

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

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29 **Abstract**

30

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

44 **Keywords:** autism spectrum conditions; perception; sensory processing; non-social;
45 activation likelihood estimation (ALE); fMRI; meta-analysis; V2; prefrontal; extrastriate

46

47 **1. Introduction**

48 Autism spectrum conditions (henceforth autism) are neurodevelopmental in origin and are
49 diagnosed on the basis of both social and non-social symptoms; namely, difficulties in
50 communication and relationships, unusually narrow interests, and strongly repetitive,
51 restrictive patterns of behaviour (American Psychiatric Association, 2013). Autism is also
52 characterized by atypical sensory perception, a feature occurring in up to 90% of autistic
53 individuals (Tavassoli et al., 2013). Autistic individuals show superior attention to detail

54 (Happé & Frith, 2006; Jolliffe & Baron-Cohen, 1997; Shah & Frith, 1983), heightened ability
55 to “systemize” (i.e, to identify *if-and-then* rules in a system) (Baron-Cohen et al., 2003, 2009;
56 Baron-Cohen & Lombardo, 2017), enhanced perceptual functioning (Mottron et al., 2006)
57 and greater perceptual load (Remington et al., 2009).

58 Sensation or sensory processing encompasses the early-stage detection of “elementary”
59 properties of stimuli (Carlson, 2010). Meanwhile, perception is a dynamic, hierarchical
60 process involving an interaction between these low-level sensations and higher-order
61 expectations (Goldstein, 2013). With reference to the visual domain, early theories of
62 perception describe the process as “unconscious inference” (von Helmholtz, 1866).

63 According to hierarchical models of the brain, feedforward connections from lower sensory
64 areas (i.e., bottom-up processes) send information to higher cortical areas, while feedback
65 connections from higher-to-lower areas (i.e., top-down processes) carry predictions or
66 expectations of low-level information (Clark, 2013; Friston, 2005; Friston & Kiebel, 2009).

67 Sensory perception is greatly influenced by prior knowledge or expectations of the external
68 world (Bar, 2004; de Lange et al., 2018; Series & Seitz, 2013). In autism, unique sensory-
69 perceptual processing may be attributed to differential weighing of either top-down prior
70 expectations (Pellicano & Burr, 2012) or bottom-up sensory processes (Mottron et al., 2006).

71 With the inclusion of sensory sensitivities (both hypo- and hyper-sensitivities) as a core
72 diagnostic criterion for autism in the *Diagnostic and Statistical Manual of Mental Disorders*
73 (*Fifth Edition*) (American Psychiatric Association, 2013), there is considerable interest in
74 understanding its neurobiological substrates.

75 Until the recent revision of its diagnostic criteria, the dominant view of autism as primarily a
76 “social” condition led to sensory symptoms being largely overlooked. While it has been
77 hypothesized that sensory differences may contribute to cognitive strengths or “talents” due
78 to superior perceptual abilities in autism (Baron-Cohen & Lombardo, 2017; Robertson &

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

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

102

103 2. Methods

104 2.1 Literature search and study selection

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

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

113 The following inclusion criteria were used:

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

121 Following the initial literature search, whole-brain task fMRI studies were categorized as
122 either social or non-social. Studies with social paradigms were checked for non-social
123 contrasts (such as neutral/control/baseline contrasts). We recorded the following details for
124 each included study: first author and year of publication, number of participants per group,
125 age, sex, task details (domain, sensory modality, and contrasts), location and direction of

126 effects, and standard stereotactic space used to spatially align imaging data for group
127 comparisons.

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

132 **2.2 Activation Likelihood Estimation Meta-Analyses**

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

135 Activation Likelihood Estimation (ALE) models the spatial agreement of foci across studies
136 or experiments with random-effects modelling (Eickhoff et al., 2009, 2012; Turkeltaub et al.,
137 2012). The algorithm treats foci as 3D spatial probability distributions and estimates the Full-
138 Width Half Maximum (FWHM) of the Gaussian distribution, which is dependent on the
139 number of participants in each primary study. The spatial probability distributions are merged
140 to create “Modelled activation” (MA) maps. By taking the union of each MA map, the
141 algorithm computes an ALE value at each voxel in the brain. These are tested against the null
142 hypothesis of random spatial convergence across studies.

143 Peak coordinates from the Autism vs Typical (henceforth Control) group comparisons of
144 each study were manually entered into GingerALE. Coordinates in Talairach space were
145 converted to Montreal Neurological Institute (MNI) space using the GingerALE ‘convert
146 foci’ tool. For our meta-analyses examining the direction of group differences, separate
147 analyses were computed for the comparisons *Autism>Control* and *Control>Autism*.

148 Specifically, *Autism>Control* foci files contained peak coordinates of regions showing more
149 activation in autistic groups compared to controls across included studies, and vice versa for

150 the *Control>Autism* foci files. We included ANOVA results, main effects, and interaction
151 effects only when group differences and direction of effects were clearly reported. For each
152 of these comparisons, the number of participants per group were appropriately coded. Studies
153 that found no group differences were included with empty coordinates. In accordance with
154 the current best practice methods for neuroimaging meta-analyses, we used the most
155 conservative field-recommend statistical thresholding approach for ALE analyses (Müller et
156 al., 2018). To limit the occurrence of false positives and artefactual results, analyses were
157 thresholded using 5000 permutations to estimate a cluster-level family-wise error (cFWE)
158 correction of $P < 0.05$ using a cluster-forming threshold of $P < 0.001$ (Eickhoff et al., 2012,
159 2016, 2017).

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

165 **2.2.1 General perception across non-social tasks**

166 To examine neural differences across a wide range of perceptual processing tasks, we first
167 meta-analysed peak coordinates from our complete list of non-social fMRI tasks. In order to
168 cover the various steps involved in perception, from stimulus detection to interpretation, the
169 included tasks ranged from sensory processing tasks, such as visuospatial reasoning,
170 visual/auditory/tactile stimulation, and target detection, to higher-level executive function
171 paradigms probing expectation, such as learning, reward anticipation, and response
172 inhibition. Foci were organized according to experimental contrast. A total of 83
173 experimental contrasts from 52 studies, encompassing 1,858 participants (891 Autism and

174 967 Control) were included in this meta-analysis. To investigate the directionality of group
175 differences, meta-analyses were computed on 307 and 369 foci for *Autism>Control* and
176 *Control>Autism* comparisons respectively.

177 **2.2.2 Sensory processing**

178 **Visual processing**

179 To investigate group differences during visual processing, we conducted more refined
180 analyses on classic visual processing paradigms. These paradigms were comprised of
181 visuospatial reasoning, target detection, and simple visual processing contrasts. In the case
182 where studies probed multiple sensory modalities, only the relevant visual contrasts were
183 included in the corresponding meta-analysis (Green et al., 2013; Keehn et al., 2017). Foci
184 were organized according to primary study, with different experiments/contrasts from the
185 study grouped together. A total of 35 experimental contrasts from 24 studies on 944
186 participants (458 Autism and 486 Control) were included. To assess the directionality of
187 group differences, separate analyses were computed on 106 and 84 foci for *Autism > Control*
188 and *Control > Autism* contrasts respectively.

189 **Auditory processing**

190 We next sought to identify brain regions consistently showing differential activation during
191 auditory processing. All non-social auditory contrasts were included in these meta-analyses.
192 A primary study which separately compared two different autism groups; that is, autism with
193 or without Speech Onset Delay, with a neurotypical group was treated as two separate entries
194 (Samson et al., 2015). Only the auditory contrasts were entered where studies examined
195 multiple sensory modalities (Green et al., 2013, 2015; Keehn et al., 2017). Our stringent
196 inclusion criteria yielded 12 experimental contrasts from 9 non-social auditory processing
197 studies with a total of 256 participants. As this number is below the minimum accepted

198 sample size of experiments required to detect effects (i.e., $n=17$) (Müller et al., 2018), we
199 mark this analysis as preliminary. Furthermore, we abstained from examining group
200 differences due to a lack of statistical power. Instead, we conducted a single pooled meta-
201 analysis on 136 peak coordinates of differential neural activity across studies. This approach
202 allowed us to identify brain regions of differential activity during auditory processing without
203 overestimating the direction of group differences.

204 **Tactile processing**

205 To examine brain regions implicated in tactile processing, we entered all non-social tactile
206 experimental contrasts into a meta-analysis. We identified 10 tactile contrasts from 4 studies
207 on a total of 120 subjects. Due to the small number of experimental contrasts in the tactile
208 domain, we followed the same approach as the auditory processing sub-analysis. A total of
209 107 peak coordinates from 10 tactile experimental contrasts were pooled together in this
210 exploratory meta-analysis which did not take directionality of group differences into account.

211 The results of the meta-analyses were visualized using the stereotactic coordinate system and
212 MNI template in MRICron (www.mccauslandcenter.sc.edu/crn1). Anatomical labelling was
213 done with in-built FSL atlases, namely the Harvard-Oxford Cortical Atlas, Juelich
214 Histological Atlas, and MNI Structural Atlas (<https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Atlases>).

215 **3 Results**

216 **3.1 General perception across non-social tasks**

217 Directional ALE analyses conducted on 83 experiments from 52 studies showed that non-
218 autistic control groups, when compared to autistic groups, showed consistently greater
219 recruitment of the frontal cortex. The *Control* > *Autism* comparison yielded a single large
220 cluster in the frontal lobe encompassing the anterior, dorsolateral, and medial prefrontal

221 cortices (BA 9,10) (*Table 2, Fig. 2*). The *Autism > Control* comparison did not find any
222 significant clusters at this conservative threshold.

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

231 **3.2 Sensory processing across studies**

232 **3.2.1 Visual processing**

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

238 Uncorrected ALE maps for the *Autism>Control* comparison across visual processing studies
239 resulted in several clusters in addition to the V2 extrastriate cortex (BA 18) cluster identified
240 in the previous meta-analysis. These additional clusters were located in the temporal (BA40)
241 and frontal (BA6) cortices as well as the insula (BA13). Additional to the conservative
242 thresholded maps, uncorrected *Control> Autism* comparisons yielded clusters – of which
243 none survived correction - in the frontal (BA6, BA9) and parietal (BA7, BA40) cortices and

244 the insula (BA 13). Further details of the uncorrected results can be found in *Fig. S2* and
245 *Table S2* of the Supplementary Material.

246 **3.2.2 Auditory processing**

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

251 **3.2.3 Tactile processing:**

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

255

256 **4 Discussion**

257 **4.1 Summary**

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

267 recruited the secondary visual cortex, V2 (BA 18), to a greater extent than controls across
268 visual processing studies.

269 **4.2 Prior ALE findings on autistic perception**

270 A number of ALE meta-analyses on autistic perception have been published in the past
271 decade. An fMRI meta-analysis of visual processing tasks with words, objects and faces as
272 stimuli found that autistic groups, compared to controls, showed more activity in occipital,
273 temporal and parietal regions and less activity in the frontal regions (Samson et al., 2012).
274 Philip et al. (2012) conducted systematic meta-analyses on different task domains: in autism,
275 visual processing tasks showed comparatively greater activity of thalamus and medial frontal
276 gyrus and less activity of the cingulate and occipital cortex, while auditory and language
277 tasks yielded more activity of the precentral gyrus and posterior cingulate, and less activity of
278 the superior temporal gyrus. In addition, Yang & Hofmann (2016) meta-analysed thirteen
279 fMRI studies on action observation in autism compared to controls. They found increased
280 activations in the frontal and parietal cortices, and decreased activity in the occipital and
281 temporal areas in autistic groups. However, the results from these meta-analyses may have
282 been compromised by implementation errors in the GingerALE software affecting multiple
283 comparisons corrections and thus leading to more liberal statistical inferences (Eickhoff et al.,
284 2017). The two errors, pertaining to False Discovery Rate (FDR) thresholding and cluster-
285 wise FWE, were rectified in versions 2.3.3 and 2.3.6 of the software. Furthermore, previous
286 meta-analyses made no distinction between social and non-social perception, rendering it
287 possible that findings may have been weighted by the high prevalence of social stimuli in the
288 primary literature. By taking a conservative thresholding approach and by focusing solely on
289 non-social experimental contrasts, we sought to provide a meaningful account of differential
290 neural activity between autistic and control individuals during non-social sensory perception.

291 **4.3 Differential activity in frontal and early visual cortices**

292 Our meta-analytic group comparisons across 83 perceptual processing experiments from 52
293 fMRI studies showed that non-autistic control groups were more likely than autistic groups to
294 show activity in the medial and dorsolateral prefrontal cortices. These differences were more
295 apparent in the uncorrected results, with control groups showing significantly more clusters
296 of activity in frontal and parietal cortices (*Table S1, Fig. S2*). These findings are in line with
297 early “underconnectivity” theories of autism which attribute autistic symptomatology to
298 impaired connections arising from higher-order brain regions (Belmonte et al., 2004; Frith,
299 2004; Geschwind & Levitt, 2007; Just et al., 2012). With the recent rise in availability of
300 large-scale brain datasets, autism-related frontal lobe anomalies have been consistently found
301 in a number of well-powered morphometric analyses, with differences in areas including, but
302 not limited to, white matter and cortical thickness (Bedford et al., 2020; Postema et al., 2019;
303 van Rooij et al., 2017).

304 The role of the prefrontal cortex in higher-order stages of perception (i.e, predictions or
305 expectations) is well-established (Friston et al., 2016; Sherman et al., 2016; Siman-Tov et al.,
306 2019; Summerfield et al., 2006; Summerfield & de Lange, 2014). Based on the limited
307 availability of suitable task fMRI contrasts and our stringent inclusion criteria, it was not
308 possible to meta-analytically pin-down the top-down processes or the “expectation”
309 components of perception. Hence, we included a range of perceptual processing paradigms
310 that encompassed the various the steps involved in non-social sensory perception, from
311 stimulus detection to interpretation. Although this approach may seem quite broad, the trade-
312 off provided a good number of suitable experiments with reasonable statistical power to draw
313 reliable inferences (Müller et al., 2018).

314 Visual processing has been prominent area of interest in autism research (Simmons et al.,
315 2009). As visual mechanisms are relatively well-defined in the typical population, visual
316 processing serves as a useful tool to investigate the differential sensory and cognitive profile
317 of autism (Heeger et al., 2017; Robertson & Baron-Cohen, 2017). Autistic individuals have
318 consistently shown differences in various visual processing domains, including: superior
319 performance on tasks related to visual search (Plaisted et al., 1998) and identifying hidden
320 figures in complex scenes (Jolliffe & Baron-Cohen, 1997; Happé & Frith, 2006); less
321 susceptibility to certain visual illusions (Chouinard et al., 2018; Happé, 1996; Manning et al.,
322 2017); diminished adaptation (Lawson et al., 2018; Pellicano et al., 2013; Turi et al., 2015);
323 and slower rates of binocular rivalry (Freyberg et al., 2015; Robertson et al., 2013).
324 Behavioural findings of atypical binocular rivalry and global motion perception have been
325 mirrored in the early visual cortices (Robertson et al., 2014, 2016).

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

336 Due to the relatively limited research, the question of whether similar differences extend to
337 other sensory domains is yet to be answered. In line with findings from vision research,
338 autistic individuals have been found to show characteristically distinct performances on

339 auditory processing tasks (Kwakye et al., 2011; Lawson et al., 2015; Millin et al., 2018;
340 O’Riordan & Passetti, 2006; Remington & Fairnie, 2017). Meanwhile, despite self-reports
341 indicating tactile sensitivities in autism, findings from tactile research have not been as
342 conclusive (Fukuyama et al., 2017; Mikkelsen et al., 2018; O’Riordan & Passetti, 2006). Our
343 exploratory sub-analyses of auditory processing studies yielded clusters of differential
344 activity in the parietal and cingulate cortices, while meta-analytical results across tactile
345 studies indicated notable activity in the primary somatosensory cortex. Due to the small
346 sample size of the included experiments, and as we did not test for directionality of group
347 differences, these findings of changes in activation across auditory and tactile studies must be
348 considered as preliminary and hence interpreted with caution.

349 **4.4 Limitations**

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

364 As several of the original papers investigated participant groups of a broad age range, and as
365 they did not test for sex differences in their fMRI analyses, it was beyond the scope of meta-
366 analysis to explore these in more detail.

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

383 Finally, we recommend caution in interpreting our results as cognitive neuroimaging findings
384 are largely based on reverse inferences (Poldrack, 2006, 2011). Moreover, the meta-analytic
385 results reflect the quality of the fMRI literature in general. Factors contributing to quality
386 range from data acquisition parameters to the pre-processing and statistical approaches
387 employed for the fMRI analyses. Important considerations include publication bias,

388 reproducibility issues, and the need for standardized analysis pipelines and best-practice
389 guidelines for fMRI research (Nichols et al., 2017).

390 **4.5 Autistic perception: current theories, challenges, and future directions**

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

398 The question of which stage of the sensory perception hierarchy to attribute autistic
399 perception to is still unanswered. While the neuroscience findings are lacking, there have
400 been attempts to formulate the relationship between high-level perception and low-level
401 sensory processing through neurocomputational models. According to Bayesian inference
402 and predictive coding, autistic individuals may: rely less on top-down expectations (i.e.,
403 hypo-priors) (Pellicano & Burr, 2012); show heightened precision of sensory evidence
404 (Friston et al., 2013; Lawson et al., 2014; Lawson, Friston, et al., 2015); form imprecise
405 sensory representations due to inflexible perceptual processing (Brock, 2012); have
406 difficulties in disentangling signal from noise (Van de Cruys et al., 2017), or show aberrant
407 updating of prior beliefs (Haker et al., 2016). Another computational perspective on autistic
408 perception is based on altered neural computations, or a failure of divisive normalization, i.e
409 when the activity of an individual neuron is divided by the total activity of the surrounding
410 neuronal population, thus making them context-sensitive (Rosenberg et al., 2015). This has
411 been linked to an imbalance in the excitation-inhibition (E/I) neural circuitry in autism

412 (Gogolla et al., 2009; Rubenstein & Merzenich, 2003). As delineating the hierarchy of
413 sensory perception is beyond the scope of meta-analysis, future empirical experiments using
414 sophisticated paradigms, computational approaches, and novel imaging methods may shed
415 light on the intricacies of these processes.

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

424

425 **5. Conclusions**

426 Using ALE, we quantitatively condensed findings from task-based fMRI studies on non-
427 social sensory perception in autism. We found that, during general perception experiments,
428 autistic groups engaged the pre-frontal cortices to a lesser extent than non-autistic controls.
429 Meanwhile, autistic groups, on average, showed greater recruitment of area V2 of the
430 occipital cortex across visual processing studies. Taken together, these findings add to the
431 current theories of autistic sensory perception. Our findings highlight some of the limitations
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434

435

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800 **List of Figures and Tables:**

801 **Fig 1.** Flowchart of the literature search and study selection process

802 **Fig 2.** ALE results across general perception experiments

803 **Fig 3.** ALE results across visual processing studies

804 **Table 1.** Complete list and relevant characteristics of whole-brain fMRI studies included in

805 ALE analyses

806 **Fig 2.** ALE results: Significant peaks of activation across ALE meta-analyses

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809 **Fig 3.** ALE results: Significant peaks of activation across ALE meta-analyses (In colour):

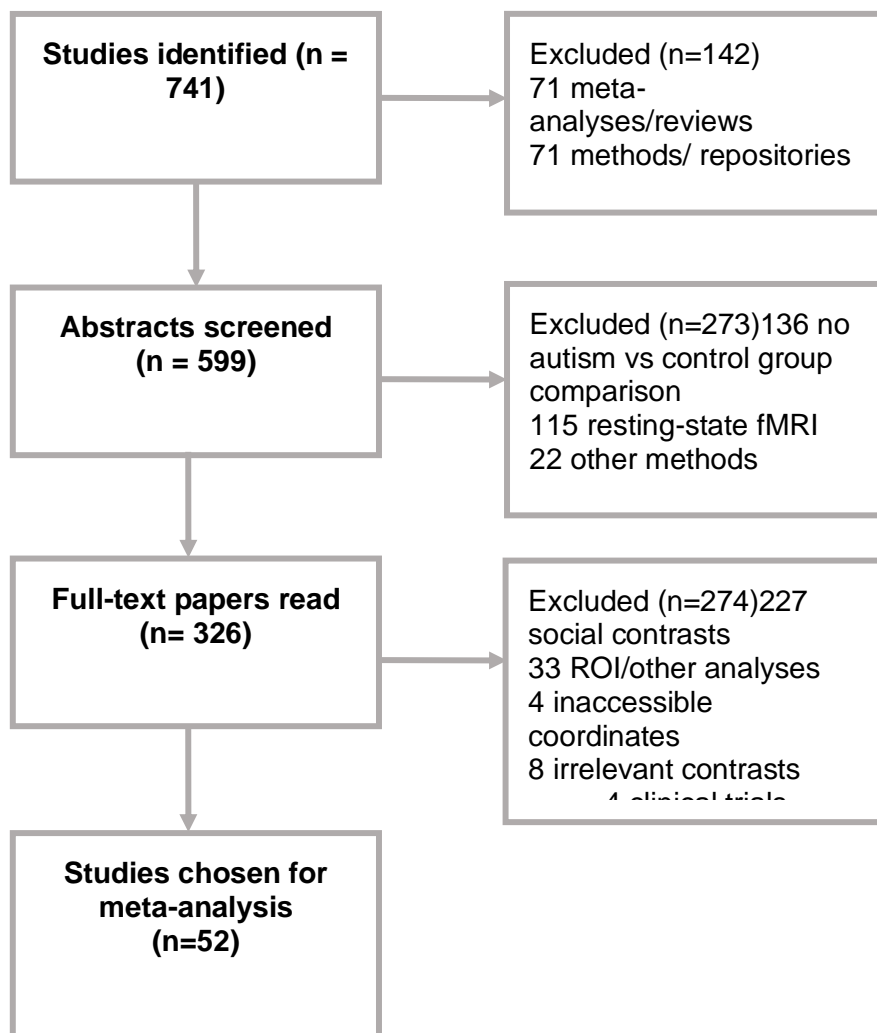
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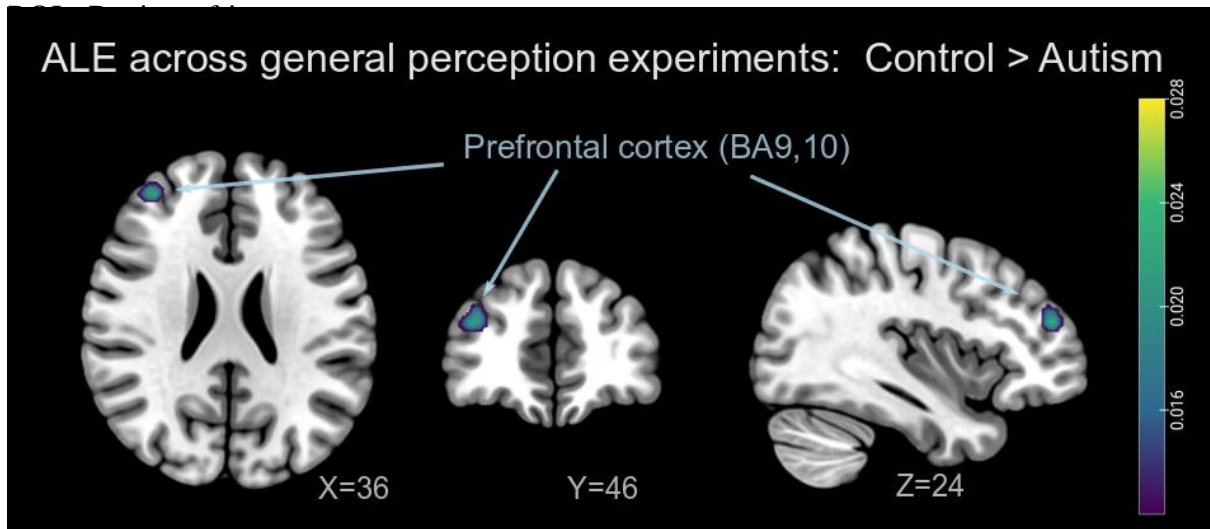
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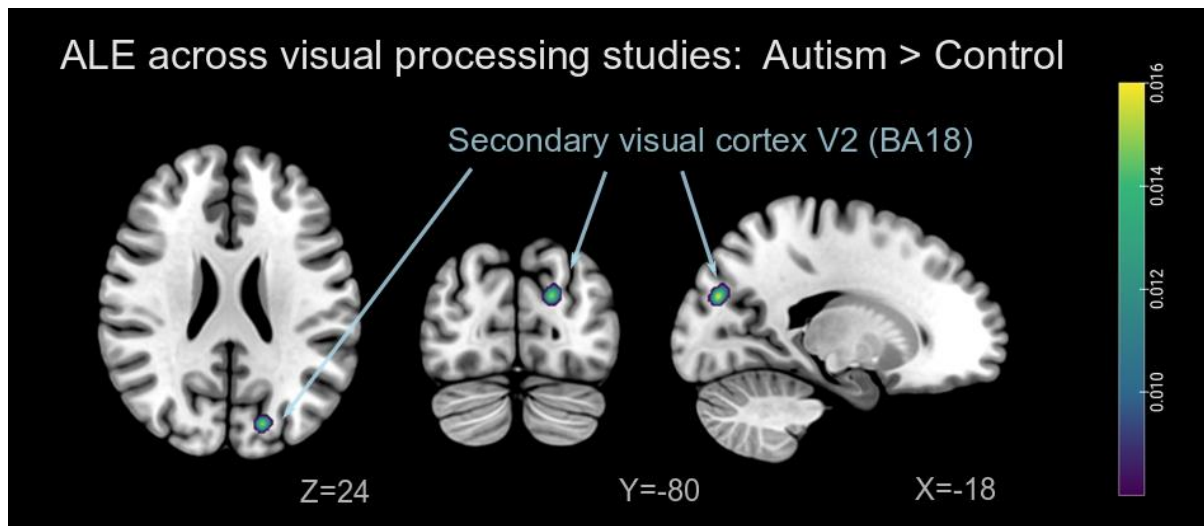
812 **Fig. 1** Flowchart representing the literature search process. n = number of publications;
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815 **Fig. 2** Significant Control > Autism ALE results across general perception experiments
 816 (cluster-level fWE-corrected at $p < 0.05$ with a cluster-forming threshold of $p < 0.001$ using
 817 5000 permutations). Coordinates are in MNI space. Colour bars indicate the ALE values.

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

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824 **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 threshold
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	Auditory vs null condition, Visual vs null condition	16 ASC	8 – 18	14:2	AFNI	FWE - corrected, $p < 0.05$

		detection, Visual- high & low spatial dot location		16 Con				
<i>Schelinksi 2016*</i>	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
<i>Kaiser 2016</i>	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
<i>Keehn 2016</i>	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

<i>Kleinhans 2016</i>	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
<i>Sharer 2015</i>	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
<i>Solomon 2015</i>	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
<i>Samson 2015</i>	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
<i>Green 2015</i>	Auditory & Tactile	Auditory stimulation: Traffic noises, Tactile stimulation: rough fabric	Auditory vs baseline, tactile vs baseline, joint auditory + tactile vs baseline	19 ASC 19 Con	9 – 17	16:3	FSL	FWE – corrected, p<0.05

Shafritz 2015	Visual	Response inhibition: Go/No Go	Letter No Go vs Go	15 ASC 18 Con	13 – 23	12:3	SPM	p <0.001, cluster-filter of 10 contiguous voxels
<i>Simhard 2015</i>	Visual	Visuospatial reasoning: Raven's Standard Progressive Matrices	Figural vs Analytical vs Complex Analytical stimuli	15 ASC 18 Con	14 – 36	13:2	SPM	p<0.001 uncorrected, extent threshold of 50 contiguous voxels
<i>Barbeau 2015</i>	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:	High-control vs low-control cue	27 ASC	12 – 18	17:10	SPM	FWE-corrected, p<0.05

		Preparing to overcome prepotency (POP) task		27 Con					
<i>Sabatino 2013</i>	Visual	Oddball target detection	High Autism Interest images vs baseline	15 ASC 17 Con	16.9 – 45.3	13:2	FSL	FWE-corrected, $p < 0.05$	
<i>Green 2013</i>	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 $z > 2.3$	
<i>Gadgil 2013</i>	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, $p < 0.05$	
<i>Spencer 2012</i>	Visual	Visuospatial reasoning: Embedded Figures Task	Embedded Figures vs Control Task	38 ASC 40 Con	12 – 18	34:4	SPMs	Uncorrected, $p < 0.001$	
<i>Yamada 2012</i>	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, $p < 0.001$	

<i>Ohta 2012*</i>	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
<i>Beacher 2012*</i>	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 $k=10$, $z > 2.5$, $P < 0.005$
<i>McGrath 2012</i>	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 ($t = 2.96$, $P < 0.005$)
<i>Cascio 2012</i>	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 $k=10$
<i>Caria 2011</i>	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 15 Con	8 – 12	8:3	SPM	Corrected $p < 0.05$
<i>Koldewyn 2011*</i>	Visual	Dot motion	Static vs coherent dot motion	16 ASC	11.41 -19.53	14:2	SPM	Voxel-wise ($t = 2.95$, $p < .005$, uncorrected)

				16 Con					and cluster-wise ($p < .05$, Bonferroni corrected)
<i>Damarla 2010</i>	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
<i>Dichter 2009</i>	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, $p < 0.05$
<i>Soulieres 2009</i>	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
<i>Keehn 2008</i>	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, $t(21) > 3.151$; $p > 0.005$
<i>Gomot 2008</i>	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, $p < 0.001$
<i>Silani 2008</i>	Visual	Viewing non-social images:	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, $p < 0.001$

		valence and colour						
<i>Shafritz 2008</i>	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, $p < 0.001$
<i>Kana 2007</i>	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, $p < 0.005$
<i>Manjaly 2007*</i>	Visual	Visuospatial reasoning: Embedded Figures Task	Embedded figures vs control task	12 ASC 12 Con	10 – 18	-	SPM	Corrected, $p < 0.05$
<i>Gomot 2006</i>	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, $p < 0.001$
<i>Schmitz 2006</i>	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, $p < 0.05$
<i>Haist 2006</i>	Visual	Spatial attention:	Short cue-to-target ISI, long cue-to-target-ISI	8 ASC 8 Con	14 – 43	All male	AFNI	Corrected, $p < 0.05$

			Cued target detection						
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, $p < 0.01$	
<i>Belmonte 2004</i>	Visual	Spatial attention: Target detection	Task vs fixation	8 ASC 6 Con	24 – 50	7:1	AFNI & SPM	-	
<i>Gervais 2004*</i>	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, $p < 0.05$	

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

828 **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				
	Autism > Control	-	-	-	-	-	-	-
General Perception								
	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 extrastriate 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 somatosensory cortex (BA2), supramarginal gyrus (BA40)

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

831

Supplementary Material**832 List of supplementary tables**

833 Table 1. Uncorrected ALE results of complex perceptual processing studies

834 Table 2. Uncorrected ALE results of visual processing studies

835

836 List of supplementary figures

837 Fig 1. Uncorrected ALE results of complex perceptual processing studies

838 Fig 2. Uncorrected ALE results of visual processing studies

839

840 Activation Likelihood Estimation

841 As an initial step, the ALE maps were thresholded using the simplest uncorrected p-value

842 method (Polyanska et al., 2017; Ding et al., 2020). Based on the recommendation of the

843 GingerALE user manual (brainmap.org/ale/manual.pdf) for uncorrected maps, the maps were844 thresholded at $p < 0.001$ with a minimum cluster volume of 100 mm³.

845

846 **Supplementary Table S1.** Uncorrected ALE results of complex perceptual processing
 847 studies

Cluster	MNI Coordinates			Cluster volume mm ³	ALE value	P Value	Label
	X	Y	Z				
Autism > Control							
1	-54	-4	6	416	0.016	3.02E-05	Precentral gyrus (BA6)
2	42	-4	58	336	0.015	8.70E-05	Precentral gyrus (BA6)
3				264			Superior temporal gyrus (BA41)
	60	-22	2		0.016	3.70E-05	
4	56	-50	22	264	0.016	2.77E-05	Supramarginal gyrus (BA40)
5	-18	-82	26	248	0.016	3.83E-05	Occipital gyrus (BA18)
6	-22	-92	18	216	0.015	4.58E-05	Occipital gyrus (BA18)
7	16	18	12	160	0.016	3.83E-05	Caudate
8	-34	-34	22	160	0.014	1.79E-04	Insula (BA13)
9	48	-20	38	160	0.014	1.50E-04	Postcentral gyrus (BA2)
10				152			Superior temporal gyrus (BA22)
	-54	-26	2		0.012	3.88E-04	
11				128			Superior temporal gyrus (BA22)
	-46	-54	22		0.013	2.03E-04	
Control > Autism							
1	50	2	26	696	0.024	2.02E-07	Precentral gyrus (BA6)
2	0	24	40	328	0.016	6.93E-05	Cingulate gyrus (BA32)
3	38	10	-2	312	0.016	7.82E-05	Clastrum
4	-2	-60	40	304	0.018	2.00E-05	Precuneus (BA7)
5	-48	-24	54	264	0.015	9.00E-05	Postcentral gyrus (BA9)
6	36	46	28	184	0.015	1.32E-04	Middle frontal gyrus (BA9)
7	-42	20	34	152	0.015	1.20E-04	Precentral gyrus (BA9)
8	-2	36	30	136	0.015	9.44E-05	Frontomedial gyrus (BA6)
9	32	-42	-24	112	0.014	1.78E-04	Culmen
10	2	20	54	112	0.014	2.73E-04	Superior frontal gyrus(BA6)

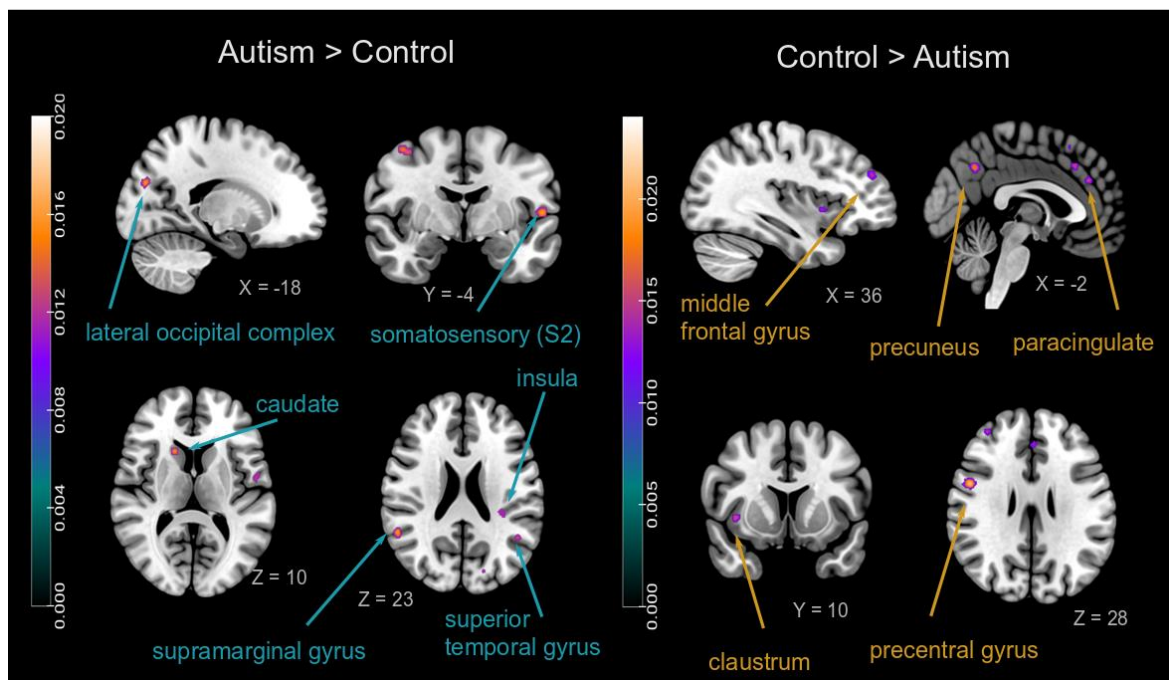
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850 **Supplementary Table S2.** Uncorrected ALE results of visual processing studies

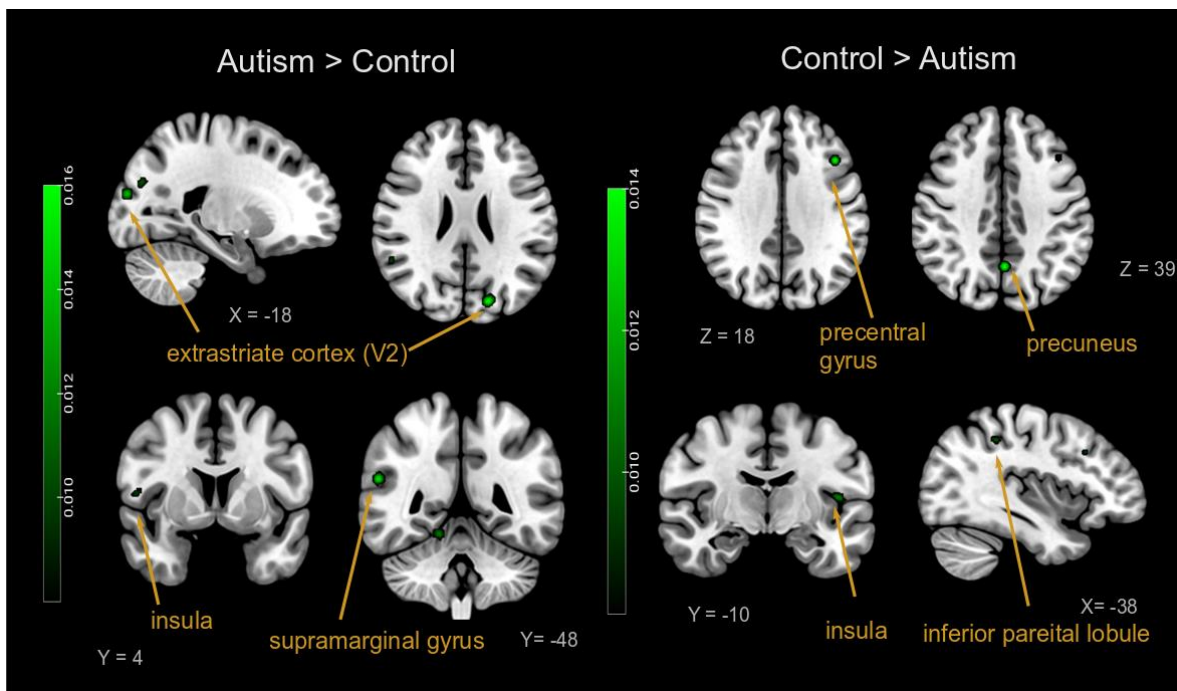
Cluster	MNI Coordinates			Cluster volume mm ³	ALE value	P Value	Label
	X	Y	Z				
Autism > Control							
1	-18	-82	26	728	0.016	1.49E-05	Occipital gyrus (BA18)
2	56	-48	22	424	0.015	7.98E-05	Supramarginal gyrus (BA40)
3	14	-46	14	384	0.013	6.51E-05	Culmen
4	-22	-90	20	384	0.013	9.01E-05	Occipital gyrus (BA18)
5	2	-16	50	208	0.010	1.62E-05	Frontomedial gyrus (BA6)
6	52	4	10	104	0.009	2.58E-05	Insula (BA13)
Control > Autism							
1	-42	2	26	416	0.024	2.45E-08	Precentral gyrus (BA9)
2	-2	46	28	416	0.015	2.85E-05	Precuneus (BA7)
3	50	42	16	336	0.013	1.24E-04	Precentral gyrus (BA6)
4	-46	46	20	256	0.011	3.38E-04	Insula (BA13)
5	-38	-40	44	114	0.010	1.11E-04	Inferior parietal lobule(BA40)

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853 **Supplementary Fig. S1** Uncorrected ALE results of 52 complex perception fMRI studies for
 854 the comparisons *Autism > Control* and *Control > Autism* ($p < 0.001$, min. cluster size 100
 855 mm³). Coordinates are in MNI space. Colour bars represent the ALE values.



856

857 **Supplementary Fig. S2** Uncorrected ALE results of 24 visual processing studies showing
 858 group differences between autism and control participants ($p < 0.001$, min. cluster size 100
 859 mm³). Coordinates are in MNI space. Colour bars represents the ALE values.

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