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Review article

Meta-analytic evidence of differential prefrontal and early sensory cortex activity during non-social sensory perception in autism

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ABSTRACT

To date, neuroimaging research has had a limited focus on non-social features of autism. As a result, neurobiological explanations for atypical sensory perception in autism are lacking. To address this, we quantitively condensed findings from the non-social autism fMRI literature in line with the current best practices for neuroimaging meta-analyses. Using activation likelihood estimation (ALE), we conducted a series of robust meta-analyses across 83 experiments from 52 fMRI studies investigating differences between autistic (n = 891) and typical (n = 967) participants. We found that typical controls, compared to autistic people, show greater activity in the prefrontal cortex (BA9, BA10) during perception tasks. More refined analyses revealed that, when compared to typical controls, autistic people show greater recruitment of the extrastriate V2 cortex (BA18) during visual processing. Taken together, these findings contribute to our understanding of current theories of autistic perception, and highlight some of the challenges of cognitive neuroscience research in autism.

1. Introduction

Autism spectrum conditions (henceforth autism) are neurodevelopmental in origin and are diagnosed on the basis of both social and non-social symptoms; namely, difficulties in communication and relationships, unusually narrow interests, and strongly repetitive, restrictive patterns of behaviour (American Psychiatric Association, 2013). Autism is also characterized by atypical sensory perception, a feature occurring in up to 90% of autistic individuals (Tavassoli et al., 2013). Autistic individuals show superior attention to detail (Happé and Frith, 2006; Jolliffe and Baron-Cohen, 1997; Shah and Frith, 1983), heightened ability to "systemize" (i.e, to identify *if-and-then* rules in a system) (Baron-Cohen et al., 2003, 2009; Baron-Cohen and Lombardo, 2017), enhanced perceptual functioning (Mottron et al., 2006) and greater perceptual load (Remington et al., 2009).

Sensation or sensory processing encompasses the early-stage detection of "elementary" properties of stimuli (Carlson, 2010). Meanwhile, perception is a dynamic, hierarchical process involving an interaction between these low-level sensations and higher-order expectations (Goldstein, 2017). With reference to the visual domain, early theories of perception describe the process as "unconscious inference" (von Helmholtz, 1866). According to hierarchical models of the brain, feedforward connections from lower sensory areas (i.e., bottom-up processes) send information to higher cortical areas, while feedback connections from higher-to-lower areas (i.e., top-down processes) carry predictions or expectations of low-level information (Clark, 2013; Friston, 2005; Friston and Kiebel, 2009). Sensory perception is greatly influenced by prior knowledge or expectations of the external world (Bar, 2004; de Lange et al., 2018; Series and Seitz, 2013). In autism, unique sensory-perceptual processing may be attributed to differential weighing of either top-down prior expectations (Pellicano and Burr, 2012) or bottom-up sensory processes (Mottron et al., 2006). With the inclusion of sensory sensitivities (both hypo- and hyper-sensitivities) as a core diagnostic criterion for autism in the *Diagnostic and Statistical Manual of Mental Disorders (Fifth Edition)* (American Psychiatric Association, 2013), there is considerable interest in understanding its neurobiological substrates.

Until the recent revision of its diagnostic criteria, the dominant view of autism as primarily a "social" condition led to sensory symptoms being largely overlooked. While it has been hypothesized that sensory differences may contribute to cognitive strengths or "talents" due to superior perceptual abilities in autism (Baron-Cohen and Lombardo,

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2017; Robertson and Baron-Cohen, 2017), it is also recognized that it may lead to high levels of anxiety due to "sensory overload" (Ben-Sasson et al., 2009; Green and Ben-Sasson, 2010). A growing body of research suggests that atypical sensory processing may be a core phenotype in autism due to its link to higher-order social and cognitive symptoms and its potential to serve as an early diagnostic marker (Robertson and Baron-Cohen, 2017). Computational theories propose a unifying framework for the social and non-social symptoms, suggesting that the two may share common neural mechanisms (Lawson et al., 2014, 2015a, 2015b; Van de Cruys et al., 2014). Meanwhile, a number of theories posit that the social and non-social core domains of autism may be dissociable (Happé et al., 2006; Happé and Ronald, 2008), a view substantiated by findings from a genome-wide association study of more than 50,000 individuals (Warrier et al., 2019). To date, neuroimaging research has had a limited focus on the non-social symptoms of autism. As a result, the neurobiology of autistic sensory perception remains poorly understood.

Here we aimed to quantitatively summarize information from the current non-social sensory perception neuroimaging literature on autism. Based on the current theories of autistic perception, we hypothesised patterns of atypical activity in higher-order association areas and in low-level sensorimotor cortices. To test these predictions, we first condensed findings across a broad range of non-social perception experiments from task-based functional Magnetic Resonance Imaging (fMRI) studies comparing autistic and non-autistic control groups. Next, based on the available literature, we conducted a more refined set of meta-analyses on studies categorized according to sensory modality. The present study provides an in-depth description of the autism task-based non-social neuroimaging data published to date and highlights important considerations for future functional neuroimaging work in autism.

2. Methods

2.1. Literature search and study selection

Based on the recommended best-practice guidelines for neuroimaging meta-analyses (Müller et al., 2018), we first pre-registered the study on PROSPERO (https://www.crd.york.ac.uk/PROSPERO/).

We conducted a comprehensive literature search in accordance with the Preferred Reporting Items for Systematic Review and Meta-Analysis (PRISMA) statement (Moher et al., 2009). A Pubmed search on the following keywords was conducted: (("autism" OR "autistic" OR "Asperger*") AND ("fMRI" OR "functional magnetic resonance imaging")). Filters were set to limit the search to English-language articles of research conducted on humans.

The following inclusion criteria were used:

1) Empirical research with original data presented
2) Task fMRI studies
3) Autism vs Typical Control group comparisons
4) Whole-brain fMRI analyses
5) No interventional clinical trials/treatment effects
6) Conducted on human participants
7) English-language articles

Following the initial literature search, whole-brain task fMRI studies were categorized as either social or non-social. Studies with social paradigms were checked for non-social contrasts (such as neutral/control/baseline contrasts). We recorded the following details for each included study: first author and year of publication, number of participants per group, age, sex, task details (domain, sensory modality, and contrasts), location and direction of effects, and standard stereotactic space used to spatially align imaging data for group comparisons.

As of December 2019, a total of 52 task fMRI studies met inclusion criteria for our meta-analyses examining differences in non-social perception between autistic and control participants (Table 1). A flowchart of the literature search and study selection process can be seen in Fig. 1.

2.2. Activation likelihood estimation meta-analyses

The meta-analyses were conducted using GingerALE v3.0.2 (www.brainmap.org/ale) (Laird et al., 2005; Eickhoff et al., 2009).

Activation Likelihood Estimation (ALE) models the spatial agreement of foci across studies or experiments with random-effects modelling (Eickhoff et al., 2009, 2012; Turkeltaub et al., 2012). The algorithm treats foci as 3D spatial probability distributions and estimates the Full-Width Half Maximum (FWHM) of the Gaussian distribution, which is dependent on the number of participants in each primary study. The spatial probability distributions are merged to create "Modelled activation" (MA) maps. By taking the union of each MA map, the algorithm computes an ALE value at each voxel in the brain. These are tested against the null hypothesis of random spatial convergence across studies.

Peak coordinates from the Autism vs Typical (henceforth Control) group comparisons of each study were manually entered into GingerALE. Coordinates in Talairach space were converted to Montreal Neurological Institute (MNI) space using the GingerALE 'convert foci' tool. For our meta-analyses examining the direction of group differences, separate analyses were computed for the comparisons *Autism* > *Control* and *Control* > *Autism*. Specifically, *Autism* > *Control* foci files contained peak coordinates of regions showing more activation in autistic groups compared to controls across included studies, and vice versa for the *Control* > *Autism* foci files. We included ANOVA results, main effects, and interaction effects only when group differences and direction of effects were clearly reported. For each of these comparisons, the number of participants per group were appropriately coded. Studies that found no group differences were included with empty coordinates. In accordance with the current best practice methods for neuroimaging meta-analyses, we used the most conservative field-recommend statistical thresholding approach for ALE analyses (Müller et al., 2018). To limit the occurrence of false positives and artefactual results, analyses were threshholded using 5000 permutations to estimate a cluster-level family-wise error (cFWE) correction of $P < 0.05$ using a cluster-forming threshold of $P < 0.001$ (Eickhoff et al., 2012, 2016, 2017).

In addition to this conservative statistical thresholding, a set of meta-analyses utilizing the simplest uncorrected p-value method was conducted on those datasets with adequate statistical power in order to gauge additional information about subthreshold clusters. Details of these uncorrected analyses and their corresponding unthresholded statistical maps are reported in the Supplementary Material.

2.2.1. General perception across non-social tasks

To examine neural differences across a wide range of perceptual processing tasks, we first meta-analysed peak coordinates from our complete list of non-social fMRI tasks (Table 1). In order to cover the various steps involved in perception, from stimulus detection to interpretation, the included tasks ranged from sensory processing tasks, such as visuospatial reasoning, visual/auditory/tactile stimulation, and target detection, to higher-level executive function paradigms probing expectation, such as learning, reward anticipation, and response inhibition. Foci were organized according to experimental contrast. A total of 83 experimental contrasts from 52 studies, encompassing 1858 participants (891 Autism and 967 Control) were included in this meta-analysis. To investigate the directionality of group differences, meta-analyses were computed on 307 and 369 foci for *Autism* > *Control* and *Control* > *Autism* comparisons respectively.

Table 1
Complete list and relevant characteristics of whole-brain fMRI studies included in the ALE analyses.

Study First Author & Year	Experiment			Participants			fMRI	
	Sensory Domain	Task	Contrast(s)	N	Age Range / Mean (SD)	Autism Sex (M: F)	Toolbox	Statistical threshhold
Schuetze 2019*	Visual	Implicit reinforcement learning	Choice behaviour to infer reward value: liked, non-liked, neutral images	32 ASC 31 Con	14–20	28:4	SPM	FWE-corrected, $p < 0.05$
Velasquez 2019	Visual	Response inhibition: Go/ No Go	Letter NoGo vs Go	19 ASC 22 Con	18–46	13:6	FSL	FWE- corrected, $p < 0.05$
Green 2018	Auditory & Tactile	Auditory sarcasm task with and without tactile stimulation & instructions	No Instructions- Tactile vs baseline, Instructions- Tactile vs baseline, Instructions- Tactile vs No Instructions- No Tactile, No Instructions-Tactile vs No Instructions- No Tactile	15 ASC 16 Con	9-17.6	11:4	FSL	FWE- corrected, $p < 0.05$
Murphy 2017	Visual	Attention orienting	Patterned vs neutral stimuli	23 ASC 35 Con	8–23	17:6	AFNI	FWE - corrected, $p < 0.05$
*Keehn 2017**	Auditory & Visual	Auditory- high & low pitch detection, Visual- high & low spatial dot location	Auditory vs null condition, Visual vs null condition	16 ASC 16 Con	8–18	14:2	AFNI	FWE - corrected, $p < 0.05$
*Schelinksi 2016**	Auditory	Sound processing	Non vocal sounds (cars, nature music) vs silence baseline	16 ASC 16 Con	18–52	13:3	SPM	Uncorrected, $P < 0.001$
D'Cruz 2017	Visual	Reversal learning: 4-choice visuospatial location	Unexpected reversal (no reinforcement) vs Expected positive reinforcement	17 ASC 23 Con	7–44	12:5	FSL	Corrected, FSL Randomize v2.1, TFCE Type 1 error rate $p < 0.01$
Prat 2016*	Visual	Response inhibition: Go / No Go	Letter No Go vs Go	16 ASC 17 Con	25.3 ± 5 (ASC), 25.6 ± 7.2 (Con)	10:6	SPM	Uncorrected, $p < 0.001$
Rahko 2016	Visual	Working memory: N-back	0-back vs baseline, 0-back vs 2-back	28 ASC 22 Con	11.4–17.6	20:8	FSL	FWE-corrected, $p < 0.05$
Kaiser 2016	Tactile	Arm and palm touch	Arm vs Palm	19 ASC 19 Con	6.43–20.26 (ASC), 5.56–17.05 (Con)	16:3	FSL	FWE-corrected, $p < 0.05$
Keehn 2016	Visual	Rapid Serial Visual Presentation	Target Present/Absent vs Target-Coloured/Neutral Distractors, Control condition: Target- Absent + Neutral-Distractors	16 ASC 21 Con	12–17	14:2	AFNI	Cluster-wise corrected ($p < 0.05$), voxel-wise uncorrected ($p < 0.01$), Monte Carlo simulation
Schipul 2016	Visual	Dot pattern learning	Encoding vs fixation	16 ASC 16 Con	16–42	14:2	SPM	Uncorrected, $p < 0.005$, spatial extent of 10 voxels
Kleinhans 2016	Visual	Habituation to houses	House 1 vs House 2	27 ASC 25 Con	18–44	25:2	FSL	Cluster-wise corrected ($p < 0.05$), voxel-wise ($z>2.3$) Monte Carlo simulation
Sharer 2015	Visual	Visuomotor learning: Serial Reaction Time task	Sequence vs random	17 ASC 32 Con	10.5 ± 1.36, (ASC) 10.46 ± 1.3, (Con)	14:3	SPM	FWE-corrected, $P < 0.05$
Solomon 2015	Visual	Transitive inference learning: Stimulus hierarchy of coloured ovals	Training phase: learning pairs, Testing phase : generalization to new pairs	21 ASC 23 Con	12.2–17	17:4	SPM	FWE – corrected, $p < 0.05$
Samson 2015	Auditory	Listening to sounds of pure tone, harmonic tone, varying levels of frequency modulation	All sound conditions vs silence baseline	27 ASC (14 + 13) 13 Con	14–39	11:2	SPM	FWE – corrected, $p < 0.05$
Green 2015	Auditory & Tactile	Auditory stimulation: Traffic noises, Tactile stimulation: rough fabric	Auditory vs baseline, tactile vs baseline, joint auditory + tactile vs baseline	19 ASC	9–17	16:3	FSL	FWE – corrected, $p < 0.05$

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Table 1 (*continued*)

Study First Author & Year	Experiment			Participants			fMRI	
	Sensory Domain	Task	Contrast(s)	N	Age Range / Mean (SD)	Autism Sex (M: F)	Toolbox	Statistical threshhold
Shafritz 2015	Visual	Response inhibition: Go/ No Go	Letter No Go vs Go	19 Con 15 ASC	13–23	12:3	SPM	p <0.001, cluster-filter of 10 contiguous voxels
Simhard 2015	Visual	Visuospatial reasoning: Raven's Standard Progressive Matrices	Figural vs Analytical vs Complex Analytical stimuli	18 Con 15 ASC	14–36	13:2	SPM	p < 0.001 uncorrected, extent threshold of 50 contiguous voxels
Barbeau 2015	Visual	Visuomotor Poffenberger task	Hand response: Left & Right, Stimulated visual field: Left & Right	34 ASC 33 Con	14–37	31:3	SPM	FWE-corrected, p < 0.05
Yerys 2015	Visual	Set shifting: Text display "STAY" or "CHANGE" with a circle and a square on either the left or right of the word	Stay + Switch vs Fixation	20 ASC 19 Con	7.17-13.33	16:4	FSL	FWE-corrected, p < 0.05
Travers 2015	Visual	Visuomotor learning: Serial Reaction Time task	Sequence vs non-sequence learning	15 ASC 15 Con	20.81 ± 3.98 (ASC), 21.41 ± 2.85 (Con)	All male	SPM	Uncorrected p < 0.001, extent threshold of 72 contiguous voxels
Solomon 2014	Visual	Cognitive control: Preparing to overcome prepotency (POP) task	High-control vs low-control cue	27 ASC 27 Con	12–18	17:10	SPM	FWE-corrected, p < 0.05
Sabatino 2013	Visual	Oddball target detection	High Autism Interest images vs baseline	15 ASC 17 Con	16.9–45.3	13:2	FSL	FWE-corrected, p < 0.05
Green 2013	Auditory & Visual	Auditory stimulation: White noise, Visual stimulation: Rotating colour wheel	Auditory vs baseline, visual vs baseline, joint auditory + visual vs baseline	25 ASC 25 Con	9–17	21:4	FSL	Uncorrected, thresholded at z>2.3
Gadgil 2013	Visual	Shape processing: Local vs global hierarchical shape recognition task	Global vs control stimulus, local vs control stimulus, global vs local	17 ASC 16 Con	18–55	14:3	SPM	FWE- corrected, p < 0.05
Spencer 2012	Visual	Visuospatial reasoning: Embedded Figures Task	Embedded Figures vs Control Task	38 ASC 40 Con	12–18	34:4	SPMs	Uncorrected, p < 0.001
Yamada 2012	Visual	Visuospatial reasoning: Raven's Standard Progressive Matrices	Easy analytical vs baseline, difficult analytical vs baseline	25 ASC 26 Con	30.7 ± 7.78 (ASC), 32.2 ± 7.7 (Con)	22:3	SPM	Uncorrected,p < 0.001
*Ohta 2012**	Visual	Selective attention/ perceptual load: Rapid Serial Visual Presentation vs checkerboard	Low vs high load, distractor vs no distractor	24 ASC 25 Con	22–40	21:3	SPM	Uncorrected, p < 0.001, voxel extent threshold = 70
*Beacher 2012**	Visual	Visuospatial reasoning: Mental rotation	Rotated letters vs control condition	29 ASC 32 Con	32.8(9.1) (ASC), 30.48 (7.7) (Con)	15:14	SPM	P < 0.001, cluster extent k = 7 voxels
Dichter 2012	Visual	Reward anticipation	Anticipation of monetary reward and autism interest object reward	15 ASC 16 Con	30 ± 11.6 (ASC), 27.5 ± 7.5 (Con)	All male	FSL	Uncorrected, cluster voxels extent k = 10, z >2.5, P < 0.005
McGrath 2012	Visual	Visuospatial reasoning: Mental rotation	3D cube stimuli: same vs mirror trials	22 ASC 22 Con	13–21	All male	AFNI	Uncorrected, voxel-wise statistical threshold ($t = 2.96$, $P < 0.005$)
Cascio 2012	Tactile	Tactile stimulation with textures	Brush vs rest, burlap vs rest, mesh vs rest	13 ASC 14 Con	28.3(10.7) (ASC), 30.8 (12) (Con)	12:1	SPM	Uncorrected, P < 0.005, z>2.3, cluster voxel extent k = 10
Caria 2011	Auditory	Passive listening to classical music	Happy vs baseline, sad vs baseline	8 ASC 14 Con	19–37	6:2	SPM	FDR- corrected, p < 0.05
Goldberg 2011	Visual	Response inhibition: Go/ No Go	Green and red spaceships: Error vs correct inhibition	11 ASC	8–12	8:3	SPM	Corrected p < 0.05

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Table 1 (*continued*)

Study First Author & Year	Experiment			Participants			fMRI	
	Sensory Domain	Task	Contrast(s)	N	Age Range / Mean (SD)	Autism Sex (M: F)	Toolbox	Statistical threshhold
*Koldewyn 2011**	Visual	Dot motion	Static vs coherent dot motion	15 Con 16 ASC 16 Con	11.41-19.53	14:2	SPM	Voxel-wise (t = 2.95, p < .005, uncorrected) and cluster-wise (p < .05, Bonferroni corrected)
Damarla 2010	Visual	Visuospatial reasoning: Embedded Figures Task	Embedded figures vs fixation	13 ASC 13 Con	15–35	11:2	SPM	Uncorrected, p < 0.005 with a spatial extent of 10 voxels
Dichter 2009	Visual	Oddball target detection	Target shape vs Novel shape	15 ASC 19 Con	23.3(11.1) (ASC), 28 (7.9) (Con)	14:1	SPM	FWE-corrected, p < 0.05
Soulieres 2009	Visual	Visuospatial reasoning: Pattern matching and Raven's Standard Progressive Matrices	Pattern matching vs fixation, Raven's matrix reasoning vs fixation	15 ASC 18 Con	14–36	13:2	SPM	Uncorrected, p < 0.001, k = 10 voxels
Keehn 2008	Visual	Visual search: Homogenous and heterogenous conditions	Baseline stimuli vs fixation, all search trials vs fixation	9 ASC 13 Con	8–19	All male	AFNI	Corrected, t(21) > 3.151; p > 0.005
Gomot 2008	Auditory	Active oddball target detection: standard, deviant, and novel sounds	Deviant vs standard, Novel vs standard	12 ASC 12 Con	12–15	All male	SPM	Uncorrected, p < 0.001
Silani 2008	Visual	Viewing non-social images: valence and colour	Judging valence (pleasant/ unpleasant/neutral) vs colour balance (black/white)	15 ASC 15 Con	36.6(11.7) (ASC), 33.7 (10.3)(Con)	13:2	SPM	Uncorrected, p < 0.001
Shafritz 2008	Visual	Target detection and set-shifting with geometric shapes	All target trials vs fixation, novel trials vs fixation	18 ASC 15 Con	22.3(8.7) (ASC), 24.3 (6.2) (Con)	16:2	SPM	Uncorrected, p < 0.001
Kana 2007	Visual	Response inhibition/ working memory: Simple inhibition and letter 1-back	Simple inhibition, 1-back	12 ASC 12 Con	26.8(7.77) (ASC), 22.5 (3.2) (Con)	11:1	SPM	Uncorrected, p < 0.005
*Manjaly 2007**	Visual	Visuospatial reasoning: Embedded Figures Task	Embedded figures vs control task	12 ASC 12 Con	10–18	–	SPM	Corrected, p < 0.05
Gomot 2006	Auditory	Passive oddball target detection: standard, deviant, and novel sounds	Deviant vs standard, Novel vs standard	12 ASC 12 Con	12–15	All male	SPM	Uncorrected, p < 0.001
Schmitz 2006	Visual	Response inhibition: Go/ No Go, Stroop, and set shifting	No Go vs Go, correct Stroop, SWITCH responses	10 ASC 12 Con	18–52	All male	SPM	Corrected, p < 0.05
Haist 2006	Visual	Spatial attention: Cued target detection	Short cue-to-target ISI, long cue-to-target-ISI	8 ASC 8 Con	14–43	All male	AFNI	Corrected, p < 0.05
Mueller 2004	Visual	Visuomotor learning: 8-digit sequence learning	Early learning and late learning	8 ASC 8 Con	15–41	All male	–	Corrected, p < 0.05, and uncorrected, p < 0.01
Belmonte 2004	Visual	Spatial attention: Target detection	Task vs fixation	8 ASC 6 Con	24–50	7:1	AFNI & SPM	–
*Gervais 2004**	Auditory	Passive listening	Non-vocal sounds vs silence	5 ASC 5 Con	25.8(5.9) (ASC), 27.9 (2.9)(Con)	All male	SPM	Random effect analysis, *P* < 0.001 Corrected
Mueller 2003	Visual	Visuomotor learning: 6-digit sequence learning	Task vs blue dot control	8 ASC 8 Con	15–41	All male	–	Bonferroni-corrected, p < 0.05

N = number of participants; ASC = Autism Spectrum Conditions; Con = Typical Controls; FWE = Family Wise Error; FDR = False Discovery Rate. Italicized studies indicate studies included in sensory processing domain-specific meta-analyses. Studies which found no group differences are indicated by an asterisk (*). Unreported items are indicated by a hyphen. Experimental contrasts, participants age and sex, and fMRI statistical thresholds are entered as reported.

2.2.2. Sensory processing

2.2.2.1. Visual processing. To investigate group differences during visual processing, we conducted more refined analyses on classic visual processing paradigms (Table 1). These paradigms were comprised of visuospatial reasoning, target detection, and simple visual processing contrasts. In the case where studies probed multiple sensory modalities, only the relevant visual contrasts were included in the corresponding meta-analysis (Green et al., 2013; Keehn et al., 2017). Foci were organized according to primary study, with different experiments/contrasts

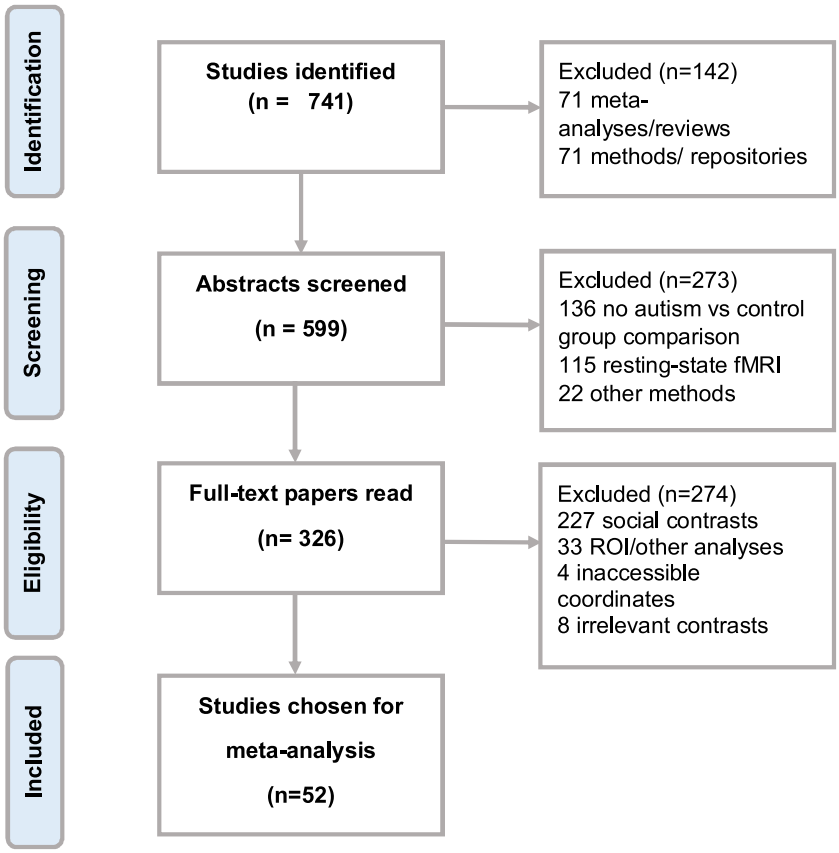

Fig. 1. Flowchart representing the literature search process. n = number of publications; ROI = Region-of-interest.

from the study grouped together. A total of 35 experimental contrasts from 24 studies on 944 participants (458 Autism and 486 Control) were included. To assess the directionality of group differences, separate analyses were computed on 106 and 84 foci for *Autism* > *Control* and *Control* > *Autism* contrasts respectively.

2.2.2.2. Auditory processing. We next sought to identify brain regions consistently showing differential activation during auditory processing. All non-social auditory contrasts were included in these meta-analyses (Table 1). A primary study which separately compared two different autism groups; that is, autism with or without Speech Onset Delay, with a neurotypical group was treated as two separate entries (Samson et al., 2015). Only the auditory contrasts were entered where studies examined multiple sensory modalities (Green et al., 2013, 2015; Keehn et al., 2017). Our stringent inclusion criteria yielded 12 experimental contrasts from 9 non-social auditory processing studies with a total of 256 participants. As this number is below the minimum accepted sample size of experiments required to detect effects (i.e., n = 17) (Müller et al., 2018), we mark this analysis as preliminary. Furthermore, we abstained from examining group differences due to a lack of statistical power. Instead, we conducted a single pooled meta-analysis on 136 peak coordinates of differential neural activity across studies. This approach allowed us to identify brain regions of differential activity during auditory processing without overestimating the direction of group differences.

2.2.2.3. Tactile processing. To examine brain regions implicated in tactile processing, we entered all non-social tactile experimental contrasts into a meta-analysis (Table 1). We identified 10 tactile contrasts from 4 studies on a total of 120 subjects. Due to the small number of experimental contrasts in the tactile domain, we followed the same approach as the auditory processing sub-analysis. A total of 107 peak coordinates from 10 tactile experimental contrasts were pooled together in this exploratory meta-analysis which did not take directionality of group differences into account.

The results of the meta-analyses were visualized using the stereotactic coordinate system and MNI template in MRICron (www.mccauslandcenter.sc.edu/crnl). Anatomical labelling was done with in-built FSL atlases, namely the Harvard-Oxford Cortical Atlas, Juelich Histological Atlas, and MNI Structural Atlas (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases).

3. Results

3.1. General perception across non-social tasks

Directional ALE analyses conducted on 83 experiments from 52 studies showed that non-autistic control groups, when compared to autistic groups, showed consistently greater recruitment of the frontal cortex. The *Control* > *Autism* comparison yielded a single large cluster in the frontal lobe encompassing the anterior, dorsolateral, and medial prefrontal cortices (BA 9,10) (Table 2, Fig. 2). The *Autism* > *Control* comparison did not find any significant clusters at this conservative threshold.

Meanwhile, uncorrected *Autism* > *Control* analyses yielded distributed clusters in the precentral gyrus (BA6), superior temporal gyrus (BA41), primary somatosensory cortex (BA2), occipital areas (BA18, BA22), the caudate, and insula (BA13). Uncorrected ALE of *Control* > *Autism* coordinates indicated several clusters in addition to the frontal (BA9,10) cluster found above: in the frontal (BA6) and parietal cortices (BA7, BA2) and the cingulate gyrus (BA32). Further details of these uncorrected ALE maps across the 52 general non-social perception studies can be found in Fig. S1 and Table S1 of the Supplementary Material.

Table 2
ALE results: Significant peaks of activation across ALE meta-analyses.

Meta-analysis	Contrast	MNI Coordinates			Cluster size mm^3	ALE value	Z- score	Neuro-anatomical labels
		X	Y	Z				
General Perception	Autism > Control	–	–	–	–	–	–	–
	Control > Autism	38	48	22	984	0.002	4.74	Prefrontal cortex, right cerebrum (BA9, BA10)
Visual Processing	Autism > Control	−18	−82	26	728	0.016	4.70	Occipital extra-striate cortex (BA18)
	Control > Autism	–	–	–	–	–	–	–
Auditory Processing	Pooled	−4	26	40	720	0.022	5.41	Dorsal anterior cingulate (BA32), frontal cortex (BA8,6)
		−40	−56	34	648	0.019	4.91	Angular gyrus (BA39)
Tactile Processing	Pooled	−52	−24	54	526	0.016	4.70	Pareital somato-sensory cortex (BA2), supramarginal gyrus (BA40)

Note: Results are cluster-level fWE-corrected at $p < 0.05$ with a cluster-forming threshold of $p < 0.001$ using 5000 permutations. Hyphens indicate null results.

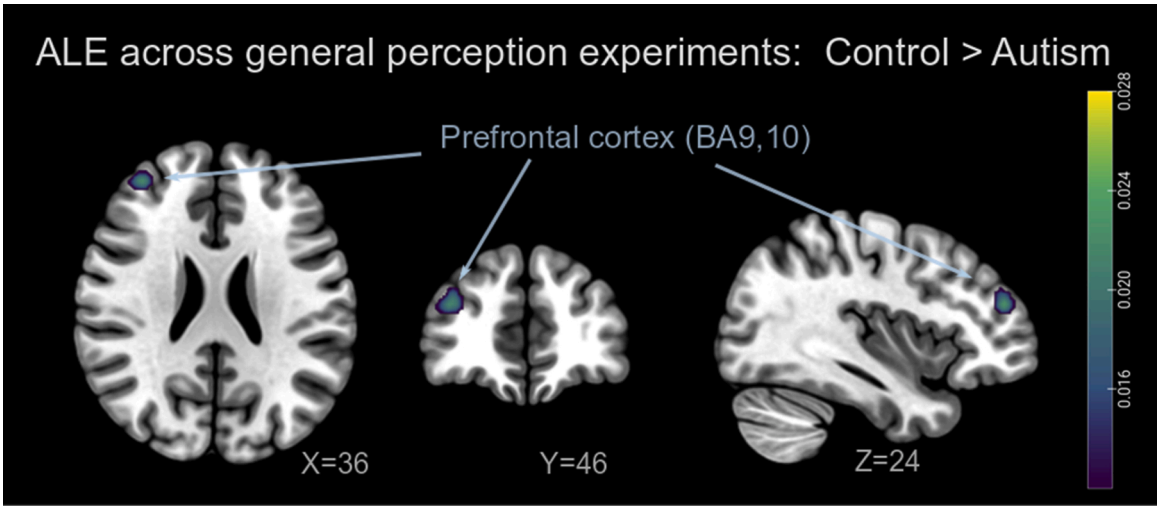

Fig. 2. Significant Control > Autism ALE results across general perception experiments (cluster-level fWE-corrected at $p < 0.05$ with a cluster-forming threshold of $p < 0.001$ using 5000 permutations). Coordinates are in MNI space. Colour bars indicate the ALE values.

3.2. *Sensory processing across studies*

3.2.1. *Visual processing*

Directional ALE across 24 visual processing studies indicated that autistic groups engaged the lateral occipital cortex to a greater extent than non-autistic controls. The *Autism* > *Control* contrast meta-analysis identified a single cluster in the occipital lobe, corresponding to the extrastriate V2 cortex (BA 18) (Table 2, Fig. 3). No significant clusters were found in the opposing direction of group comparisons.

Uncorrected ALE maps for the *Autism* > *Control* comparison across

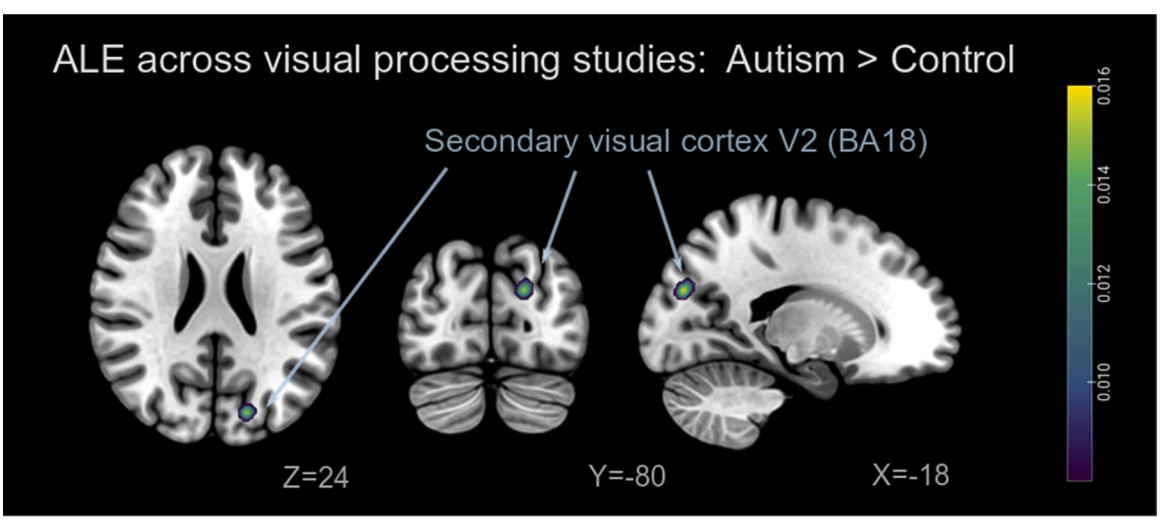

Fig. 3. Significant Autism > Control ALE results across visual processing studies (cluster-level fWE-corrected at $p < 0.05$ with a cluster-forming threshold of $p < 0.001$ using 5000 permutations). Coordinates are in MNI space. Colour bars indicate the ALE values.

visual processing studies resulted in several clusters in addition to the V2 extrastriate cortex (BA 18) cluster identified in the corrected meta-analysis. These additional clusters were located in the temporal (BA40) and frontal (BA6) cortices as well as the insula (BA13). Additional to the conservative threshholded maps, uncorrected Control > Autism comparisons yielded clusters – of which none survived correction - in the frontal (BA6, BA9) and parietal (BA7, BA40) cortices and the insula (BA 13). Further details of the uncorrected results can be found in Fig. S2 and Table S2 of the Supplementary Material.

3.2.2. Auditory processing

Exploratory ALE sub-analyses on the pooled peak coordinates from 9 auditory processing studies with 12 experimental contrasts yielded 2 clusters of differential activity spanning the anterior cingulate (BA32) and frontal cortices (BA8, BA6) and the angular gyrus (BA39) (Table 2).

3.2.3. Tactile processing

Exploratory ALE sub-analyses on the pooled peak coordinates from 4 tactile processing studies with 10 experimental contrasts yielded a single cluster of differential activity in the primary somatosensory cortex (BA2) and supramarginal gyrus (BA40) (Table 2).

4. Discussion

4.1. Summary

We quantitatively summarized evidence from task-based fMRI studies of non-social sensory perception in autistic compared to typical control participants by conducting a series of conservatively-thresholded ALE meta-analyses. First, we investigated neural group differences across a wide range of experiments probing general perceptual processes. Next, by confining the analyses to more homogenous sets of studies, we examined task activation patterns of sensory processing across different sensory domains. The most robust findings from these meta-analyses were that, compared to autistic groups, non-autistic control participants showed consistently greater engagement of the anterior, dorsolateral and medial prefrontal cortices (BA9,10) across general perception tasks. In addition, autistic groups recruited the secondary visual cortex, V2 (BA 18), to a greater extent than controls across visual processing studies.

4.2. Prior ALE findings on autistic perception

A number of ALE meta-analyses on autistic perception have been published in the past decade. An fMRI meta-analysis of visual processing tasks with words, objects and faces as stimuli found that autistic groups, compared to controls, showed more activity in occipital, temporal and parietal regions and less activity in the frontal regions (Samson et al., 2012). Philip et al. (2012) conducted systematic meta-analyses on different task domains: in autism, visual processing tasks showed comparatively greater activity of thalamus and medial frontal gyrus and less activity of the cingulate and occipital cortex, while auditory and language tasks yielded more activity of the precentral gyrus and posterior cingulate, and less activity of the superior temporal gyrus. In addition, Yang and Hofmann (2016) meta-analysed thirteen fMRI studies on action observation in autism compared to controls. They found increased activations in the frontal and parietal cortices, and decreased activity in the occipital and temporal areas in autistic groups. However, the results from these meta-analyses may have been compromised by implementation errors in the GingerALE software affecting multiple comparisons corrections and thus leading to more liberal statistical inferences (Eickhoff et al., 2017). The two errors, pertaining to False Discovery Rate (FDR) thresholding and cluster-wise FWE, were rectified in versions 2.3.3 and 2.3.6 of the software. Furthermore, previous meta-analyses made no distinction between social and non-social perception, rendering it possible that findings may have been weighted by the high prevalence of social stimuli in the primary literature. By taking a conservative thresholding approach and by focusing solely on non-social experimental contrasts, we sought to provide a meaningful account of differential neural activity between autistic and control individuals during non-social sensory perception.

4.3. Differential activity in frontal and early visual cortices

Our meta-analytic group comparisons across 83 perceptual processing experiments from 52 fMRI studies showed that non-autistic control groups were more likely than autistic groups to show activity in the medial and dorsolateral prefrontal cortices. These differences were more apparent in the uncorrected results, with control groups showing significantly more clusters of activity in frontal and parietal cortices (Table S1, Fig. S2). These findings are in line with early "underconnectivity" theories of autism which attribute autistic symptomatology to impaired connections arising from higher-order brain regions (Belmonte et al., 2004; Frith, 2004; Geschwind and Levitt, 2007; Just et al., 2012). With the recent rise in availability of large-scale brain datasets, autism-related frontal lobe anomalies have been consistently found in a number of well-powered morphometric analyses, with differences in areas including, but not limited to, white matter and cortical thickness (Bedford et al., 2020; Postema et al., 2019; van Rooij et al., 2017).

The role of the prefrontal cortex in higher-order stages of perception (i.e, predictions or expectations) is well-established (Friston et al., 2016; Sherman et al., 2016; Siman-Tov et al., 2019; Summerfield et al., 2006; Summerfield and de Lange, 2014). Based on the limited availability of suitable task fMRI contrasts and our stringent inclusion criteria, it was not possible to meta-analytically pin-down the top-down processes or the "expectation" components of perception. Hence, we included a range of perceptual processing paradigms that encompassed the various the steps involved in non-social sensory perception, from stimulus detection to interpretation. Although this approach may seem quite broad, the trade-off provided a good number of suitable experiments with reasonable statistical power to draw reliable inferences (Müller et al., 2018).

Visual processing has been prominent area of interest in autism research (Simmons et al., 2009). As visual mechanisms are relatively well-defined in the typical population, visual processing serves as a useful tool to investigate the differential sensory and cognitive profile of autism (Heeger et al., 2017; Robertson and Baron-Cohen, 2017). Autistic individuals have consistently shown differences in various visual processing domains, including: superior performance on tasks related to visual search (Plaisted et al., 1998) and identifying hidden figures in complex scenes (Jolliffe and Baron-Cohen, 1997; Happé and Frith, 2006); less susceptibility to certain visual illusions (Chouinard et al., 2018; Happé, 1996; Manning et al., 2017); diminished adaptation (Lawson et al., 2018; Pellicano et al., 2013; Turi et al., 2015); and slower rates of binocular rivalry (Freyberg et al., 2015; Robertson et al., 2013). Behavioural findings of atypical binocular rivalry and global motion perception have been mirrored in the early visual cortices (Robertson et al., 2014, 2016).

After refining the meta-analysis to a more homogenous set of visual processing studies, our second robust finding was heightened occipital activity, localized to area V2 or the secondary visual cortex (BA18), in autistic compared to non-autistic control groups. The extrastriate V2 plays a distinct role in early visual processing, with reference to detecting orientation, contours/edges, and colours of objects (Anzai et al., 2007; Boynton and Hegdé, 2004; Hegdé and Essen, 2000; Heydt et al., 1984; Hubel and Livingstone, 1987; Hubel and Wiesel, 1965; Rowekamp and Sharpee, 2017). Furthermore, the V2 receives feedforward sensory input from the V1 (i.e, the primary visual cortex) and feeds back predictions and inferences to V1 in a well-defined, hierarchical manner (Lee and Mumford, 2003; Muckli and Petro, 2013; Rao and Ballard, 1999; Roelfsema et al., 2000; Smith and Muckli, 2010).

Due to the relatively limited research, the question of whether similar differences extend to other sensory domains is yet to be answered. In line with findings from vision research, autistic individuals have been found to show characteristically distinct performances on auditory processing tasks (Kwakye et al., 2011; Lawson et al., 2015a, 2015b; Millin et al., 2018; O'Riordan and Passetti, 2006; Remington and Fairnie, 2017). Meanwhile, despite self-reports indicating tactile sensitivities in autism, findings from tactile research have not been as conclusive (Fukuyama et al., 2017; Mikkelsen et al., 2018; O'Riordan and Passetti, 2006). Our exploratory sub-analyses of auditory processing studies yielded clusters of differential activity in the parietal and cingulate cortices, while meta-analytical results across tactile studies indicated notable activity in the primary somatosensory cortex. Due to the small sample size of the included experiments, and as we did not test for directionality of group differences, these findings of changes in activation across auditory and tactile studies must be considered as preliminary and hence interpreted with caution.

4.4. Limitations

A number of limitations are pertinent to the interpretation of our ALE results. First, a general challenge of ALE meta-analyses is the issue of heterogeneity across included studies. Despite our use of stringent, pre-registered inclusion criteria, we had to make some compromises in homogeneity to maintain an acceptable sample size. The recommended number of studies to yield sufficient statistical power for ALE meta-analyses is 17–20 (Eickhoff et al., 2016; Müller et al., 2018). In addition, we acknowledge that the range of task contrasts included is quite broad, encompassing several perceptual processes. Although it would have been ideal to restrict our inclusion criteria to specific sensory modalities and paradigms, our decisions were driven by the need for sufficient statistical power to draw reliable inferences. Limitations pertaining to participant groups across studies include: 1) heterogeneity across age and gender, and b) the sampling bias of the population under study, namely autistic individuals who were not contraindicated for the MRI environment. The former is important as autism is notably a neurodevelopmental condition with marked sex differences in its symptom presentation (American Psychiatric Association, 2013; Lai et al., 2017; Mandy et al., 2012). As several of the original papers investigated participant groups of a broad age range, and as they did not test for sex differences in their fMRI analyses, it was beyond the scope of meta-analysis to explore these in more detail.

Due to our focus on whole-brain fMRI studies, these findings are not representative of the entire task-based fMRI literature on non-social sensory perception in autism. We were limited by whole-brain analyses as the inclusion of region-specific analyses would violate the assumptions of the coordinate-based voxel-wise meta-analysis (Radua and Mataix-Cols, 2009; Wager et al., 2007; Eickhoff et al., 2012). By excluding hypothesis-driven fMRI studies employing ROI analyses, we may be missing out on subtle, low-level neural differences identified in the early sensory cortices. Using ROI-based approaches, studies have identified early, autism-specific neural responses in a number of regions including: the primary visual cortex and middle temporal gyrus during visual global motion perception (Robertson et al., 2014) ; intraparietal sulcus, primary and secondary visual cortex, precuneus, cerebellum and middle temporal gyrus during passive and active visual movement tracking (Takarae et al., 2014); and extrastriate population receptive fields during visual stimulation (Schwarzkopf et al., 2014). Although some of these regions feature in the uncorrected ALE results (Supplementary Material), we note that the exclusion of such studies may have attenuated the effects of certain regions commonly activated during autistic perception.

Finally, we recommend caution in interpreting our results as cognitive neuroimaging findings are largely based on reverse inferences (Poldrack, 2006, 2011). Moreover, the meta-analytic results reflect the quality of the fMRI literature in general. Factors contributing to quality range from data acquisition parameters to the pre-processing and statistical approaches employed for the fMRI analyses. Important considerations include publication bias, reproducibility issues, and the need for standardized analysis pipelines and best-practice guidelines for fMRI research (Nichols et al., 2017).

4.5. Autistic perception: current theories, challenges, and future directions

Taken together, our meta-analysis findings of comparatively increased frontal activity in typical controls across general perception experiments and heightened extrastriate activity in autistic groups across visual processing studies, add to the literature of sensory perception in autism. Notably, our findings of differential higher-order prefrontal and low-level extrastriate activity help inform some of the current theories of autistic perception. However, these results also highlight that synthesizing the non-social perception fMRI literature on autism yields only a small number of significant clusters of groups differences.

The question of which stage of the sensory perception hierarchy to attribute autistic perception to is still unanswered. While the neuroscience findings are lacking, there have been attempts to formulate the relationship between high-level perception and low-level sensory processing through neurocomputational models. According to Bayesian inference and predictive coding, autistic individuals may: rely less on top-down expectations (i.e., hypo-priors) (Pellicano and Burr, 2012); show heightened precision of sensory evidence (Friston et al., 2013; Lawson et al., 2014, 2015b); form imprecise sensory representations due to inflexible perceptual processing (Brock, 2012); have difficulties in disentangling signal from noise (Van de Cruys et al., 2017), or show aberrant updating of prior beliefs (Haker et al., 2016). Another computational perspective on autistic perception is based on altered neural computations, or a failure of divisive normalization, i.e when the activity of an individual neuron is divided by the total activity of the surrounding neuronal population, thus making them context-sensitive (Rosenberg et al., 2015). This has been linked to an imbalance in the excitation-inhibition (E/I) neural circuitry in autism (Gogolla et al., 2009; Rubenstein and Merzenich, 2003). As delineating the hierarchy of sensory perception is beyond the scope of meta-analysis, future empirical experiments using sophisticated paradigms, computational approaches, and novel imaging methods may shed light on the intricacies of these processes.

The lack of consistent neuroscience findings in autism is an area of concern. Indeed, our meta-analytical results indicate that the brain regions showing differential activity between autistic and non-autistic controls during non-social perception, although notable, are few in number. This highlights one of the key challenges of autism research in general - the heterogeneity across the clinical profile of the condition (An and Claudianos, 2016). To address this, current research is striving to refine the study of autism through brain- and behaviour-based sub--typing (Hong et al., 2020; Kim, 2020; Lombardo et al., 2019; Tang et al., 2020; Tillmann et al., 2020).

5. Conclusions

Using ALE, we quantitatively condensed findings from task-based fMRI studies on non-social sensory perception in autism. We found that, during general perception experiments, autistic groups engaged the pre-frontal cortices to a lesser extent than typical controls. Meanwhile, autistic groups, on average, showed greater recruitment of area V2 of the occipital cortex across visual processing studies. Taken together, these findings add to the current theories of autistic sensory perception. Our findings highlight some of the limitations of fMRI research in autism and may help guide future research to focus on relevant brain mechanisms associated with autistic perception.

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Data availability

Jassim, Nazia (2021), "Meta-analytic evidence of differential prefrontal and early sensory cortex activity during non-social sensory perception in autism", Mendeley Data, V3, doi:10.17632/pwgdfd88cy.3.

Declaration of Competing Interest

None

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.neubiorev.2021.04.014.

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