprehension; mean language score (MLS) was calculated for each child (Arutiunian et al., 2022).

2.3. Stimuli and procedure

Auditory stimuli were pure tones with a duration of 1 s with amplitude modulation set up at 2 Hz (modulation depth of 100 %). A total of 90 auditory stimuli with 2000 ms inter-stimulus intervals were presented binaurally at the 83.7 dB sensation level and were transmitted through plastic tubes with foam tips inserted into the ears. During the recording the children were instructed to minimize physical activity and look at the static image of a fixation cross on the screen in front of them.

2.4. Structural magnetic resonance imaging (MRI) data acquisition

The T1 weighted MRI images 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 = $1.0 \times 1.0 \times 1.0$ mm^3. For MRI segmentation and reconstruction of cortical surface we used FreeSurfer (Dale et al., 1999). The co-registration of structural (MRI) and functional (MEG) data was performed in the Brainstorm toolbox (Tadel et al., 2011) using six reference points: left and right pre-auricular points, nasion anterior and posterior commissure, and interhemispheric point and about 150 digitized head points.

Not all subjects with ASD were able to tolerate the MRI procedure. Thus, for 5 out of 20 children with ASD we used the template anatomy ("MRI: ICBM152") applying the special warping procedure implemented in Brainstorm. This algorithm allowed us to build a pseudo-individual brain based on the head points digitized before the MEG data collection and represent the real head shape of each child.

2.5. MEG data collection and pre-processing

MEG was collected using 306-channel MEG (Vectorview, Elekta Neuromag) with a sampling rate of 1000 Hz. The position of children's heads within the MEG helmet was monitored every 4 ms during the experiment via four head position indicator (HPI) coils digitized together with fiducial points using 3D digitizer 'Fastrak' (Polhemus). We applied the temporal signal space separation (Taulu and Simola, 2006) and movement compensation procedures implemented in MaxFilter software (Elekta Neuromag) to remove external interference signals generated outside the brain and to compensate for head movements. An electrooculogram (EOG) was recorded using four electrodes placed above and below the left eye (to detect the blinks) as well as at the left and right outer canthi (to detect horizontal eye movements). An electrocardiograph (ECG) was monitored with ECG electrodes to compensate for cardiac artifacts. MEG was recorded at 1000 Hz sampling rate and filtered off-line with a band-pass (0.1–330 Hz) and notch (50 Hz) filters which were applied to continuous MEG files. The artifacts (heartbeats and eye movements) were cleaned with the EEGLAB's (Delorme and Makeig, 2004) Independent Component Analysis (ICA) implemented in Brainstorm. The filtered MEG recording was segmented into epochs with a duration of 6000 ms ranging from −2000 ms to 4000 ms, and DC offset correction from −100 ms to −2 ms was applied.

2.6. MEG source analysis

For our analysis, we utilized only gradiometers because of the current debates over mixing both magnetometers and gradiometers, which have different levels of noise (see Seymour et al., 2020). The head model for each participant was built using the "Overlapping spheres" method (Huang et al., 1999), which fits one sphere for each sensor. The inverse problem was solved using the depth-weighted linear L2-minimum norm estimate (MNE) method, (Lin et al., 2006), with the dipole orientation constrained to be normal to the cortical surface. To prevent numerical instability (Hämäläinen and Ilmoniemi, 1994), we used a regularization parameter ($\lambda = 0.33$) when computing the inverse operator. To obtain single epoch cortical reconstructions, a common imaging kernel was computed and then applied. We calculated a noise covariance matrix for source estimation from a 2-min empty room recording taken after each participant's recording session. To enable comparisons between participants, we projected the individual MNEs onto the "MRI: ICBM152" template brain provided by Brainstorm.

According to previous studies (Farahani et al., 2021), cortical generators of ASSR are spread over the auditory regions in both hemispheres. To assess the sources of the 2 Hz ASSR, we identified the following regions of interest (ROI): transverse temporal gyrus (Heschl's gyrus) and superior temporal gyrus. Both frequency and Event-Related Field (ERF) analysis was performed at the source level. Power spectral density (PSD) was calculated using the Welch method (time window: 0–1000 ms, window length: 1000 ms, window overlap ratio: 50 %, unit: physical: U^2/Hz). Then the averaged power in the delta frequency (2 Hz) was calculated in the interval from 0 to 1000 ms. Considering participants' individual variability, we selected 15 voxels in the left and right hemisphere (total $n = 30$) within the selected ROIs with the highest mean values. We chose such an approach in order to take into account the individual variability of responses within the 'core auditory area' (defined ROIs), which provides a more precise source estimation (Arutiunian et al., 2023; Stroganova et al., 2020). For the analysis, we extracted PSD averaged over these 15 vertices in the 0 and 1000 ms time interval in each auditory ROI for each child.

To conduct an ERF analysis, we first averaged the signal over epochs and calculated an individual time course for each of the 15,000 vertices. We normalized the cortical map using a z-score, with a pre-stimulus time of −100 to −2 ms. For each child, z-score normalized absolute values were averaged in the time interval between 0 ms and 1000 ms and were extracted for the same functional regions as for frequency analysis in the left and right auditory ROIs.

3. Results

3.1. Phenotypic characteristics of participants

Between-group comparisons in the total AQ scores revealed a significantly higher presence of autistic traits in the ASD group: $t = 6.23$, $p < 0.001$. Significant differences were also found in language skills (measured with MLS): $t = -4.04$, $p < 0.001$. The ASD group was highly heterogeneous, and there was variability (from impaired to normal) in non-verbal IQ and language abilities (see Table 1).

3.2. Source estimation of 2 Hz ASSR

In order to reveal the sources of 2 Hz ASSR in the left and right auditory cortices, we calculated PSD for the stimulation frequency (2 Hz) in the 0–1000 ms time window (stimulus presentation time) and estimated MNI coordinates for 15 vertices in each ROI with the highest 2 Hz PSD values. The grand average MNI coordinates are presented in Table 2 for both groups of children.

The results of source estimation (grand average MNI coordinates) showed that the location of 2 Hz ASSR in the left and right hemispheres was the transverse temporal sulcus and the planum temporale of the superior temporal gyrus. To estimate whether the localization of 2 Hz ASSR is different between the ASD and TD groups, we provided a between-group comparison of MNI coordinates in each hemisphere. The results revealed significant differences in Y and Z coordinates in the right hemisphere, indicating that the topology of 2 Hz ASSR was more superior ($t = -2.03$, $p = 0.02$) and posterior ($t = 1.77$, $p = 0.03$) in TD children compared with children with ASD (Fig. 1). Other effects were non-significant: X coordinate in the right hemisphere ($t = 0.08$, $p = 0.46$) and X coordinate ($t = 0.47$, $p = 0.31$), Y coordinate ($t = -0.47$, p = 0.31) and Z coordinate ($t = 0.006$, $p = 0.49$) in the left hemisphere.

Fig. 2 shows the cortical distribution of auditory response averaged in 0–1000 ms time windows as well as time courses for the identified left and right auditory regions of interest.

3.3. The comparison of auditory responses between children with and without ASD

In order to assess between-group differences in the power of 2 Hz ASSR, we fitted a linear mixed-effects model including the main effects of Hemisphere (right vs. left), Group (ASD vs. TD), and Group × Hemisphere interaction as fixed effects, and participants as a random intercept, according to the formula: lmer(Power ~ Hemisphere*Group + (1 | ID), data = data). The results showed a significant main effect of the Group, indicating that the ASD group had lower power; other effects were not significant (Table 3, Fig. 3A).

To compare amplitude of the ERF of 2 Hz ASSR between children with ASD and TD children, we used a linear mixed-effects model of similar structure as for power: lmer(ERF ~ Hemisphere*Group + (1 | ID), data = data). The results revealed a significant main effect of the Hemisphere, so that the amplitude of response was higher in the right hemisphere; other effects were non-significant (Table 4, Fig. 3B).

3.4. The relationships between neural responses and behavioral measures in children with ASD

In order to assess the relationships between neural responses and behavioral measures (language comprehension skills, nonverbal IQ, and the severity of autistic traits) in children with ASD, we fitted two linear mixed-effects models with neural activity as the dependent variable, main effects of three behavioral measures, and their interaction with hemisphere as fixed effects, and participants as a random intercept. The results revealed no relationships between power of 2 Hz ASSR and behavioral measures, but for the amplitude of ERF there was a significant main effect of mean language score: lower amplitude was associated with lower language skills (Tables 5, 6, Fig. 4).

Table 2
Grand average MNI coordinates for 2 Hz Auditory Steady-State Response for ASD and TD groups of children.

Group	Left auditory ROI			Right auditory ROI		
	Coordinate	Mean	SD	Coordinate	Mean	SD
ASD	X	−50.66	5.89	X	53.53	3.84
	Y	−21.29	7.77	Y	−11.06	4.46
	Z	6.27	4.22	Z	3.37	3.02
TD	X	−49.11	5.36	X	52.02	5.71
	Y	−25.39	6.21	Y	−17.98	6.29
	Z	10.44	3.62	Z	7.55	3.79

4. Discussion

In this study, we used MEG to examine 2 Hz ASSR (the power and the amplitude of ERF) at the source-level in children with ASD. We also evaluated how these responses were associated with behavioral measures such as language abilities, non-verbal IQ, and the severity of autistic symptoms in the ASD group. We found that children with ASD have a different topology of the auditory response and reduced power of 2 Hz ASSR in comparison to TD children, as well as a significant association between the amplitude of ERF and language skills.

The analysis of source localization for 2 Hz ASSR showed that the neural generators of the response were located in the primary auditory cortex (A1) and adjacent regions in the left and right hemispheres in both groups of children, which is consistent with previous ASSR studies (Arutiunian et al., 2023; Edgar et al., 2016; Seymour et al., 2020; Stroganova et al., 2020). The direct between-group comparison of MNI coordinates revealed significant differences in Y and Z coordinates in the right hemisphere. This means that in the group of TD children the location of 2 Hz ASSR was more superior and posterior in comparison to the ASD group. These findings are in line with previous studies that showed structural abnormalities in the auditory cortex in individuals with ASD compared to TD controls (Boddaert et al., 2004; De Fossé et al., 2004; Gage et al., 2009; Herbert et al., 2002; Hyde et al., 2010). For instance, Stroganova et al. (2020) using periodic stimuli at 40 Hz have found significant differences in the MNI coordinates of the response in the left but not right auditory ROI between children with and without ASD, indicating that the topology of ASSR was more medial in children with ASD.

In both groups, we observed a right hemispheric dominance in the amplitude of ERF in response to the pure tones presented at a frequency of 2 Hz. This finding is in line with studies indicating that the right hemisphere is dominant in pure tone processing, a phenomenon observed in both TD individuals (Ross et al., 2005; Schoonhoven et al., 2003) and those with ASD (Edgar et al., 2016; Ono et al., 2020; Poulsen et al., 2009; Stroganova et al., 2020). Some authors hypothesized that this asymmetry can be explained by the fact that the right auditory cortex is specialized for processing the temporal periodicity of sound (Ross et al., 2005). Overall, the hemispheric asymmetry of auditory responses can be associated with both morphological and functional differences between left and right auditory cortices (Boemio et al., 2005; Devlin et al., 2003; Hine and Debener, 2007).

The present study identified a significant reduction in the power of 2 Hz ASSR in children with ASD when compared to TD children, indicating that children with ASD have a deficit in synchronizing brain oscillations with incoming non-speech auditory rhythmic stimulation in the delta band. To the best of our knowledge, our study is the only research providing evidence on the auditory synchronization in response to non-linguistic stimuli of 2 Hz in children with ASD. Revealed group differences in the power of 2 Hz are consistent with the findings in other neurodevelopmental disorders. For example, some studies have shown an atypical auditory synchronization in the delta frequency range in response to linguistic and non-linguistic stimuli in children with developmental dyslexia, and found that this was associated with poorer phonological and reading skills (Di Liberto et al., 2018; Keshavarzi et al., 2022; Mandke et al., 2022; Molinaro et al., 2016; Power et al., 2016, 2013). Authors proposed that atypical auditory synchronization in children with developmental dyslexia may be due to their brains utilizing a different preferred phase of neural synchronizations (Keshavarzi et al., 2022; Power et al., 2013), but in children with ASD it can be also associated with atypical processing in cerebellum due to disruptions in specific cerebro-cerebellar loops in ASD (D'Mello and Stoodley, 2015; Mosconi et al., 2015).

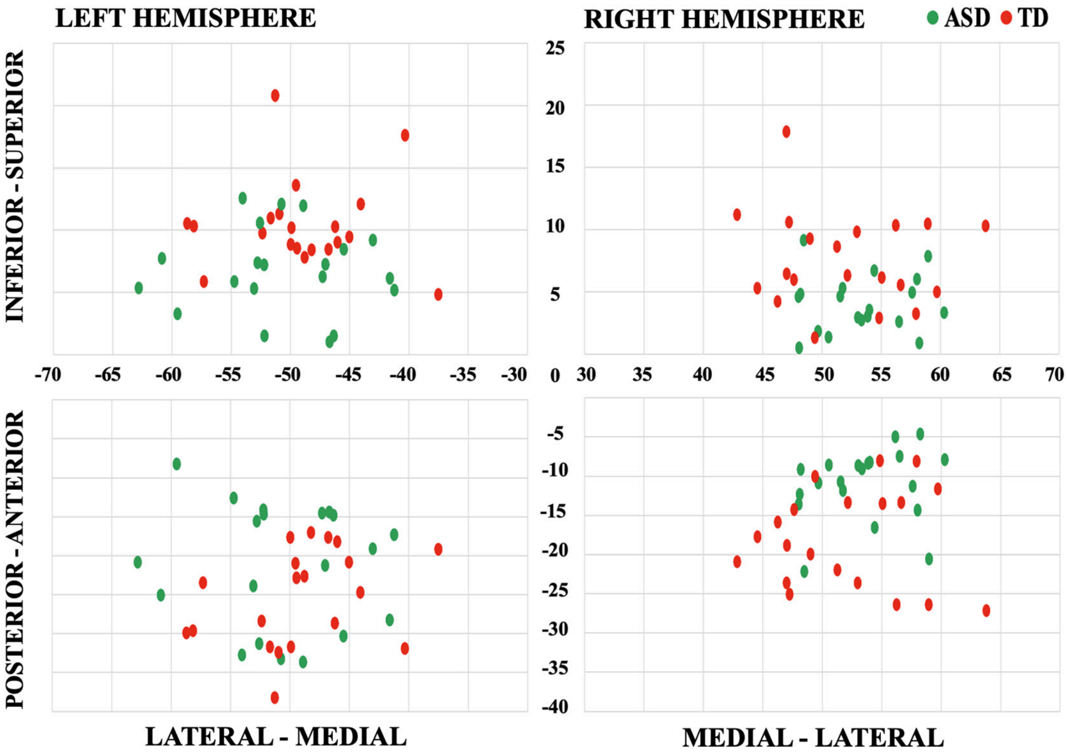

Fig. 1. MNI coordinates of 2 Hz ASSR power in the left and right hemispheres: green dots represent the individual MNI coordinates of each child with ASD, red dots represent the individual MNI coordinates of each TD child. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

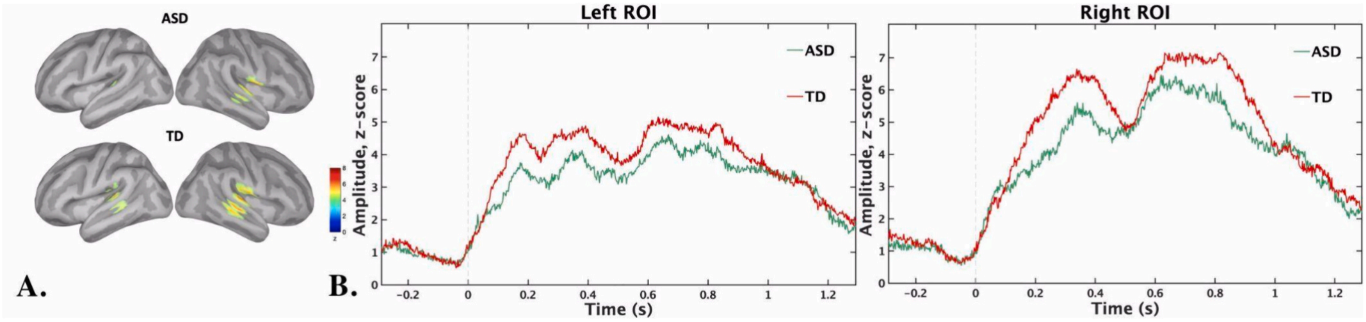

Fig. 2. Source localization of auditory response in children with and without ASD: (A) distribution of z-score absolute values in the left and right hemispheres averaged in 0–1000 ms time intervals; (B) timecourses of the ERF response in the left and right auditory ROI.

Table 3

The comparison of power of 2 Hz Auditory Steady-State Response between the ASD and TD groups. The significance is labeled with *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$ and highlighted in bold.

Predictor	Estimate	Standard error	*t*	*p*
Intercept	0.75	0.2	3.71	<**0.001***
Hemisphere	−0.21	0.18	−1.13	0.26
Group	0.59	0.28	2.06	**0.04***
Group × Hemisphere	−0.21	0.26	−0.8	0.42

We observed that the lower amplitude of ERF in response to 2 Hz pure tones was correlated with lower language skills in children with ASD. A possible explanation was provided in previous studies showing that auditory synchronization in delta frequency band is associated with the phonological system, and especially with prosodic features, i.e., pauses, stress, and intonation (Bourguignon et al., 2012; Ding and Simon, 2014; Giraud and Poeppel, 2012; Keitel et al., 2017). In addition, recent studies have shown that atypical auditory processing in the primary auditory cortex within the delta frequency range may impact both speech processing and the acquisition of an efficient phonological system (Attaheri et al., 2022; Goswami, 2019; Keshavarzi et al., 2022). Based on Temporal Sampling theory, for efficient auditory processing, rhythmic neuronal activity must coincide with the perceived rhythmic structure of the stimulus (Goswami, 2011). According to this theory, difficulties with slower temporal modulations can be related to the difficulties with syllable parsing and perceiving both syllable stress and the phonetic constituents of the syllable in children with developmental dyslexia. Furthermore, it has been shown that the oscillatory neural activity at different frequency bands corresponds to a different level of language processing, and the accuracy of the synchronization of these oscillations with the perceived input is positively correlated with language ability (Ding and Simon, 2014). The results of our study demonstrated a positive correlation between the amplitude of ERF at delta frequency range and language abilities, which may hypothetically reflect the level of development of the phonological system of children

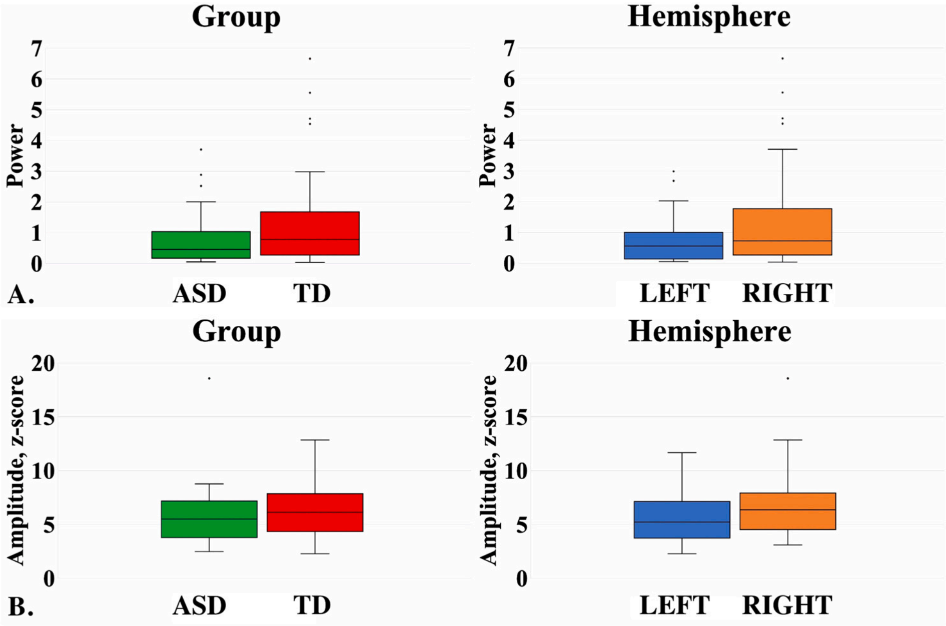

Fig. 3. Group and Hemispheric differences in (A) the power of 2 Hz ASSR and (B) the amplitude of the ERF of 2 Hz ASSR in children with and without ASD.

Table 4
The comparison of the amplitude of the ERF of 2 Hz ASSR between the ASD and TD groups. The significance is labeled with $*p < 0.05$, $**p < 0.01$, $***p < 0.001$ and highlighted in bold.

Predictor	Estimate	Standard error	*t*	*p*
Intercept	5.73	0.45	12.73	<**0.001*****
Hemisphere	−0.76	0.37	−2.03	**0.04***
Group	0.78	0.63	1.23	0.22
Group × Hemisphere	0.16	0.53	0.31	0.75

Table 5
The relationship between the power of 2 Hz ASSR and behavioral characteristics of children with ASD.

Predictor	Estimate	Standard Error	*t*	*p*
(Intercept)	0.28	0.85	0.33	0.74
Hemisphere	−0.1	0.82	−0.12	0.9
Mean language score	0.85	0.72	1.22	0.23
IQ	−0.002	0.009	−0.21	0.83
AQ	0.00001	0.007	0.002	0.99
Hemisphere × MLS	−0.78	0.69	−1.13	0.27
Hemisphere × IQ	0.0005	0.009	0.06	0.95
Hemisphere × AQ	0.005	0.007	0.69	0.49

Table 6
The relationship between the amplitude of the ERF of 2 Hz ASSR and behavioral characteristics of children with ASD. The significance is labeled with $*p < 0.05$, $**p < 0.01$, $***p < 0.001$ and highlighted in bold.

Predictor	Estimate	Standard error	*t*	*p*
(Intercept)	6.61	2.66	2.48	**0.02***
Hemisphere	−3.05	2.55	−1.19	0.24
Mean language score	4.77	2.24	2.12	**0.04***
IQ	−0.04	0.03	−1.65	0.11
AQ	−0.001	0.02	−0.74	0.94
Hemisphere × MLS	−1.002	2.15	−0.46	0.64
Hemisphere × IQ	0.005	0.02	0.18	0.85
Hemisphere × AQ	0.03	0.02	1.36	0.19

with ASD.

Summarizing, the present study revealed a significant reduction in the power of 2 Hz ASSR in children with ASD and the relationship between the neural response and language skills in autistic individuals. Overall, our findings contribute to the study of auditory processing in children with ASD, emphasizing the significance of the synchronization in the delta frequency band and its correlation with language abilities. These findings contribute to the broader understanding of sensory processing mechanisms in ASD and may inform future interventions targeting auditory and language impairments in this population.

4.1. Limitations and future directions

The study has some limitations. First of all, our sample sizes are relatively small, and, in addition, there is a high variability in the ASD group. To generalize and to confirm the main findings (both between-group comparisons and brain–behavior relationships), it is necessary to include larger samples in the future studies. Second, we did not register individual differences of hearing thresholds, which can affect the strengths of both types of auditory responses and future studies would require to register individual sensitive variability in ASD participants to account the hypersensitiveness. Third, our sample includes primary-school-aged children, but it is known that the strength of ASSR responses typically increase with development, with the magnitude of phase locking increasing up to the age of 14–16 years (Cho et al., 2015). Hence, future studies of an older group of participants are needed to understand whether the findings in younger children with ASD are age-specific or can be generalized to the broader population (Ahlfors et al., 2023). Fourth, our samples are sex-imbalanced and future studies would benefit from including an equal number of males and females in each group as the previous studies have identified differences in general and domain-specific brain functioning between male and female autistic individuals (e.g., Baron-Cohen, 2002; Mo et al., 2021; Neuhaus et al., 2021). Finally, due to the critical role of cerebellum in ASD symptomatology as well as in rhythmic movements, future studies would benefit from combining both functional and structural imaging to investigate the contribution of primary auditory areas and cerebellum in the neural processing and its relation to language functioning in children with ASD.

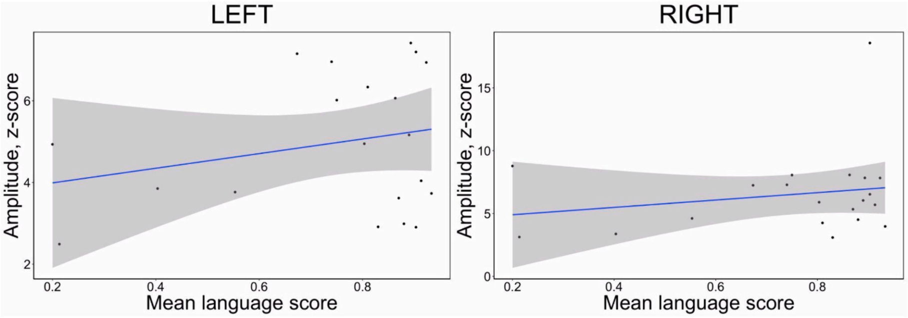

Fig. 4. The relationship between the amplitude of the ERF of 2 Hz ASSR and mean language score in children with ASD.

Funding

This work is an output of a research project implemented as part of the Basic Research Program at HSE University.

CRediT authorship contribution statement

Ilya Samoylov: Writing – review & editing, Writing – original draft, Formal analysis. **Giorgio Arcara:** Methodology, Formal analysis. **Irina Buyanova:** Investigation. **Elizaveta Davydova:** Investigation. **Darya Pereverzeva:** Investigation. **Alexander Sorokin:** Investigation. **Svetlana Tyushkevich:** Investigation. **Uliana Mamokhina:** Investigation. **Kamilla Danilina:** Investigation. **Olga Dragoy:** Writing – review & editing, Resources. **Vardan Arutiunian:** Writing – review & editing, Project administration, Investigation, Formal analysis, Data curation, Methodology, Conceptualization.

Declaration of competing interest

The authors have no conflict to disclose.

Acknowledgements

We would especially like to thank all children taking part in this study – without them such a study would not be possible.

References

Ahlfors, S., Graham, S., Bharadwaj, H., Mamashli, F., Khan, S., Joseph, R., et al., 2023. No differences in auditory steady-state responses in children with autism spectrum disorder and typically developing children. J. Autism Dev. Disord. 1–14. https://doi.org/10.1007/s10803-023-05907-w.

American Psychiatric Association (Ed.), 2013. Diagnostic and Statistical Manual of Mental Disorders: DSM-5, 5th ed. American Psychiatric Association, Washington, D. C.

Arutiunian, V., Lopukhina, A., Minnigulova, A., Shlyakhova, A., Davydova, E., Pereverzeva, D., et al., 2022. 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., Davydova, E., Pereverzeva, D., Sorokin, A., et al., 2023. Neuromagnetic 40 Hz auditory steady-state response in the left auditory cortex is related to language comprehension in children with autism spectrum disorder. Prog. Neuro-Psychopharmacol. Biol. Psychiatry 122, 110690. https://doi.org/10.1016/j.pnpbp.2022.110690.

Attaheri, A., Choisdealbha, Á.N., Di Liberto, G.M., Rocha, S., Brusini, P., Mead, N., et al., 2022. Delta- and theta-band cortical tracking and phase-amplitude coupling to sung speech by infants. Neuroimage 247, 118698. https://doi.org/10.1016/j.neuroimage.2021.118698.

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.

Baron-Cohen, S., 2002. The extreme male brain theory of autism. Trends Cogn. Sci. 6, 248–254. https://doi.org/10.1016/s1364-6613(02)01904-6.

Berman, J.I., Edgar, J.C., Blaskey, L., Kuschner, E.S., Levy, S.E., Ku, M., et al., 2016. Multimodal diffusion-MRI and MEG assessment of auditory and language system development in autism spectrum disorder. Front. Neuroanat. 10. https://doi.org/10.3389/fnana.2016.00030.

Boddaert, N., Chabane, N., Gervais, H., Good, C.D., Bourgeois, M., Plumet, M.-H., et al., 2004. Superior temporal sulcus anatomical abnormalities in childhood autism: a voxel-based morphometry MRI study. NeuroImage 23, 364–369. https://doi.org/10.1016/j.neuroimage.2004.06.016.

Boemio, A., Fromm, S., Braun, A., Poeppel, D., 2005. Hierarchical and asymmetric temporal sensitivity in human auditory cortices. Nat. Neurosci. 8, 389–395. https://doi.org/10.1038/nn1409.

Bourguignon, M., De Tiège, X., de Beeck, M.O., Ligot, N., Paquier, P., Van Bogaert, P., et al., 2012. The pace of prosodic phrasing couples the listener's cortex to the reader's voice. Hum. Brain Mapp. 34, 314–326. https://doi.org/10.1002/hbm.21442.

Cho, R.Y., Walker, C.P., Polizzotto, N.R., Wozny, T.A., Fissell, C., Chen, C.-M.A., et al., 2015. Development of sensory gamma oscillations and cross-frequency coupling from childhood to early adulthood. Cereb. Cortex 25, 1509–1518. https://doi.org/10.1093/cercor/bht341.

Clumeck, C., Garcia, S.S., Bourguignon, M., Wens, V., Beeck, M.O. de, Marty, B., et al., 2014. Preserved coupling between the reader's voice and the listener's cortical activity in autism spectrum disorders. PLoS One 9, e92329. https://doi.org/10.1371/journal.pone.0092329.

Cogan, G.B., Poeppel, D., 2011. A mutual information analysis of neural coding of speech by low-frequency MEG phase information. J. Neurophysiol. 106, 554–563. https://doi.org/10.1152/jn.00075.2011.

Dale, A.M., Fischl, B., Sereno, M.I., 1999. Cortical surface-based analysis: I. Segmentation and surface reconstruction. NeuroImage 9, 179–194. https://doi.org/10.1006/nimg.1998.0395.

De Fossé, L., Hodge, S.M., Makris, N., Kennedy, D.N., Caviness, V.S., McGrath, L., et al., 2004. Language-association cortex asymmetry in autism and specific language impairment. Ann. Neurol. 56, 757–766. https://doi.org/10.1002/ana.20275.

De Stefano, L.A., Schmitt, L.M., White, S.P., Mosconi, M.W., Sweeney, J.A., Ethridge, L. E., 2019. Developmental effects on auditory neural oscillatory synchronization abnormalities in autism spectrum disorder. Front. Integr. Neurosci. 13, 34. https://doi.org/10.3389/fnint.2019.00034.

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.

Demopoulos, C., Yu, N., Tripp, J., Mota, N., Brandes-Aitken, A.N., Desai, S.S., et al., 2017. Magnetoencephalographic imaging of auditory and somatosensory cortical responses in children with autism and sensory processing dysfunction. Front. Hum. Neurosci. 11. https://doi.org/10.3389/fnhum.2017.00259.

Devlin, J.T., Raley, J., Tunbridge, E., Lanary, K., Floyer-Lea, A., Narain, C., et al., 2003. Functional asymmetry for auditory processing in human primary auditory cortex. J. Neurosci. 23, 11516–11522. https://doi.org/10.1523/JNEUROSCI.23-37-11516.2003.

Di Liberto, G.M., Peter, V., Kalashnikova, M., Goswami, U., Burnham, D., Lalor, E.C., 2018. Atypical cortical entrainment to speech in the right hemisphere underpins phonemic deficits in dyslexia. Neuroimage 175, 70–79. https://doi.org/10.1016/j.neuroimage.2018.03.072.

Ding, N., Simon, J.Z., 2014. Cortical entrainment to continuous speech: functional roles and interpretations. Front. Hum. Neurosci. 8. https://doi.org/10.3389/fnhum.2014.00311.

D'Mello, A.M., Stoodley, C.J., 2015. Cerebro-cerebellar circuits in autism spectrum disorder. Front. Neurosci. 9. https://doi.org/10.3389/fnins.2015.00408.

Dunlop, W.A., Enticott, P.G., Rajan, R., 2016. Speech discrimination difficulties in high-functioning autism spectrum disorder are likely independent of auditory hypersensitivity. Front. Hum. Neurosci. 10. https://doi.org/10.3389/fnhum.2016.00401.

Edgar, J.C., CLF, I.V., Berman, J.I., Chudnovskaya, D., Liu, S., Pandey, J., et al., 2015. Auditory encoding abnormalities in children with autism spectrum disorder suggest delayed development of auditory cortex. Mol. Autism 6, 69. https://doi.org/10.1186/s13229-015-0065-5.

Edgar, J.C., Fisk IV, C.L., Liu, S., Pandey, J., Herrington, J.D., Schultz, R.T., et al., 2016. Translating adult electrophysiology findings to younger patient populations: difficulty measuring 40-Hz auditory steady-state responses in typically developing children and children with autism spectrum disorder. Dev. Neurosci. 38, 1–14. https://doi.org/10.1159/000441943.

Farahani, E.D., Wouters, J., Wieringen, A. van, 2021. Brain mapping of auditory steady-state responses: a broad view of cortical and subcortical sources. Hum. Brain Mapp. 42, 780–796. https://doi.org/10.1002/hbm.25262.

Gage, N.M., Siegel, B., Callen, M., Roberts, T.P.L., 2003. Cortical sound processing in children with autism disorder: an MEG investigation. NeuroReport 14, 2047–2051. https://doi.org/10.1097/00001756-200311140-00008.

Gage, N.M., Juranek, J., Filipek, P.A., Osann, K., Flodman, P., Isenberg, A.L., et al., 2009. Rightward hemispheric asymmetries in auditory language cortex in children with autistic disorder: an MRI investigation. J. Neurodev. Disord. 1, 205–214. https://doi.org/10.1007/s11689-009-9010-2.

Galambos, R., Makeig, S., Talmachoff, P.J., 1981. A 40-Hz auditory potential recorded from the human scalp. Proc. Natl. Acad. Sci. 78, 2643–2647. https://doi.org/10.1073/pnas.78.4.2643.

Giraud, A.-L., Poeppel, D., 2012. Cortical oscillations and speech processing: emerging computational principles and operations. Nat. Neurosci. 15, 511–517. https://doi.org/10.1038/nn.3063.

Giraud, A.-L., Kleinschmidt, A., Poeppel, D., Lund, T.E., Frackowiak, R.S.J., Laufs, H., 2007. Endogenous cortical rhythms determine cerebral specialization for speech perception and production. Neuron 56, 1127–1134. https://doi.org/10.1016/j.neuron.2007.09.038.

Goswami, U., 2011. A temporal sampling framework for developmental dyslexia. Trends Cogn. Sci. 15, 3–10. https://doi.org/10.1016/j.tics.2010.10.001.

Goswami, U., 2019. Speech rhythm and language acquisition: an amplitude modulation phase hierarchy perspective. Ann. N. Y. Acad. Sci. 1453, 67–78. https://doi.org/10.1111/nyas.14137.

Gross, J., Hoogenboom, N., Thut, G., Schyns, P., Panzeri, S., Belin, P., et al., 2013. Speech rhythms and multiplexed oscillatory sensory coding in the human brain. PLoS Biol. 11, e1001752 https://doi.org/10.1371/journal.pbio.1001752.

Haesen, B., Boets, B., Wagemans, J., 2011. A review of behavioural and electrophysiological studies on auditory processing and speech perception in autism spectrum disorders. Res. Autism Spectr. Disord. 5, 701–714. https://doi.org/10.1016/j.rasd.2010.11.006.

Hämäläinen, M.S., Ilmoniemi, R.J., 1994. Interpreting magnetic fields of the brain: minimum norm estimates. Med. Biol. Eng. Comput. 32, 35–42. https://doi.org/10.1007/BF02512476.

Herbert, M.R., Harris, G.J., Adrien, K.T., Ziegler, D.A., Makris, N., Kennedy, D.N., et al., 2002. Abnormal asymmetry in language association cortex in autism. Ann. Neurol. 52, 588–596. https://doi.org/10.1002/ana.10349.

Hertrich, I., Mathiak, K., Ackermann, H., 2016. Chapter 2 - the role of the cerebellum in speech perception and language comprehension. In: Mariën, P., Manto, M. (Eds.), The Linguistic Cerebellum. Academic Press, San Diego, pp. 33–50. https://doi.org/10.1016/B978-0-12-801608-4.00002-5.

Hine, J., Debener, S., 2007. Late auditory evoked potentials asymmetry revisited. Clin. Neurophysiol. 118, 1274–1285. https://doi.org/10.1016/j.clinph.2007.03.012.

Huang, M.X., Mosher, J.C., Leahy, R.M., 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.

Hyde, K.L., Samson, F., Evans, A.C., Mottron, L., 2010. Neuroanatomical differences in brain areas implicated in perceptual and other core features of autism revealed by cortical thickness analysis and voxel-based morphometry. Hum. Brain Mapp. 31, 556–566. https://doi.org/10.1002/hbm.20887.

Jochaut, D., Lehongre, K., Saitovitch, A., Devauchelle, A.-D., Olasagasti, I., Chabane, N., et al., 2015. Atypical coordination of cortical oscillations in response to speech in autism. Front. Hum. Neurosci. 9. https://doi.org/10.3389/fnhum.2015.00171.

Kaufman, A.S., Kaufman, N.L., 2004. Kaufman Assessment Battery for Children, 2nd ed. American Guidance Service.

Keitel, A., Gross, J., Kayser, C., 2017. Speech tracking in auditory and motor regions reflects distinct linguistic features. Neuroscience. https://doi.org/10.1101/195941.

Keshavarzi, M., Mandke, K., Macfarlane, A., Parvez, L., Gabrielczyk, F., Wilson, A., et al., 2022. Atypical delta-band phase consistency and atypical preferred phase in children with dyslexia during neural entrainment to rhythmic audio-visual speech. Neuroimage Clin. 35, 103054 https://doi.org/10.1016/j.nicl.2022.103054.

Kuwada, S., Batra, R., Maher, V.L., 1986. Scalp potentials of normal and hearing-impaired subjects in response to sinusoidally amplitude-modulated tones. Hear. Res. 21, 179–192. https://doi.org/10.1016/0378-5955(86)90038-9.

Legget, K.T., Hild, A.K., Steinmetz, S.E., Simon, S.T., Rojas, D.C., 2017. MEG and EEG demonstrate similar test-retest reliability of the 40Hz auditory steady-state response. Int. J. Psychophysiol. 114, 16–23. https://doi.org/10.1016/j.ijpsycho.2017.01.013.

Lin, F.-H., Witzel, T., Ahlfors, S.P., Stufflebeam, S.M., Belliveau, J.W., Hämäläinen, M.S., 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, P.C., Risi, S., Gotham, K., Bishop, S.L., 2012. Autism Diagnostic Observation Schedule, 2nd ed. Western Psychological Services.

Luo, H., Poeppel, D., 2012. Cortical oscillations in auditory perception and speech: evidence for two temporal windows in human auditory cortex. Front. Psychol. 3. https://doi.org/10.3389/fpsyg.2012.00170.

Mandke, K., Flanagan, S., Macfarlane, A., Gabrielczyk, F., Wilson, A., Gross, J., et al., 2022. Neural sampling of the speech signal at different timescales by children with dyslexia. Neuroimage 253, 119077. https://doi.org/10.1016/j.neuroimage.2022.119077.

Matsuzaki, J., Kuschner, E.S., Blaskey, L., Bloy, L., Kim, M., Ku, M., et al., 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.

McFadden, K.L., Steinmetz, S.E., Carroll, A.M., Simon, S.T., Wallace, A., Rojas, D.C., 2014. Test-retest reliability of the 40 Hz EEG auditory steady-state response. PLoS One 9, e85748. https://doi.org/10.1371/journal.pone.0085748.

Mo, K., Sadoway, T., Bonato, S., Ameis, S.H., Anagnostou, E., Lerch, J.P., et al., 2021. Sex/gender differences in the human autistic brains: a systematic review of 20 years of neuroimaging research. Neuroimage Clin. 32, 102811 https://doi.org/10.1016/j.nicl.2021.102811.

Molinaro, N., Lizarazu, M., Lallier, M., Bourguignon, M., Carreiras, M., 2016. Out-of-synchrony speech entrainment in developmental dyslexia. Hum. Brain Mapp. 37, 2767–2783. https://doi.org/10.1002/hbm.23206.

Mosconi, M.W., Wang, Z., Schmitt, L.M., Tsai, P., Sweeney, J.A., 2015. The role of cerebellar circuitry alterations in the pathophysiology of autism spectrum disorders. Front. Neurosci. 9. https://doi.org/10.3389/fnins.2015.00296.

Murphy, E., Benítez-Burraco, A., 2017. Language deficits in schizophrenia and autism as related oscillatory connectomopathies: an evolutionary account. Neurosci. Biobehav. Rev. 83, 742–764. https://doi.org/10.1016/j.neubiorev.2016.07.029.

Nadig, A., Shaw, H., 2012. Acoustic and perceptual measurement of expressive prosody in high-functioning autism: increased pitch range and what it means to listeners. J. Autism Dev. Disord. 42, 499–511. https://doi.org/10.1007/s10803-011-1264-3.

Nallet, C., Gervain, J., 2022. Atypical neural oscillations in response to speech in infants and children with speech and language impairments: a systematic review. Hear. Balance Commun. 20, 145–154. https://doi.org/10.1080/21695717.2022.2084864.

Nash-Kille, A., Sharma, A., 2014. Inter-trial coherence as a marker of cortical phase synchrony in children with sensorineural hearing loss and auditory neuropathy spectrum disorder fitted with hearing aids and cochlear implants. Clin. Neurophysiol. 125, 1459–1470. https://doi.org/10.1016/j.clinph.2013.11.017.

Neuhaus, E., Lowry, S.J., Santhosh, M., Kresse, A., Edwards, L.A., Keller, J., et al., 2021. Resting state EEG in youth with ASD: age, sex, and relation to phenotype. J. Neurodev. Disord. 13, 1–15. https://doi.org/10.1186/s11689-021-09390-1.

Ono, Y., Kudoh, K., Ikeda, T., Takahashi, T., Yoshimura, Y., Minabe, Y., et al., 2020. Auditory steady-state response at 20 Hz and 40 Hz in young typically developing children and children with autism spectrum disorder. Psychiatry Clin. Neurosci. 74, 354–361. https://doi.org/10.1111/pcn.12998.

Palana, J., Schwartz, S., Tager-Flusberg, H., 2022. Evaluating the use of cortical entrainment to measure atypical speech processing: a systematic review. Neurosci. Biobehav. Rev. 133, 104506 https://doi.org/10.1016/j.neubiorev.2021.12.029.

Park, H., Ince, R.A.A., Schyns, P.G., Thut, G., Gross, J., 2015. Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. Curr. Biol. 25, 1649–1653. https://doi.org/10.1016/j.cub.2015.04.049.

Paul, R., Shriberg, L.D., McSweeny, J., Cicchetti, D., Klin, A., Volkmar, F., 2005. Brief report: relations between prosodic performance and communication and socialization ratings in high functioning speakers with autism spectrum disorders. J. Autism Dev. Disord. 35, 861–869. https://doi.org/10.1007/s10803-005-0031-8.

Peelle, J.E., Davis, M.H., 2012. Neural oscillations carry speech rhythm through to comprehension. Front. Psychol. 3, 320. https://doi.org/10.3389/fpsyg.2012.00320.

Peelle, J., Gross, J., Davis, M., 2012. Phase-locked responses to speech in human auditory cortex are enhanced during comprehension. Cereb. Cortex 23. https://doi.org/10.1093/cercor/bhs118.

Picton, T.W., Skinner, C.R., Champagne, S.C., Kellett, A.J.C., Maiste, A.C., 1987. Potentials evoked by the sinusoidal modulation of the amplitude or frequency of a tone. J. Acoust. Soc. Am. 82, 165–178. https://doi.org/10.1121/1.395560.

Picton, T.W., John, M.S., Dimitrijevic, A., Purcell, D., 2003. Human auditory steady-state responses: respuestas auditivas de estado estable en humanos. Int. J. Audiol. 42, 177–219. https://doi.org/10.3109/14992020309101316.

Poeppel, D., Teng, X., 2020. 2.06 - entrainment in human auditory cortex: mechanism and functions. In: Fritzsch, B. (Ed.), The Senses: A Comprehensive Reference, Second edition. Elsevier, Oxford, pp. 63–76. https://doi.org/10.1016/B978-0-12-805408-6.00018-X.

Poulsen, C., Picton, T.W., Paus, T., 2009. Age-related changes in transient and oscillatory brain responses to auditory stimulation during early adolescence. Dev. Sci. 12, 220–235. https://doi.org/10.1111/j.1467-7687.2008.00760.x.

Power, A.J., Mead, N., Barnes, L., Goswami, U., 2013. Neural entrainment to rhythmic speech in children with developmental dyslexia. Front. Hum. Neurosci. 7. https://doi.org/10.3389/fnhum.2013.00777.

Power, A.J., Colling, L.J., Mead, N., Barnes, L., Goswami, U., 2016. Neural encoding of the speech envelope by children with developmental dyslexia. Brain Lang. 160, 1–10. https://doi.org/10.1016/j.bandl.2016.06.006.

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.

Rees, A., Green, G.G.R., Kay, R.H., 1986. Steady-state evoked responses to sinusoidally amplitude-modulated sounds recorded in man. Hear. Res. 23, 123–133. https://doi.org/10.1016/0378-5955(86)90009-2.

Roberts, T.P.L., Khan, S.Y., Rey, M., Monroe, J.F., Cannon, K., Blaskey, L., et al., 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, T.P.L., Heiken, K., Zarnow, D., Dell, J., Nagae, L., Blaskey, L., et al., 2014. Left hemisphere diffusivity of the arcuate fasciculus: influences of autism spectrum disorder and language impairment. Am. J. Neuroradiol. 35, 587–592. https://doi.org/10.3174/ajnr.A3754.

Roberts, T.P.L., 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. https://doi.org/10.3389/fnhum.2021.787229.

Ross, B., Herdman, A.T., Pantev, C., 2005. Right hemispheric laterality of human 40 Hz auditory steady-state responses. Cereb. Cortex 15, 2029–2039. https://doi.org/10.1093/cercor/bhi078.

Schelinski, S., Tabas, A., von Kriegstein, K., 2022. Altered processing of communication signals in the subcortical auditory sensory pathway in autism. Hum. Brain Mapp. 43, 1955–1972. https://doi.org/10.1002/hbm.25766.

Schoonhoven, R., Boden, C.J.R., Verbunt, J.P.A., de Munck, J.C., 2003. A whole head MEG study of the amplitude-modulation-following response: phase coherence, group delay and dipole source analysis. Clin. Neurophysiol. 114, 2096–2106. https://doi.org/10.1016/s1388-2457(03)00200-1.

Schwartze, M., Kotz, S.A., 2016. Contributions of cerebellar event-based temporal processing and preparatory function to speech perception. Brain Lang. 161, 28–32. https://doi.org/10.1016/j.bandl.2015.08.005.

Seymour, R.A., Rippon, G., Gooding-Williams, G., Sowman, P.F., 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.

Stapells, D.R., Galambos, R., Costello, J.A., Makeig, S., 1988. Inconsistency of auditory middle latency and steady-state responses in infants. Electroencephalogr. Clin. Neurophysiol. 71, 289–295. https://doi.org/10.1016/0168-5597(88)90029-9.

Stroganova, T.A., Komarov, K.S., Sysoeva, O.V., Goiaeva, D.E., Obukhova, T.S., Ovsiannikova, T.M., et al., 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, J.C., Pantazis, D., Leahy, R.M., 2011. Brainstorm: a user-friendly application for MEG/EEG analysis. Comput. Intell. Neurosci. 2011, 1–13. https://doi.org/10.1155/2011/879716.

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.

Thaut, M.H., Stephan, K.M., Wunderlich, G., Schicks, W., Tellmann, L., Herzog, H., et al., 2009. Distinct cortico-cerebellar activations in rhythmic auditory motor synchronization. Cortex 45, 44–53. https://doi.org/10.1016/j.cortex.2007.09.009.

Thut, G., Schyns, P.G., Gross, J., 2011. Entrainment of perceptually relevant brain oscillations by non-invasive rhythmic stimulation of the human brain. Front. Psychol. 2. https://doi.org/10.3389/fpsyg.2011.00170.

Wang, X., Delgado, J., Marchesotti, S., Kojovic, N., Sperdin, H.F., Rihs, T.A., et al., 2023. Speech reception in young children with autism is selectively indexed by a neural oscillation coupling anomaly. J. Neurosci. 43, 6779–6795. https://doi.org/10.1523/JNEUROSCI.0112-22.2023.

Wechsler, D., 1991. The Wechsler Intelligence Scale for Children, Third edition. The Psychological Corporation.

Wolff, J.J., Gu, H., Gerig, G., Elison, J.T., Styner, M., Gouttard, S., et al., 2012. Differences in white matter fiber tract development present from 6 to 24 months in infants with autism. Am. J. Psychiatry 169, 589–600. https://doi.org/10.1176/appi.ajp.2011.11091447.