

## TITLE PAGE

## Title: Global MEG Resting State Functional Connectivity in Children with Autism and Sensory Processing Dysfunction

## Running Title: MEG Functional Connectivity in ASD & SPD

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## Abstract

51       Sensory processing dysfunction not only affects most individuals with autism spectrum  
52       disorder (ASD), but at least 5% of children without ASD also experience dysfunctional sensory  
53       processing. Our understanding of the relationship between sensory dysfunction and resting state  
54       brain activity is still emerging. This study compared long-range resting state functional  
55       connectivity of neural oscillatory behavior in children aged 8-12 years with autism spectrum  
56       disorder (ASD; N=18), those with sensory processing dysfunction (SPD; N=18) who do not meet  
57       ASD criteria, and typically developing control participants (TDC; N=24) using  
58       magnetoencephalography (MEG). Functional connectivity analyses were performed in the alpha  
59       and beta frequency bands, which are known to be implicated in sensory information processing.  
60       Group differences in functional connectivity and associations between sensory abilities and  
61       functional connectivity were examined. Distinct patterns of functional connectivity differences  
62       between ASD and SPD groups were found only in the beta band, but not in the alpha band. In  
63       both alpha and beta bands, ASD and SPD cohorts differed from the TDC cohort. Somatosensory  
64       cortical beta-band functional connectivity was associated with tactile processing abilities, while  
65       higher-order auditory cortical alpha-band functional connectivity was associated with auditory  
66       processing abilities. These findings demonstrate distinct long-range neural synchrony alterations  
67       in SPD and ASD that are associated with sensory processing abilities. Neural synchrony  
68       measures could serve as potential sensitive biomarkers for ASD and SPD.

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## Introduction

74       Sensory dysfunction is estimated to impact at least 70% of individuals with Autism  
75       Spectrum Disorders (ASD; Adamson, Hare, & Graham, 2006; Al-Heizan, AlAbdulwahab,  
76       Kachanathu, & Natho, 2015; Greenspan & Wieder, 1997; Mayes & Calhoun, 1999; Tomcheck &  
77       Dunn, 2007), and with its recognition as a core symptom in DSM-5 (American Psychiatric  
78       Association 2013), there is a rapidly growing body of research focused on understanding the  
79       causes and impact of sensory dysfunction in ASD. This line of research can be advanced not  
80       only by studying sensory dysfunction in individuals with ASD and other clinical populations, but  
81       also through examination of the estimated >5% of non-autistic individuals who experience  
82       clinically significant sensory processing dysfunction (SPD) (Ahn et al. 2004). Yet, despite the  
83       impairment in adaptive functioning associated with SPD, the absence of a recognized categorical  
84       diagnosis limits access to resources for research and treatment in affected individuals.

85       Nevertheless, biological differences, such as white matter abnormalities (Chang et al. 2014;  
86       Owen et al. 2013) and cortical response latencies (Demopoulos et al. 2017), have been identified  
87       in children with SPD and these measurable structural and physiologic differences have been  
88       associated with sensory processing behaviors (Chang et al., 2016). While some features of  
89       sensory dysfunction may be shared among children with SPD and those with ASD, such as  
90       tactile processing deficits (Demopoulos, Brandes-Aitken, et al. 2015), some domains of sensory  
91       dysfunction may identify important distinctions between these populations. For example,  
92       auditory processing abnormalities have been identified as distinguishing ASD from SPD groups  
93       in both behavioral tasks and neural response latencies (Demopoulos et al. 2017; Demopoulos,  
94       Brandes-Aitken, et al. 2015). Understanding these similarities and differences in sensory  
95       processing dysfunction among children with and without ASD can not only help delineate the

96 sensory dysfunction that is specific to ASD, but it can also heighten our understanding of sensory  
97 information processing more broadly and guide treatment strategies.

98       Because differences in resting state oscillatory activity can be indicative of functional  
99 pathology (Papanicolaou 2009), there has been extensive research examining differences in  
100 resting state brain activity in individuals with and without ASD diagnoses. While previous  
101 sensory processing research has focused on differences in performance-based measures of, and  
102 neural responses to, sensory processing (Chang et al., 2014; Demopoulos et al., 2015, 2017), our  
103 understanding of the relationship between sensory dysfunction and resting state brain activity is  
104 still emerging. This study will be the first to use using silently acquired recording via  
105 magnetoencephalography (MEG) to examine whole brain functional connectivity during rest in  
106 participants with ASD, SPD, and typically developing children (TDC). The goal of this study is  
107 to identify relevant differences in whole brain functional connectivity that may be associated  
108 with sensory dysfunction. Concurrent examination of these three groups offers two key benefits.  
109 First, it will add to the emerging literature identifying the shared and distinct patterns of neural  
110 activity in children with ASD and SPD. Second, it will allow us to examine differences in  
111 functional connectivity and behavioral measures of sensory discrimination in affected children.  
112 Prior research has suggested that auditory and tactile processing are particularly impacted in  
113 children with ASD (Fernandez-Andres et al. 2015), and that auditory processing has been  
114 associated with the communication impairments that are core to ASD (Demopoulos et al. 2017;  
115 Demopoulos, Brandes-Aitken, et al. 2015; Demopoulos, Hopkins, et al. 2015; Edgar et al. 2013,  
116 2014; Lerner, McPartland, and Morris 2013; Oram-Cardy et al. 2005; Oram Cardy et al. 2008;  
117 Roberts et al. 2011, 2012, 2019, 2008, 2010). As such, we also examine associations between

118 functional connectivity and performance-based measures of auditory and tactile processing and  
119 verbal abilities.

120 Our functional connectivity analyses were performed in the alpha and beta frequency  
121 bands, which are known to be implicated in sensory information processing. Specifically, these  
122 frequency bands have been associated with sensory gating (Buchholz, Jensen, and Medendorp  
123 2014) and direction of sensory attention in the auditory and visual cortex for alpha (Foxe and  
124 Snyder 2011) and in the somatosensory cortex for beta (Bauer, Kennett, and Driver 2012; van  
125 Ede, Jensen, and Maris 2010). Further, the role of alpha activity in states of psychological  
126 distress has been widely studied (Adolph and Margraf 2017; Bouthcher and Landers 1998;  
127 Demerdzieva and Pop-Jordanova 2015; Fingelkurts et al. 2007; Knyazev, Savostyanov, and  
128 Levin 2006; Mennella, Patron, and Palomba 2017; Smith, Zambrano-Vazquez, and Allen 2016),  
129 and may be relevant to differences in psychological response to sensory input in our clinical  
130 groups.

131 Prior research has demonstrated that both children with SPD and ASD were impaired on  
132 behavioral and neural measures of tactile processing, but only the ASD group demonstrated  
133 auditory dysfunction (Demopoulos et al. 2017; Demopoulos, Brandes-Aitken, et al. 2015). This  
134 work is consistent with structural findings that children with ASD and SPD demonstrate  
135 decreased connectivity in parieto-occipital tracts, but connectivity in temporal tracts was only  
136 reduced in the ASD group (Chang et al., 2014). Thus, given these shared and divergent sensory  
137 findings between children with ASD and SPD, and given that alpha and beta connectivity has  
138 been associated with sensory gating and sensory attention in these frequency bands (Buchholz et  
139 al. 2014; Foxe and Snyder 2011), we hypothesize that similar shared and divergent MEG-derived  
140 findings of resting state functional connectivity in the alpha and beta ranges will be identified

141 between children with ASD, SPD, and TDC participants. In addition, based on work implicating  
142 alpha oscillations in the direction of auditory attention (Bauer et al. 2012) and evidence of  
143 somatosensory cortex beta band modulation in advance of tactile stimuli (van Ede et al. 2010),  
144 we also hypothesize that alpha connectivity will be associated with auditory processing and beta  
145 connectivity will be associated with tactile processing. To test these hypotheses, these frequency  
146 bands were subjected to source space reconstruction for analysis of differences in long-range  
147 neural synchrony and associations with sensory processing abilities.

## Methods

## 149 Participants

150 Participants were 60 boys aged 8-12 years (ASD N=18; SPD N=18; typically developing  
151 controls (TDC) N=24) who were recruited from the UCSF Sensory Neurodevelopmental and  
152 Autism Program (SNAP) participant registry and website, UCSF SNAP clinic, and local online  
153 parent groups. Experimental protocols were approved by the UCSF IRB and carried out in  
154 accordance with those approved procedures. Participants provided their written assent and  
155 written informed consent was obtained from parents or legal guardians prior to enrollment.  
156 Consent and assent procedures were witnessed by a member of the study team. Participants were  
157 recruited between 5/22/2003 and 10/26/2015. All participants who were taking medication were  
158 on a stable dose for at least six weeks prior to testing as reported in our previously published  
159 studies that recruited from this pool of participants (Demopoulos et al. 2017; Demopoulos,  
160 Brandes-Aitken, et al. 2015). Specifically, in the TDC group one participant regularly used an  
161 antihistamine and a leukotriene inhibitor for seasonal allergies as well as melatonin for sleep.  
162 Another TDC participant regularly used steroid medications paired with a bronchodilator as  
163 needed for asthma and allergies and omeprazole for reflux. A third TDC participant regularly

164 used methylphenidate for attention. In the SPD group, one participant was prescribed  
165 lisdexamfetamine, sertraline, and valproic acid for inattention and challenging behavior, and four  
166 others were taking stimulants (amphetamine/dextroamphetamine and methylphenidate) for  
167 inattention. One additional SPD participant was taking nonstimulant medication (atomoxetine)  
168 for inattention and montelukast for allergies, and another was taking steroid medication for  
169 asthma. In the ASD group, one participant was taking a chelation agent (DMSA), another  
170 participant was taking escitalopram for anxiety, and a third was taking guanfacine and  
171 methylphenidate for calming and inattention.

172 Inclusion/exclusion criteria and diagnostic classification followed the criteria utilized in  
173 previous studies (Demopoulos et al. 2017; Demopoulos, Brandes-Aitken, et al. 2015).

174 Specifically, exclusion criteria included (1) bipolar disorder, psychotic disorder, or other  
175 neurological disorder or injury, and (2) a score of 70 or below on the Wechsler Intelligence Scale  
176 for Children-Fourth Edition (WISC-IV; Wechsler, 2003) Perceptual Reasoning Index (PRI). The  
177 PRI rather than the Full Scale Intelligence Quotient (FSIQ) was utilized for exclusion criteria  
178 because verbal abilities (represented in the Verbal Comprehension Index and incorporated into  
179 the FSIQ) were examined as an outcome measure in this study. Specifically, those with prior  
180 clinical diagnosis of ASD and those scoring  $\geq 15$  on the Social Communication Questionnaire  
181 (SCQ; Rutter, Bailey, & Lord, 2003), regardless of previous diagnostic status, were evaluated  
182 with the Autism Diagnostic Inventory-Revised (ADI-R; Lord, Rutter, & Le Couteur, 1994) and  
183 the Autism Diagnostic Observation Schedule (ADOS; Lord et al., 1989). Diagnostic cutoffs on  
184 both of these measures were met for participants in the ASD group, who also met DSM-IV-TR  
185 criteria for Autistic Disorder, confirmed by a pediatric neurologist (EJM). SPD participants were  
186 previously diagnosed with SPD by a community occupational therapist. Inclusion criteria for this

187 group were included (1) SCQ score <15 and (2) a score in the “Definite Difference” range in one  
188 or more of the auditory, visual, oral/olfactory, tactile, vestibular, or multisensory processing  
189 domains of the Sensory Profile (Dunn 1999). All SCQ and Sensory Profile scores for the TDC  
190 group were not in clinical ranges. Demographic characteristics of the study sample are presented  
191 in Table 1.

192 [Table 1]

193 Table 1

194  
195 *Group Characteristics (M ± SD [range])*

	ASD	SPD	TDC	Statistics	
200					
201	Age	$9.88 \pm 1.32$ [8.13-12.00]	$9.94 \pm 1.29$ [8.28-12.08]	$10.18 \pm .1.13$ [8.18-11.94]	$F(2,57) = .36$
202					
203					
204	FSIQ	$96.94 \pm 13.54^{\text{ac}}$ [71-121]	$109.39 \pm 11.35$ [89-131]	$114.92 \pm 9.31$ [97-135]	$F(2,57)=13.20^{***}$
205					
206					
207	PRI	$103.17 \pm 8.56^{\text{d}}$ [94-123]	$113.11 \pm 11.63$ [92-131]	$111.00 \pm 12.29$ [89-129]	$F(2,57)=4.09^*$
208					
209					
210	VCI	$98.56 \pm 21.81^{\text{bd}}$ [59-140]	$113.11 \pm 14.63$ [83-136]	$118.46 \pm 13.08$ [93-144]	$F(2,57)=7.65^{**}$
211					
212					
213	Sensory Profile Total Score	$135.78 \pm 16.92^{\text{ac}}$ [102-160]	$119.11 \pm 17.38^{\text{a}}$ [74-145]	$172.04 \pm 10.38$ [145-187]	$F(2,57)=71.12^{***}$
214					
215					
216	Ethnicity (N)				
217	Caucasian	10	12	17	
218					
219	Asian	4	1	1	
220					
221	Multiracial	4	3	4	
222					
223	Hispanic	0	1	0	
224					
225	Unknown	0	1	2	
226					
227	Handedness				
228	Right	15	17	20	
229					
230	Left	1	1	2	
231					
232	Ambidextrous	2	0	1	
233					

234      Unknown      0      0      1

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236      \*p < .05

237      \*\*p < .01

238      \*\*\*p < .001

239      a Significantly different from TDC at p<.001 following Bonferroni correction for multiple comparisons

240      b Significantly different from TDC at p<.01 following Bonferroni correction for multiple comparisons

241      c Significantly different from SPD at p<.01 following Bonferroni correction for multiple comparisons

242      d Significantly different from SPD at p<.05 following Bonferroni correction for multiple comparisons

243

## 244      Measures

245            *Tactile Processing.* Tactile processing measures were assessed according to previously  
246      published procedures (Demopoulos et al. 2017; Demopoulos, Brandes-Aitken, et al. 2015).

247      Tactile form discrimination was assessed using the Van Boven Domes task (Van Boven &  
248      Johnson, 1994) and quantified by the lowest grating size of passed trials. Tactile proprioception  
249      was measured according to the total score of the right and left hand scores of the graphesthesia  
250      subtest of the Sensory Integration Praxis Tests (Ayres 1989).

251            *Auditory Processing.* Auditory processing also was assessed according to previously  
252      published procedures (Demopoulos, Brandes-Aitken, et al. 2015; Demopoulos et al., 2017) via  
253      the Acoustic (AI) and Acoustic-Linguistic Index (ALI) of the Differential Screening Test for  
254      Processing (DSTP; Richard & Ferre, 2006). The AI is derived from performance on measures of  
255      dichotic listening, temporal sequencing, and auditory filtering skills. The ALI assesses auditory  
256      processing skills associated with language via tasks focused on phonic and phonemic  
257      manipulation.

258            *Verbal Abilities.* Because auditory processing dysfunction has been repeatedly associated  
259      with weaker verbal abilities in children with ASD (Demopoulos et al. 2017; Edgar et al. 2013;  
260      Oram-Cardy et al. 2005; Roberts et al. 2011; Russo et al. 2009; Schmidt et al. 2009), we also  
261      assessed for associations between functional connectivity and verbal abilities in the ASD group  
262      using established protocols for our assessment of verbal abilities (Demopoulos et al. 2017;

263 Demopoulos, Brandes-Aitken, et al. 2015). The Linguistic Index (LI) of the DSTP was used to  
264 evaluate semantic and pragmatic aspects of language. The VCI of the WISC-IV (Wechsler,  
265 2003) was used to index verbal intellectual abilities.

266 *Magnetic Resonance Image (MRI) Acquisition and Processing.* Structural MRIs were  
267 acquired for co-registration with MEG functional data on a 3T Siemens MRI scanner at the  
268 UCSF Neuroscience Imaging Center. T1-weighted images were spatially normalized to the  
269 standard Montreal Neurological Institute template brain using 5mm voxels in SPM8  
270 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). Normalization results were manually verified  
271 in all participants.

272 *Magnetoencephalographic Image Acquisition and Processing.* Methods for acquisition  
273 and processing of MEG data follow protocols similar to those used in prior research employing  
274 these imaginary coherence metrics (Demopoulos et al. 2020; Ranasinghe et al. 2017).  
275 Specifically, MEG data were acquired at a 1200 Hz sampling rate using a 275-channel CTF  
276 System whole-head biomagnetometer (MEG International Services Ltd., Coquitlam, BC,  
277 Canada). Fiducial coils were placed at the nasion and bilateral peri-auricular points to localize  
278 the head to the sensor array. These localizations were utilized for coregistration to the T1-  
279 weighted MRI and generation of a head shape. Four minutes of continuous recording was  
280 collected from each subject while awake with eyes closed in a supine position. While keeping  
281 eyes closed can increase alpha in resting state activity, it also serves to control visual stimulation  
282 and because this procedure was implemented for all participants, this would not confound group  
283 contrasts. As such, we elected to use an eyes closed approach, as has been used in many previous  
284 studies of resting state activity in children with ASD (Berman et al. 2015; Brodski-Guerniero et  
285 al. 2018; Cornew et al. 2012; Edgar et al. 2019; Edgar, Heiken, et al. 2015; Green et al. 2020,

286 2022; Port et al. 2019). Based on previous studies demonstrating reliable results from 60 second  
287 segments of MEG resting state data (Guggisberg et al. 2008; Hinkley 2010; Hinkley et al. 2011),  
288 we selected a 60-second artifact-free epoch. Artifact rejection criteria were signal amplitude  
289 >10pT or visual evidence of movement or muscle contractions.

290 A whole brain lead field was computed according to a spatially normalized MRI with a  
291 10mm voxel size. The Neurodynamic Utility Tool for MEG (NUTMEG;  
292 <http://nutmeg.berkeley.edu>; Dalal et al., 2011) was used for source-space reconstruction and  
293 functional connectivity analyses. Source-space was reconstructed from filtered sensor (fourth-  
294 order Butterworth filter of 1–20 Hz). A linear combination of spatial weighting and sensor data  
295 matrices were used to estimate each voxel's amplitudes (Hinkley et al., 2011).

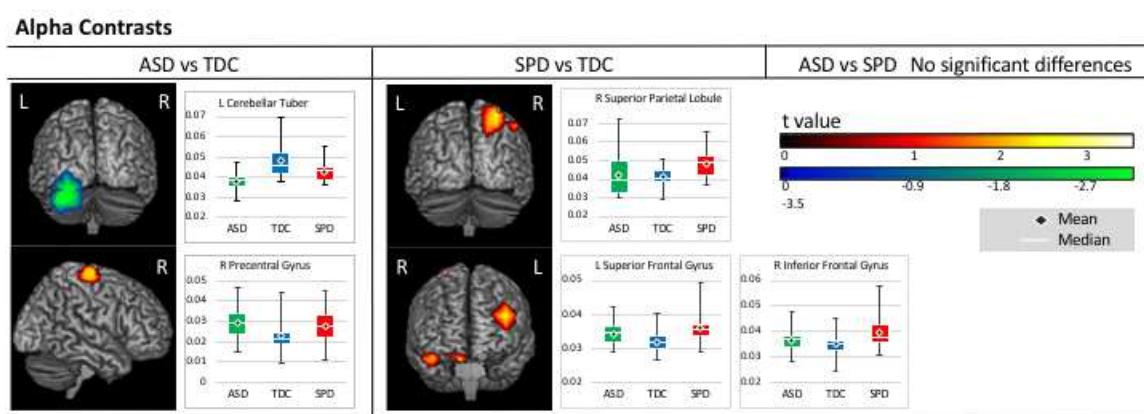
296 Following source space reconstruction, functional connectivity analysis was performed  
297 by computing imaginary coherence. The imaginary coherence approach excludes zero- or  $\pi$ -  
298 phase-lag-connectivity to eliminate neural synchrony attributable to volume spread (Nolte et al.  
299 2004). This approach has been documented as a reliable method for estimating long-range neural  
300 synchrony (Engel et al. 2013; Guggisberg et al. 2008; Martino et al. 2011; Nolte et al. 2004), and  
301 has been shown to reduce overestimation (Guggisberg et al. 2008; Martino et al. 2011; Nolte et  
302 al. 2004). Imaginary coherence values were transformed to Fisher's Z prior to calculating  
303 associations between each voxel and all other voxels. These associations were averaged within  
304 each voxel to derive voxel wise global connectivity values for group contrasts in the alpha and  
305 beta frequency bands. Correlations also were performed between behavioral measures and global  
306 connectivity values at each voxel for the combined group study sample. All voxel-wise results  
307 with uncorrected  $p < 0.05$  were further subjected to a 5% False Discovery Rate multiple  
308 comparisons correction (Benjamini and Hochberg 1995) and a 5-voxel cluster correction.

309 *Missing Data.* Data from the sensory battery tasks are missing for some participants  
310 because these tasks were added to the protocol after these participants were enrolled. Thus, these  
311 data can be considered missing at random. DSTP data was available for 17 ASD participants, 17  
312 TDC participants, and 11 SPD participants. Van Boven Domes were administered to 16  
313 participants in the ASD group, 16 in the TDC group, and 11 in the SPD group. Graphesthesia  
314 was administered to 17 ASD participants, 15 TDC participants, and 11 SPD participants.

## 315 Results

316 *Group Contrasts in Alpha Connectivity.* Group contrasts in alpha coherence indicated  
317 that, relative to TDC participants, the ASD group showed reduced connectivity in the left  
318 fusiform and inferior occipital gyri and cerebellum and increased connectivity in the right pre-  
319 and postcentral gyri. No significant differences were identified between the ASD and SPD  
320 groups; however, the SPD group showed increased connectivity compared to TDC participants  
321 in the left middle and superior frontal gyri and in the right inferior frontal gyrus, precuneus, and  
322 inferior and superior parietal lobules. Alpha contrast results are presented in Figure 1 and  
323 summarized in Table 2.

324 [Figure 1]



325

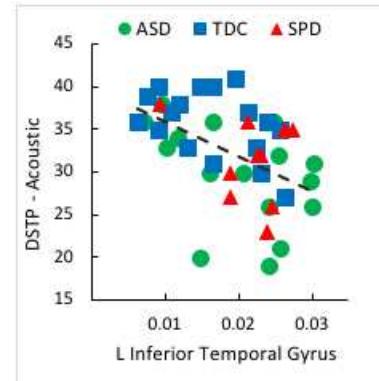
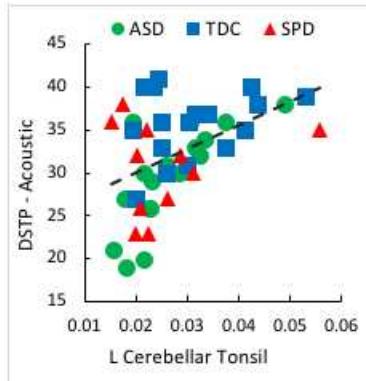
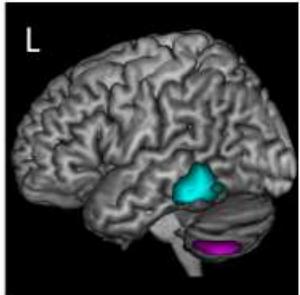
326 Figure 1. Alpha Contrasts. Areas of significantly increased (warm) and reduced (cool) alpha  
327 connectivity are presented on figures for each pairwise contrast. Accompanying boxplots are  
328 presented for each cluster showing imaginary coherence values for all groups at the voxel within  
329 that cluster that demonstrated the greatest pairwise difference.

330 *Correlations Between Alpha Connectivity and Sensory Processing/Verbal Abilities.*

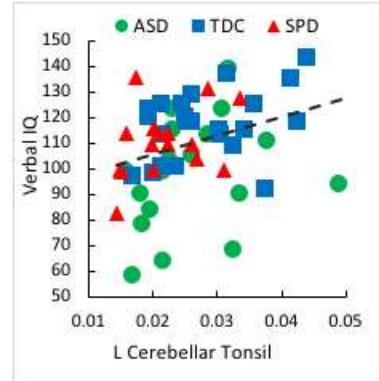
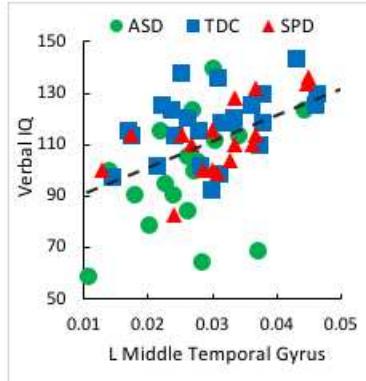
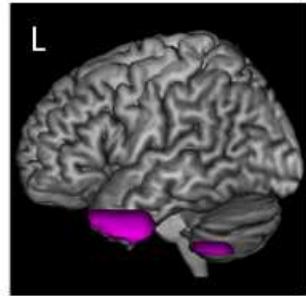
331 Correlation analyses were performed on all study participants combined across groups to  
332 examine the relations between functional connectivity and the range of sensory processing and  
333 verbal abilities in our sample. No significant associations were identified between tactile  
334 processing performance and measures of alpha coherence; however, significant associations  
335 were identified between measures of alpha coherence and auditory processing performance.  
336 Specifically, scores on the DSTP Acoustic scale were positively associated with alpha coherence  
337 in the left cerebellar tonsil and negatively associated with alpha coherence in the left inferior and  
338 middle temporal gyri. A significant positive association also was identified between VIQ and  
339 alpha coherence in the left uncus, cerebellar tonsil, and anterior superior, middle, and inferior  
340 temporal gyri (Figure 2). A summary of correlation results is presented in Table 3.  
341 [Figure 2]

## Alpha Connectivity Correlations: Combined Sample

### Auditory Processing

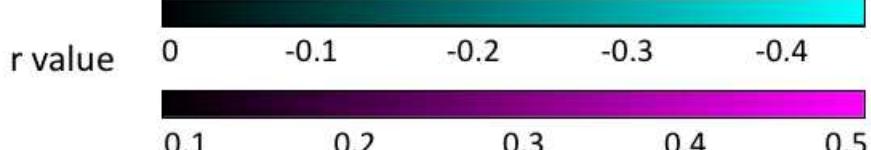


### Verbal Abilities



### Tactile Processing

No Significant Associations



342

343 Figure 2. Alpha Correlations in the Combined Participant Sample. Positive associations between  
344 auditory processing/verbal abilities and alpha connectivity values are identified in magenta  
345 clusters for the sample of all participants in the study. Negative associations between auditory  
346 processing and imaginary coherence values are identified in cyan clusters. Corresponding  
347 scatterplots are presented for the voxel with the greatest correlation value within each cluster,

348 with groups identified by color and shape (ASD group = yellow circle, SPD group = green  
349 triangle, and TDC group = grey square).

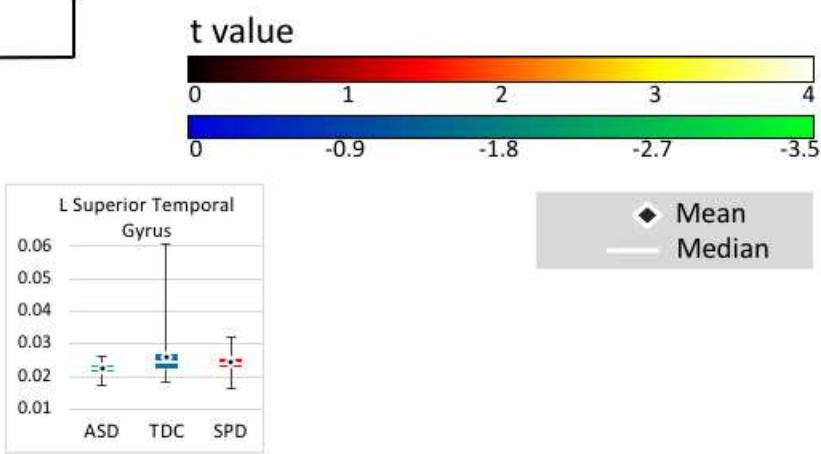
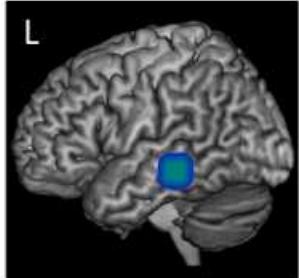
350

351 *Group Contrasts in Beta Connectivity.* Group contrasts in beta coherence indicated that,  
352 relative to TDC participants, the ASD group showed reduced connectivity in the left middle and  
353 inferior temporal gyri. Relative to SPD participants, however, the ASD group showed a pattern  
354 of increased beta connectivity in the right cingulate, middle frontal, and precentral gyri, and  
355 bilaterally in the superior and medial frontal gyri, the postcentral gyrus, the inferior parietal  
356 lobule, and in the supramarginal gyrus. Finally, when compared to TDC participants, the SPD  
357 group demonstrated a pattern of reduced beta connectivity bilaterally in the superior and middle  
358 frontal gyri, insula and putamen, as well as in the left inferior frontal gyrus, cingulate gyrus,  
359 caudate body, pre- and postcentral gyri, and inferior parietal lobule, and in the right superior  
360 temporal gyrus, lentiform nucleus, globus pallidus, and caudate. Beta contrasts are presented in  
361 Figure 3 and summarized in Table 2.

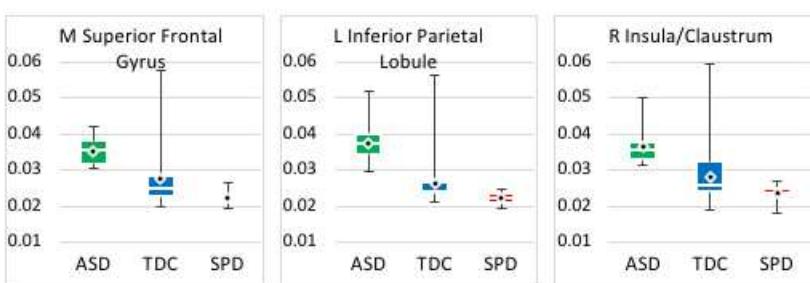
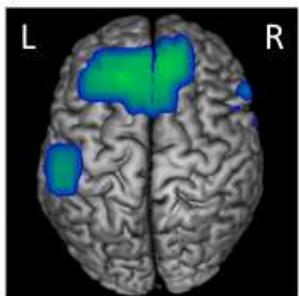
362 [Figure 3]

## Beta Contrasts

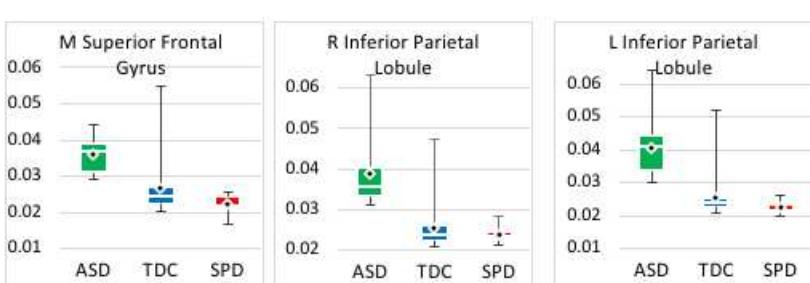
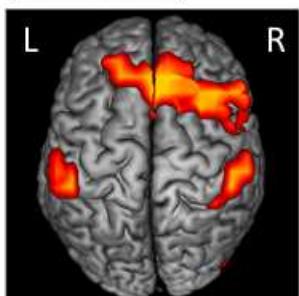
### ASD vs TDC



### SPD vs TDC



### ASD vs SPD



363

364 Figure 3. Beta Contrasts. Areas of significantly increased (warm) and reduced (cool) beta  
365 connectivity are presented on figures for each pairwise contrast. Accompanying boxplots are  
366 presented for each cluster showing imaginary coherence values for all groups at the voxel within  
367 that cluster that demonstrated the greatest pairwise difference.

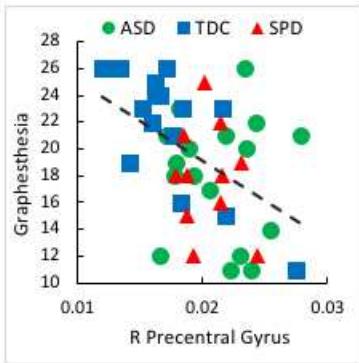
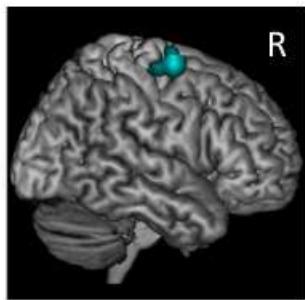
368

369 *Correlations Between Beta Connectivity and Sensory Processing.* A significant negative  
370 association was identified between beta coherence in the right precentral gyrus and performance  
371 on the graphesthesia task (Figure 4). No significant associations were identified between beta  
372 coherence and measures of auditory processing or verbal abilities in the combined groups  
373 sample. A summary of correlation results is presented in Table 3.

374 [Figure 4]

### Beta Connectivity Correlations: Combined Sample

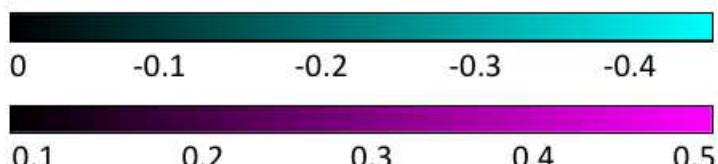
#### Tactile Processing



#### Auditory Processing & Verbal Abilities

No Significant Associations

375 r value



375

376 Figure 4. Beta Correlations in the Combined Participant Sample. Negative associations between  
377 tactile processing abilities and beta connectivity values are identified in the cyan cluster for the  
378 sample of all participants in the study. The corresponding scatterplot is presented for the voxel  
379 with the greatest correlation value within each cluster, with groups identified by color and shape  
380 (ASD group = yellow circle, SPD group = green triangle, and TDC group = grey square).

381

382 [Table 2]

383 Table 2. Summary of Group Contrast Results

Group	Band	Regions	Direction of Difference
ASD vs. TDC	$\alpha$	left fusiform and inferior occipital gyri and cerebellum	Decreased
		right pre- and postcentral gyri	Increased
	$\beta$	left middle and inferior temporal gyri	Decreased
SPD vs. TDC	$\alpha$	left middle and superior frontal gyri and in the right inferior frontal gyrus, precuneus, and inferior and superior parietal lobules	Increased
	$\beta$	bilaterally in the superior and middle frontal gyri, insula and putamen, as well as in the left inferior frontal gyrus, cingulate gyrus, caudate body, pre- and postcentral gyri, and inferior parietal lobule, and the right superior temporal gyrus, lentiform nucleus, globus pallidus, and caudate	Decreased
ASD vs. SPD	$\alpha$	no significant differences	N/A
	$\beta$	right cingulate, middle frontal, and precentral gyri, and bilaterally in the superior and medial frontal gyri, the postcentral gyrus, the inferior parietal lobule, and in the supramarginal gyrus	Increased

384

385 [Table 3]

386 Table 3. Summary of Correlation Results for the Combine Groups Sample

Band	Domain	Task	Regions	Direction of Correlation
$\alpha$	tactile		no significant associations	N/A
	auditory	DSTP Acoustic Scale	left cerebellar tonsil	+
			left inferior and middle temporal gyri	-
	verbal	VIQ	left uncus, cerebellar tonsil, and anterior superior, middle, and inferior temporal gyri	+
$\beta$	tactile	Graphesthesia	right precentral gyrus	-
	auditory		no significant associations	N/A
	verbal		no significant associations	N/A

387

388

Discussion

389 This study used two methods to investigate associations between direct assessment of  
390 auditory and tactile sensory processing and resting state functional connectivity in the brain.  
391 First, we examined differences between groups that would allow us to isolate the sensory  
392 processing dysfunction that presents as part of an ASD from that which manifests in the absence  
393 of the other defining features of ASD. Second, we directly examined associations between  
394 functional connectivity and auditory and tactile processing and verbal abilities in a combined  
395 participant sample including all three groups, allowing us to examine the distribution of these  
396 variables across children with a range of sensory functioning.

397 *Group Contrasts in Functional Connectivity*

398 *ASD vs TDC Contrasts.* Relative to the TDC group, participants with ASD showed  
399 increased alpha connectivity in the right sensorimotor cortex and decreased connectivity in left  
400 posterior fusiform, occipital, and cerebellar regions. Notably, increased alpha power (Edgar,  
401 Heiken, et al. 2015) in a similar region in the right medial sensorimotor cortex, and increased  
402 alpha to low-gamma phase amplitude coupling in this central midline region (Port et al. 2019)  
403 has been reported in prior ASD samples. The present results also recapitulate our previous  
404 structural findings in children with ASD, in which we reported decreased structural connectivity  
405 in the inferior fronto-occipital fasciculus and the fusiform-hippocampus and fusiform-amygdala  
406 tracts (Chang et al., 2014). Our findings of increased cerebellar connectivity are also consistent  
407 with considerable prior research implicating the cerebellum in the pathology of ASD.  
408 Specifically, cerebellar anomalies, including abnormal anatomy, neurotransmission, oxidative  
409 stress, neuroinflammation, and cerebellar motor and cognitive deficits are among the most  
410 replicated findings in individuals with ASD (Fatemi et al. 2012).

411            In the beta range, the ASD group demonstrated decreased beta connectivity in left  
412    temporal regions relative to TDC participants. Stronger beta connectivity in TDC relative to  
413    ASD participants in temporal regions has been demonstrated in prior work (Kitzbichler et al.  
414    2015). Beta power in the auditory cortex has been hypothesized to be involved in auditory-motor  
415    communication (Fujioka et al. 2009) and recent work has demonstrated increases in sensorimotor  
416    low beta power in response to perceived self-produced vocal errors on an altered auditory  
417    feedback speech paradigm (Franken et al. 2018). The decreased beta connectivity in the left  
418    auditory cortex demonstrated in the present study may reflect under-recruitment of this area  
419    needed for auditory processing and auditory motor communication in participants with ASD.

420            *SPD vs TDC Contrasts.* The SPD group differed from the TDC group via increased alpha  
421    connectivity in bilateral frontal and right posterior parietal regions and reduced beta connectivity  
422    in left parietal and medial and right frontal regions. These differences in functional connectivity  
423    identified in these regions may be associated with the impairments in visuomotor skills and  
424    attention previously reported in the SPD population (Brandes-Aitken et al., 2018). In fact, prior  
425    work examining diffusion imaging in children with SPD identified associations between  
426    visuomotor and cognitive control abilities and structural connectivity in regions of the superior  
427    longitudinal fasciculus that run adjacent to the parietal regions identified in this study (Brandes-  
428    Aitken et al., 2019).

429            *ASD vs SPD Alpha and Beta Contrasts.* Notably, the ASD and SPD groups did not show  
430    significant differences in alpha connectivity. In fact, it was beta connectivity that distinguished  
431    these two groups. Specifically, the SPD group showed a pattern of reduced beta connectivity  
432    relative to both the TDC and ASD groups in bilateral and medial frontal and left parietal regions.  
433    Taken together, these findings suggest that decreased beta connectivity in medial frontal and

434 parietal regions may be involved in, or a response to, the sensory disturbance experienced by  
435 children with SPD. Beta activity has been previously reported to be associated with  
436 somatosensory gating and attention (Bauer et al. 2012; Buchholz et al. 2014; van Ede et al.  
437 2010). Our previous work has demonstrated common tactile processing deficits in both ASD and  
438 SPD groups (Demopoulos, Brandes-Aitken, et al. 2015), although when MEG-acquired  
439 somatosensory latencies were compared between these groups, the SPD group demonstrated an  
440 intermediate latency and did not significantly differ from TDC or ASD participants (Demopoulos  
441 et al. 2017). These previous results, in conjunction with the present finding that beta activity  
442 distinguished the ASD and SPD groups in the bilateral somatosensory cortex, may suggest that  
443 the pathology underlying tactile dysfunction in these two groups is divergent.

444 *Combined Groups Correlation Results.* When correlation analyses were performed on all  
445 participants combined into one group, alpha connectivity was positively associated with auditory  
446 and verbal abilities, whereas beta connectivity was negatively associated with tactile processing.  
447 Specifically, there was a common area of positive correlation between left cerebellar alpha  
448 connectivity and both auditory processing and verbal abilities; however, an additional positive  
449 association was identified between left anterior temporal alpha connectivity and verbal abilities.  
450 Previous work has identified an association between increased anterior temporal alpha power and  
451 autism symptomatology measured via the SRS total score (Cornew et al. 2012), whereas an  
452 additional negative association was identified between posterior temporal alpha connectivity and  
453 auditory processing. Taken together, these findings may suggest that increased cerebellar alpha  
454 recruitment may be utilized to address auditory processing weakness that affects not only basic  
455 auditory processing abilities, a deficit that is common in individuals with ASD (Abdeltawwab  
456 and Baz 2015; Alcántara et al. 2004; Demopoulos et al. 2017; Demopoulos, Hopkins, et al. 2015;

457 Demopoulos and Lewine 2016; DePape et al. 2012; Edgar et al. 2013, 2014; Edgar, Fisk IV, et  
458 al. 2015; Gage, Siegel, Callen, et al. 2003; Gage, Siegel, and Roberts 2003; Hitoglou et al. 2010;  
459 Järvinen-Pasley and Heaton 2007; Kargas et al. 2015; Oram-Cardy et al. 2005; Oram Cardy et al.  
460 2005; Tecchio et al. 2003; Tomcheck and Dunn 2007), but also verbal abilities. Indeed, prior  
461 work has demonstrated links between cortical auditory processing abnormalities and verbal  
462 abilities (Berman et al. 2016; Demopoulos et al. 2017; Edgar et al. 2013; Oram-Cardy et al.  
463 2005; Oram Cardy et al. 2008; Roberts et al. 2011, 2012; Schmidt et al. 2009). With regard to  
464 beta connectivity, increases in the right somatosensory cortex were associated with poorer  
465 performance on the graphesthesia task. Examination of the scatterplot distribution suggests that  
466 somatosensory processing limitations may drive the graphesthesia impairments demonstrated in  
467 the two clinical groups. Correlation results were consistent with our hypothesis that beta  
468 connectivity would be associated with tactile processing and alpha connectivity would be  
469 associated with auditory processing. This is consistent with prior work in which alpha  
470 oscillations were associated with direction of auditory attention (Bauer et al. 2012) and  
471 somatosensory cortex beta band modulation was reported in advance of tactile stimuli (van Ede  
472 et al. 2010).

473

474 *Limitations and Future Directions*

475 Several limitations of the present study must be acknowledged. First, the participant  
476 sample was restricted to males between the ages of 8-12 years. Prior studies examining resting  
477 state neural oscillatory behavior have also restricted analyses to males given the high prevalence  
478 of ASD in males and sex differences in peak alpha frequency (Edgar et al. 2019; Green et al.  
479 2022; Manyukhina et al. 2022). While these restrictions result in more homogenous groups and

480 minimize confounds of sex and age differences in neurobiology, they also create limitations for  
481 the generalizability of these results to females and children and adolescents outside the age range  
482 studies. Future research is necessary to understand the applicability of these findings across ages  
483 and sexes. This study also included only children with a nonverbal IQ>70, which limits the  
484 generalizability of these results to lower functioning individuals. Further, this study focused on  
485 only two frequency bands (alpha and beta) and only two sensory domains, auditory and tactile  
486 processing. While prior research suggests that these domains may be the most severely impacted  
487 in individuals with ASD (Fernandez-Andres et al. 2015), sensory dysfunction is heterogeneous in  
488 its presentation among individuals with and without ASD, and understanding neurobiological  
489 factors associated with dysfunction in other sensory domains also will be important to inform  
490 treatment development. Finally, this study focused on specific aspects of sensory processing  
491 (e.g., discrimination, temporal processing, etc.), but did not incorporate measures of sensory  
492 responsivity or sensory seeking behavior. Further, this work only focused on two frequency  
493 bands, alpha and beta. Future studies could expand upon this work to examine relations between  
494 sensory processing dysfunction and functional connectivity in other frequency bands, as gamma  
495 oscillatory behavior has been associated with multisensory communication (Misselhorn et al.  
496 2019) and sensory sensitivity (Manyukhina et al. 2021). Future studies are needed to characterize  
497 differences in functional connectivity that may account for these heterogeneous sensory  
498 responses or behaviors in children with ASD and SPD.

#### 499 *Conclusions*

500 This study was the first to use MEG to examine participants with ASD and SPD in  
501 relation to neurotypical children to identify relevant differences in resting state whole brain  
502 functional connectivity that may be associated with sensory dysfunction. This study design

503 allowed us to identify both shared and distinct patterns of neural activity in two groups affected  
504 by sensory dysfunction. Specifically, both clinical groups were distinguished from the TDC  
505 group by patterns of functional connectivity differences in the alpha and beta bands, whereas the  
506 clinical groups were only distinguished from each other on measures of beta connectivity.  
507 Associations between functional connectivity and behavior identified that sensorimotor regions  
508 were associated with tactile processing performance and temporal and cerebellar regions were  
509 associated with auditory processing and language abilities. These results suggest that resting  
510 state differences in oscillatory brain activity in the alpha and beta frequencies is associated with  
511 the sensory dysfunction that characterizes children with ASD and SPD.

512

513

514

515

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### Author Contribution Statement

843

844 C.D., E.J.M., and S.S.N. conceived the project and methodological approach. S.D., S.H., A.F.,  
845 and D.M. participated in data acquisition. C.D. and X.D. performed data analysis with  
846 consultation from A.F., L.B.H. and K.G.R. C.D., X.D., and B.G.J. created the figures. C.D. and  
847 M.R.G. created the tables. C.D. wrote the manuscript in consultation with E.J.M. and S.S.N.

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### Data Availability Statement

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852 The data that support the findings of this study are available on request from the corresponding  
853 author. The data are not publicly available due to privacy or ethical restrictions.

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### Additional Information

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The authors have no competing interests to declare.

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## Figure Legends

864 Figure 1. Alpha Contrasts. Areas of significantly increased (warm) and reduced (cool) alpha  
865 connectivity are presented on figures for each pairwise contrast. Accompanying boxplots are  
866 presented for each cluster showing imaginary coherence values for all groups at the voxel within  
867 that cluster that demonstrated the greatest pairwise difference.

868

Figure 2. Alpha Correlations in the Combined Participant Sample. Positive associations between auditory processing/verbal abilities and alpha connectivity values are identified in magenta clusters for the sample of all participants in the study. Negative associations between auditory processing and imaginary coherence values are identified in cyan clusters. Corresponding scatterplots are presented for the voxel with the greatest correlation value within each cluster, with groups identified by color and shape (ASD group = yellow circle, SPD group = green triangle, and TDC group = grey square).

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Figure 3. Beta Contrasts. Areas of significantly increased (warm) and reduced (cool) beta connectivity are presented on figures for each pairwise contrast. Accompanying boxplots are presented for each cluster showing imaginary coherence values for all groups at the voxel within that cluster that demonstrated the greatest pairwise difference.

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882 Figure 4. Beta Correlations in the Combined Participant Sample. Negative associations between  
883 tactile processing abilities and beta connectivity values are identified in the cyan cluster for the  
884 sample of all participants in the study. The corresponding scatterplot is presented for the voxel

885 with the greatest correlation value within each cluster, with groups identified by color and shape

886 (ASD group = yellow circle, SPD group = green triangle, and TDC group = grey square).

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893 Table 1

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895 *Group Characteristics (M ± SD [range])*

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	ASD	SPD	TDC	Statistics
Age	9.88 ± 1.32 [8.13-12.00]	9.94 ± 1.29 [8.28-12.08]	10.18 ± 1.13 [8.18-11.94]	F(2,57) = .36
FSIQ	96.94 ± 13.54 <sup>ac</sup> [71-121]	109.39 ± 11.35 [89-131]	114.92 ± 9.31 [97-135]	F(2,57)=13.20***
PRI	103.17 ± 8.56 <sup>d</sup> [94-123]	113.11 ± 11.63 [92-131]	111.00 ± 12.29 [89-129]	F(2,57)=4.09*
VCI	98.56 ± 21.81 <sup>bd</sup> [59-140]	113.11 ± 14.63 [83-136]	118.46 ± 13.08 [93-144]	F(2,57)=7.65**
Ethnicity (N)				
Caucasian	10	12	17	
Asian	4	1	1	
Multiracial	4	3	4	
Hispanic	0	1	0	
Unknown	0	1	2	
Handedness				
Right	15	17	20	
Left	1	1	2	
Ambidextrous	2	0	1	
Unknown	0	0	1	

933 \*p < .05

934 \*\*p < .01

935 \*\*\*p < .001

936 <sup>a</sup> Significantly different from TDC at p<.001 following Bonferroni correction for multiple comparisons

937 <sup>b</sup> Significantly different from TDC at p<.01 following Bonferroni correction for multiple comparisons

938 <sup>c</sup> Significantly different from SPD at p<.01 following Bonferroni correction for multiple comparisons

939 <sup>d</sup> Significantly different from SPD at p<.05 following Bonferroni correction for multiple comparisons

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942 Table 2. Summary of Group Contrast Results

Group	Band	Regions	Direction of Difference
ASD vs. TDC	α	left fusiform and inferior occipital gyri and cerebellum	Decreased
		right pre- and postcentral gyri	Increased
	β	left middle and inferior temporal gyri	Decreased
SPD vs. TDC	α	left middle and superior frontal gyri and in the right inferior frontal gyrus, precuneus, and inferior and superior parietal lobules	Increased
	β	bilaterally in the superior and middle frontal gyri, insula and putamen, as well as in the left inferior frontal gyrus, cingulate gyrus, caudate body, pre- and postcentral gyri, and inferior parietal lobule, and the right superior temporal gyrus, lentiform nucleus, globus pallidus, and caudate	Decreased
ASD vs. SPD	α	no significant differences	N/A
	β	right cingulate, middle frontal, and precentral gyri, and bilaterally in the superior and medial frontal gyri, the postcentral gyrus, the inferior parietal lobule, and in the supramarginal gyrus	Increased

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946 [Table 3]

947 Table 3. Summary of Correlation Results for the Combine Groups Sample

Band	Domain	Task	Regions	Direction of Correlation
<b>α</b>	<b>tactile</b>		no significant associations	N/A
	<b>auditory</b>	DSTP Acoustic Scale	left cerebellar tonsil	+
			left inferior and middle temporal gyri	-
	<b>verbal</b>	VIQ	left uncus, cerebellar tonsil, and anterior superior, middle, and inferior temporal gyri	+
<b>β</b>	<b>tactile</b>	Graphesthesia	right precentral gyrus	-
	<b>auditory</b>		no significant associations	N/A
	<b>verbal</b>		no significant associations	N/A

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## Alpha Contrasts

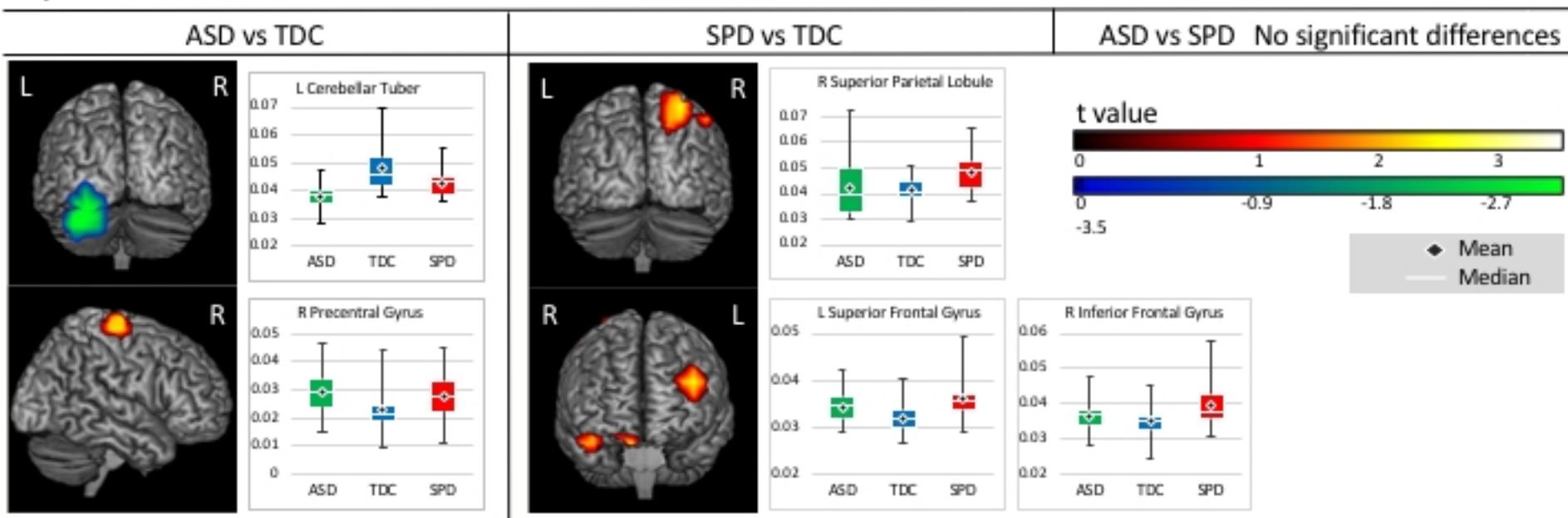
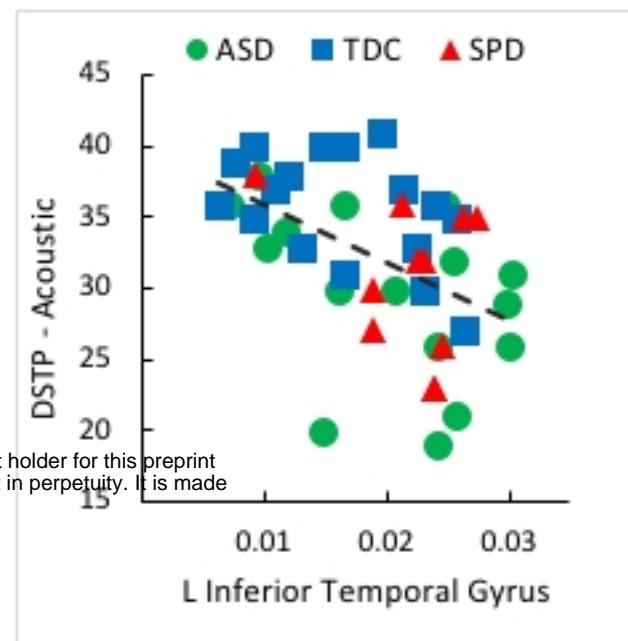
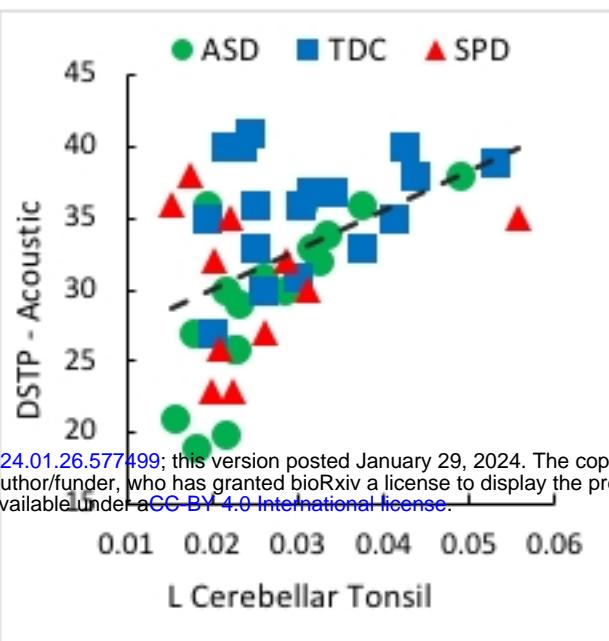
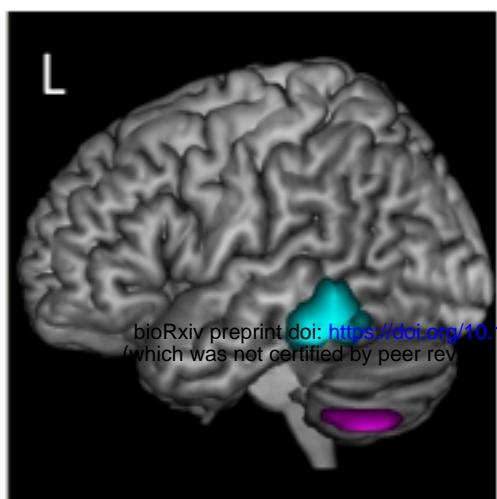


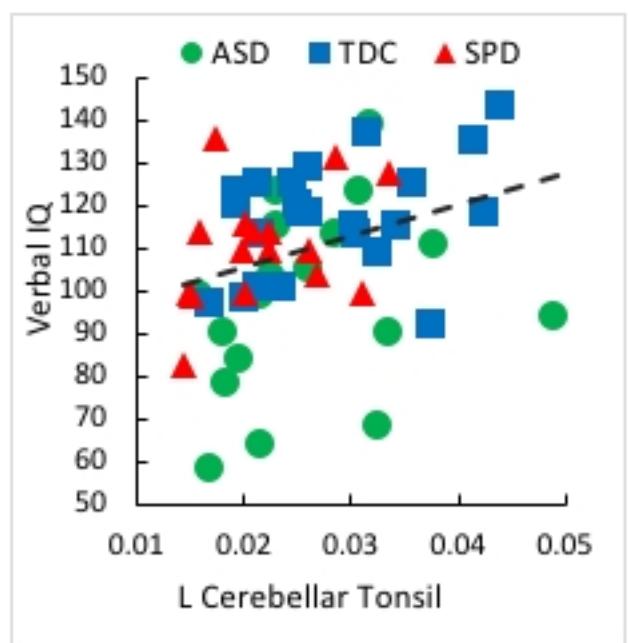
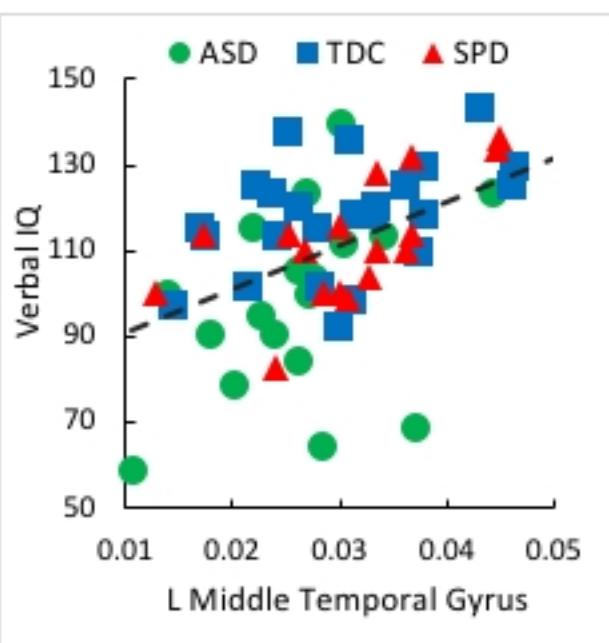
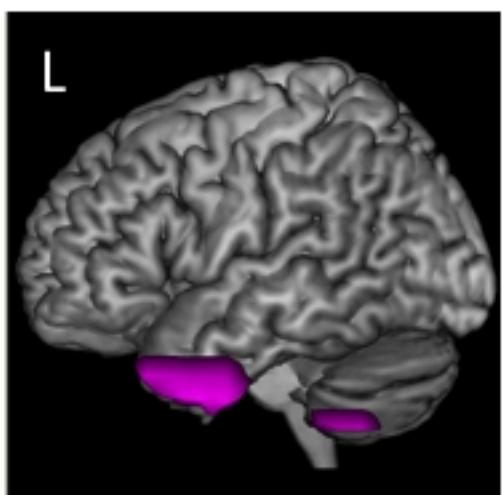
Figure 1

# Alpha Connectivity Correlations: Combined Sample

## Auditory Processing



## Verbal Abilities



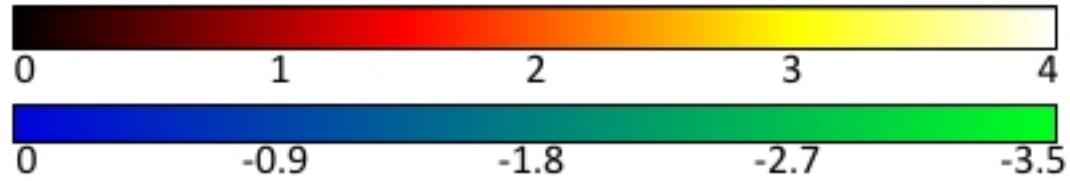
## Tactile Processing

No Significant Associations

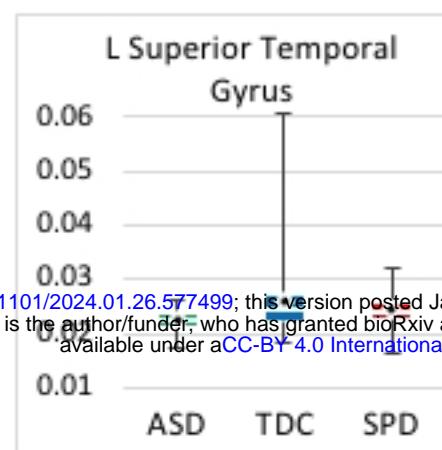
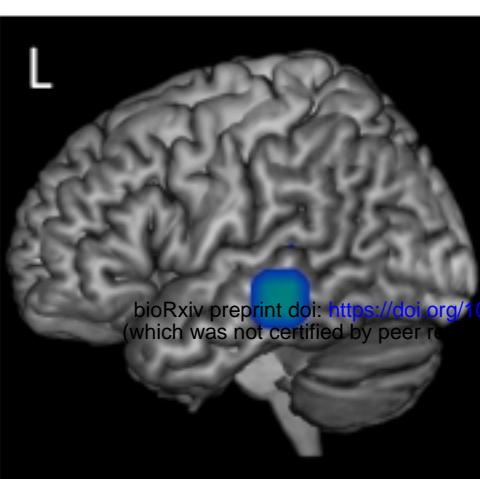


# Beta Contrasts

t value

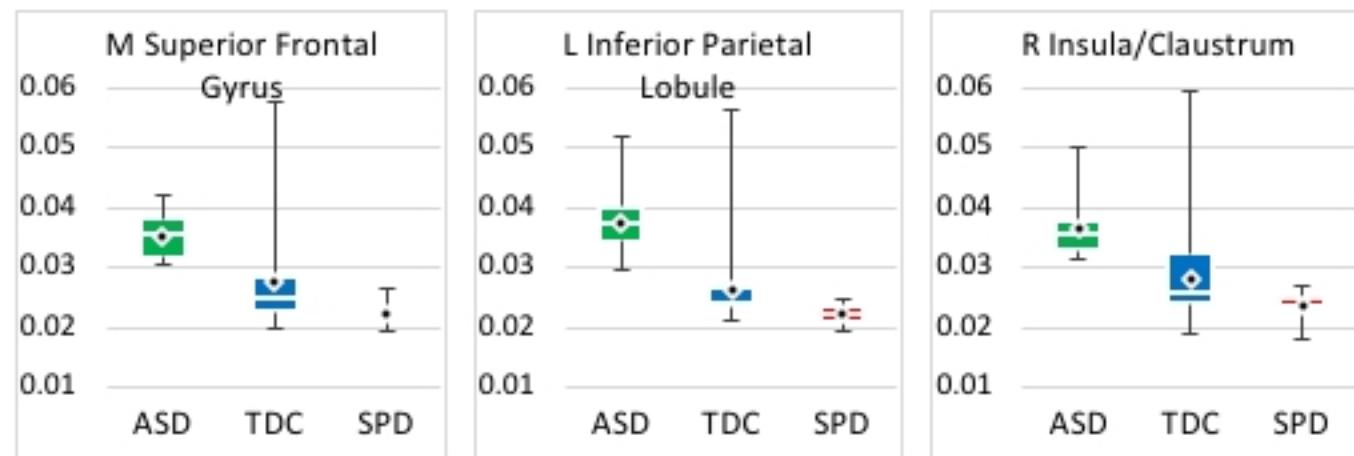
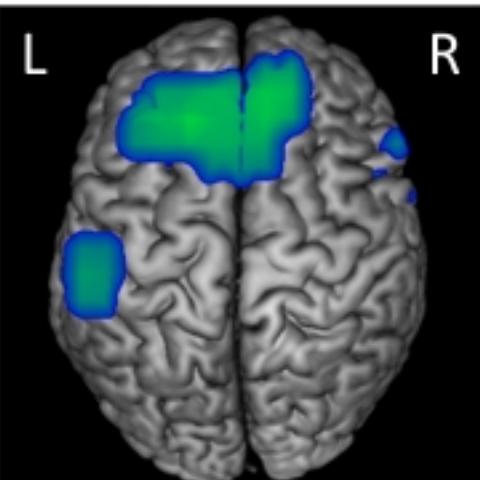


## ASD vs TDC



◆ Mean  
— Median

## SPD vs TDC



## ASD vs SPD

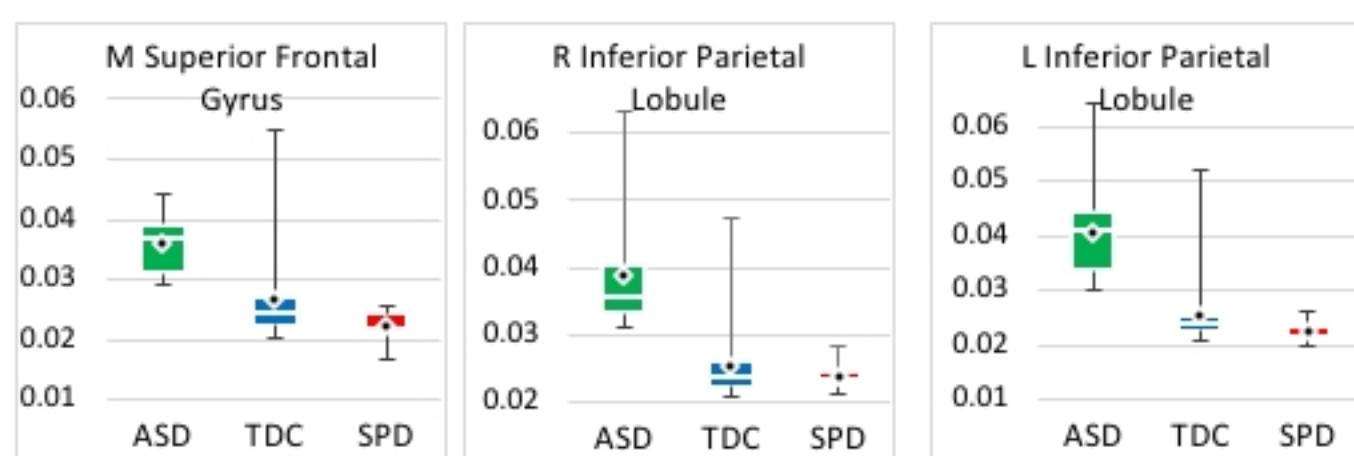
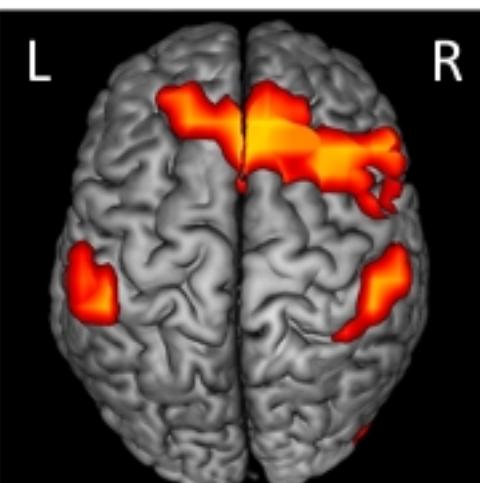
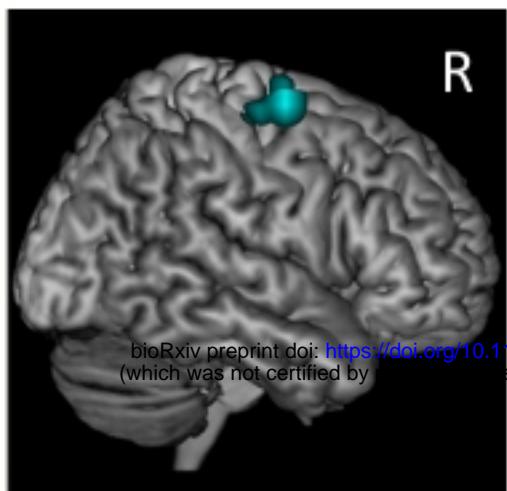


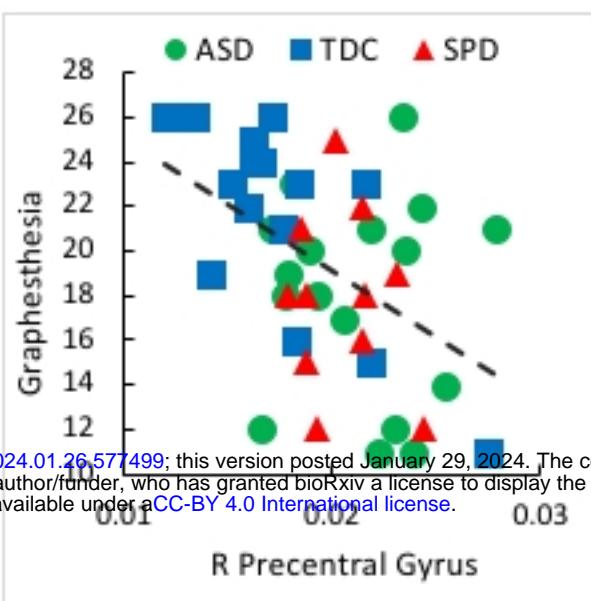
Figure 3

# Beta Connectivity Correlations: Combined Sample

## Tactile Processing



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## Auditory Processing & Verbal Abilities

No Significant Associations

