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Adults with high functioning autism display idiosyncratic behavioral patterns, neural representations and connectivity of the ‘Voice Area’ while judging the appropriateness of emotional vocal reactions

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ABSTRACT

Understanding others in everyday situations requires multiple types of information processing (visual, auditory, higher order...) which implicates the use of multiple neural circuits of the human brain. Here, using a multisensory paradigm we investigate one aspect of social understanding less explored in the literature: instead of focusing on the capacity to infer what a specific person is thinking, we explore here how people with high functioning autism (HFA) and matched controls with typical development (TD) infer the “population thinking”. For this we created an audio-visual ‘social norm inference’ task. Participants were required to imagine how most people would judge the appropriateness of vocal utterances in relation to different emotional visual contexts. Behavioral findings demonstrated that HFA individuals show more interindividual variability in these judgments despite equal within-participant reliability relative to TD. This was also the case for judgements of the valence of these vocalizations when presented in isolation. At the neural level, multivoxel pattern analysis of functional magnetic resonance imaging data revealed strikingly similar neural representations between HFA and TD participants at the group level across different hierarchical levels and neural systems. However, analyses at the individual-participant level revealed that the “Temporal Voice Area” (TVA) shows more interindividual variability in the HFA group, both for neural representations and functional connectivity. Thus, this larger neural idiosyncrasy in a high-level auditory area matches with the larger

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behavioral idiosyncrasy in HFA individuals, when judging auditory valence and its adequacy in different social scenarios. These results suggest that idiosyncrasy in task-relevant sensory areas in HFA participants could underlie their greater difficulties to estimate how others can think.

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1. Introduction

The capacity to understand others, i.e., “mindreading” or Theory of [others’] Mind (ToM) is highly developed in humans. The cognitive and neural basis of ToM has been investigated extensively, but typically focused on the understanding of a specific agent, e.g., one person. This has, for instance, been implemented by paradigms requiring participants to infer mental representations of a person based on facial emotional information, cognitive knowledge about a person (cf. false belief tasks), or verbal descriptions of personality traits (Schurz, Radua, Aichhorn, Richlan, & Perner, 2014). However, much less attention has been devoted to the understanding of how we infer the ‘population mind’. In fact, this type of “theory of population mind” is probably a very prevalent cognitive activity in our daily lives, as we constantly evaluate what ‘others’ would think about our behaviors, decisions or opinions. In other words, we are constantly estimating “social norms”.

Recently, we developed an audio-visual social norm inference paradigm to tackle this issue (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018; Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018). In short, participants watch emotionally evocative pictures and must indicate whether concurrent vocal utterances would be experienced as emotionally congruent or incongruent, according to the perspective of “most people”. We also showed in healthy young adults that performance on this task necessitates to access a shared social norm (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018).

Here we extend this investigation to adults with autism spectrum disorder (ASD), characterized by symptoms in several domains, in particular with regards to social interaction, behavior and communication (American Psychiatric Association, 2013). The deficits can be very specific and subtle, especially in people with high-functioning autism (HFA). In addition, recent studies have shown that samples of individuals with HFA patients are not always characterized by differences at the group level (Bernas et al., 2018), but rather by more idiosyncratic behavioral and neural functioning at the individual level [3–8]. Several theoretical frameworks have been proposed trying to explain the co-occurrence of this wide range of symptoms in ASD, including for instance accounts on theory of mind deficits (Baron-Cohen, 2001), weak central coherence (Happé & Frith, 2006) or prediction abnormalities (Sinha et al., 2014; Van de Cruys et al., 2014).

The characterization of ASD as a disorder that encompasses multiple domains confronts researchers with important challenges when they want to pinpoint the biological

basis of the disorder in general and of particular symptoms. Often, studies focus upon one particular deficit, somewhere along the pathway from sensory processing (Behrmann, Thomas, & Humphreys, 2006) to high-level cognitive processes involved in mentalizing (Koster-Hale, Saxe, Dungan, & Young, 2013; Philip et al., 2012) studying these different levels and systems in a isolate manner. In real-life situations however, social cognition is performed under multisensory scenarios requiring information processing from different senses in parallel, e.g., auditory processing of prosodic information in a given visual context. Further, sensory information is processed at different hierarchical levels (e.g., from low-level luminance detection to high-level object identification) and this sensory information should be related to higher-order cognition to perform social judgements such as judging the adequacy of behaviors. An experimental paradigm that is exclusively tailored towards studying one level in this processing chain, may miss problems at other levels that actually cause the observed differences.

Against this background, our paradigm is particularly relevant to assess social cognition in HFA, given the reported difficulties in other social tasks and given the observed idiosyncrasy in HFA samples. Importantly, the design allows a characterization of the neural content of information processing at multiple perceptual and cognitive levels and modalities (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018). In adults having a typical development (TD) we previously assessed the representational content related to visual, auditory and social congruency processing in a series of visual, auditory and social processing brain areas. In particular, we investigated the quality of neural representations in Early Visual Cortex, Lateral Occipital Complex, Early Auditory Cortex, Temporal Voice Area, Precuneus, Temporal Parietal Junction, and medial Prefrontal Cortex by testing a series of explicit models (related to low-level sensory feature, high-level sensory information, emotional information, etc.) to explain the neural representation patterns in these areas.

In the current study, we use this new paradigm to compare adults with HFA with a matched sample of TD adults at different levels: behavioral responses, brain representations (at multiple levels) and connectivity patterns. This both at the group level and individual level.

We predict to find reduced capacity in HFA to infer social norms, as found in previous behavioral works (Loveland, Pearson, Tunali-Kotoski, Ortegón, & Gibbs, 2001; Nah & Poon, 2011; Tine & Lucariello, 2012) giving us the opportunity to investigate its neural correlates. We also expect to find reduced neural information at the group level in HFA for all hierarchical brain levels, as found when studying these different levels in an isolate manner. Finally, we predict to

observe more unique patterns of brain activity in HFA participants, either globally as recently observed [9,10] or more locally on task-related brain regions.

2. Methods

We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study (Simmons, Nelson, & Simonsohn, 2012). No part of the study procedures or analyses was pre-registered in a time-stamped, institutional registry prior to the research being conducted. Note however that we applied here the same analyses procedure as in previous studies [2, 3], that were themselves preceded by a pilot study with 13 typically developing participants in order to determine the required sample size and how the analysis would be performed (models, GLMs, ROIs, potential use of localizers, etc.). Further, we extend here the individual variability analysis previously performed at the behavioral level in the general population (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018) to the neural level, for two reasons: because we found important group differences in terms of individual variability and also to probe neural idiosyncrasies in HFA as recently reported in the literature (Hahamy, Behrmann, & Malach, 2015; Nunes, Peatfield, Vakorin, & Doesburg, 2018). Functional connectivity analysis was performed in the same way as in previous work from our laboratory (Boets et al., 2013; Bulthé et al., 2019).

2.1. Participants

Forty-eight male participants (24 HFA, 24 TD) were recruited to take part in this study. Based on a previous exploratory pilot study described in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018) the cost-effective sample size was estimated to preferably be of at least 20 participants. Two participants from each group were excluded from analysis: one TD for excessive head movement (see criteria in “data quality check” section), one TD who did not follow the button press instructions correctly, one HFA for excessive anxiety in the scanner (interrupted) and one HFA who presented abnormally enlarged ventricles (which was known by the participant since infancy but was not mentioned during recruitment). The remaining 22 participants in each group were included in the study and analyzed (see Table 1 for participant characteristics and group matching).

Inclusion and exclusion criteria for both groups were established previous to data acquisition. For the HFA group inclusion requested a formal diagnosis of autism spectrum disorder, established by a multidisciplinary team following DSM-IV or DSM-V criteria, for male adults in the 18-35 years old range. Exclusion criteria were the following: presence of comorbid neurological, psychiatric or genetic condition diagnosis (such as epilepsy, traumatic brain injury, attention deficit/hyperactivity disorder, or active depression). They were recruited through the Leuven Autism Expertise Centre and the Psychiatric Clinic at the University Hospitals Leuven. For the TD group, participants were recruited

through online advertising at KU Leuven University and technical schools in Leuven. Inclusion criteria consisted of male adults in the 18-35 years old range. Exclusion criteria were the following: presence for the participants or first degree relatives of a history of neurological, psychiatric, or medical conditions known to affect brain structure or function. A rudimentary screening of autism and depressive symptoms was additionally performed by means of the Social Responsiveness Scale for Adults (SRS-A) (Constantino et al., 2003) and the Beck Depression Inventory (BDI) (Beck, Ward, Mendelson, Mock, & Erbaugh, 1961). None of the participants in both groups took psychotropic medication and all had normal or corrected-to-normal vision. The two groups were matched for gender (all male), age, and IQ, as assessed with the Wechsler Adult Intelligence Scale (WAIS-IV-NL) (Wechsler, 2008). Participants received a financial compensation for their participation. The study was approved (No. S58997) by the Medical Ethics Committee UZ/ KU Leuven University. All participants provided written informed consent prior to scanning.

2.2. Task during the scanner

Participants were lying in the scanner while watching a visual display and hearing auditory input through headphones. They were instructed to imagine they were seeing images (photographs) together with other unknown people. For each image, after a short 600 ms delay, participants hear a vocal reaction (emotional utterance) that could be more or less congruent with the particular scene. The task was to evaluate the congruency of the vocal reaction in relation to the visual context. Yet, they did not have to judge this congruency from their own personal perspective, but they were explicitly instructed to evaluate whether most people would consider this vocal response appropriate or not (i.e., inferring the ‘social norm’) and respond accordingly. The two assigned buttons (congruent vs incongruent) were switched after 3 runs out of 6, and the assigned order was balanced across participants. We have previously validated this task as sensitive to the particular perspective adopted by the participants, with higher inter-participant agreement when adopting the allocentric perspective (i.e., social norm inference task) versus the self-related perspective (see (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018) in open access: <https://www.nature.com/articles/s41598-018-31260-5>).

Table 1 – Groups' matching. The High-Functioning Autism (HFA) group (n = 22) and the Typically Developing (TD) group (n = 22) were matched in terms of Age, Intelligence Quotient (IQ), and Gender (all males). The groups differed in scores of the Social Responsiveness Scale (SRS). Averages (+/- 1 Standard Deviation).

	HFA (22 males)	TD (22 males)	t-statistic	p-value
Age (years)	22.5 (4.09)	22.8 (2.94)	t(42) = .34	p = .74
IQ	108.6 (14.5)	112.4 (15.4)	t(42) = .84	p = .40
SRS	63.0 (13.0)	49.0 (8.0)	t(42) = 4.28	p = .0001

Note. Standard Deviations between parentheses for the second and third columns.

2.2.1. Visual stimuli

Twelve images were selected from the standardized and widely used emotional pictures set IAPS (International Affective Picture System) (Lang, Bradley, & Cuthbert, 2008), based on extreme valence ratings (positive vs negative) and on animacy categorization (animate vs inanimate). The six animate (e.g., humans, animals...) and the six non-animate pictures (e.g., landscapes, objects...) were orthogonal to the image valence, with half of them rated positively (e.g., happy baby), and half of them negatively (e.g., people being threatened with a gun). Based upon the quality of the brain responses evoked by a larger dataset of 24 IAPS images present in a pilot fMRI study [described in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018)], this final set of 12 images was selected: numbered 2341, 1710, 1750, 5760, 5825, 7492, 3530, 1300, 1930, 9290, 9300, 9301 in

the IAPS database (see Fig. 1 for illustration; note that IAPS policy requests to not publish the original images).

2.2.2. Auditory stimuli

Eight different non-verbal vocal utterances were used, inspired by previous work on universal (cross-cultural) emotional vocal expressions (Sauter, Eisner, Ekman, & Scott, 2010). The utterances express four different emotional reactions that could be more or less congruent with the pictures previously selected. Utterances expressing disgust, fear, admiration and cuteness, were recorded in an expressive but still natural manner (not an exaggerated caricature). Each emotional vocalization was performed by one male and one female actor. They were recorded in a sound-proof room at 96 kHz sampling rate and 32-bit resolution, and were down-

Fig. 1 – Experimental Design. A) *Audio-Visual stimuli combinations.* Visual images were combined with auditory stimuli (vocal utterances), simulating social reactions for different scenarios. F = female voice; M = male voice. B) *Experimental trials.* Participants were asked to judge the appropriateness of the social reactions (vocal utterances), responding ‘congruent’ or ‘incongruent’ with assigned buttons. Importantly, they were explicitly instructed not to use their own personal opinion (self-reference) but to infer what most of people would answer and to respond accordingly. To mimic a natural timing of social reactions, vocal utterances started .6 s after the visual scene. Respecting the IAPS (International Affective Picture System) policy, the images presented are not the original ones.

sampled to 44 kHz and 16-bit mono-recordings to reduce the size of the audio files. All stimuli had a fixed duration of 700 ms and an equivalent total Root Mean Square (RMS) power ($-17.4 \pm .17$ dB). Stimuli were then processed in Cool Edit Pro software and Adobe Audition CC 2015 software. Identical 600 ms silent periods were added before the onset of each auditory stimulus to create a natural delay from the visual stimulus onset, and a 100 ms silent period was added after the end of the utterance to provide stable ending transitions.

The aforementioned pilot fMRI study aided us in determining the low-level auditory features that had to be controlled for, such as the duration and sound level, which very much determined responses in early auditory areas. Stimuli can be found here (<https://osf.io/hgyzf/>).

2.3. Experimental runs

The fMRI session consisted of 6 runs, with 96 pseudo-randomly presented experimental trials, i.e., all 12 visual stimuli paired with all 8 auditory stimuli, to make the design orthogonal for each sensory dimension (Fig. 1A). Additionally, 10 silent fixation trials were included among them, as well as 3 initial and 3 final dummy trials, making a total of 112 trials per run, each lasting 4.5 s (total duration of the run = 504 s). Each experimental trial started with a visual image for 2.5 s during which an auditory utterance was played via headphones (from .6 to 1.3 s) to simulate a natural delay before the vocal reaction. A 2 s fixation cross was then displayed until the end of the trial (Fig. 1B). Participants could respond any time within the trial and were instructed to press the buttons as soon as they knew the answer.

2.4. fMRI data acquisition

Imaging data were acquired using a 3T Philips Ingenia CX scanner (Department of Radiology of the University of Leuven) with a 32-channel head coil. Each functional run consisted of T2*-weighted echoplanar images (EPis), with voxel size = $2.2 \times 2.2 \times 2.7$ mm, interslice gap .2 mm, TR = 2550 ms, TE = 30 ms, matrix = 84×82 , 45 slices, field of view (FOV) = $211 \times 211 \times 121$. In addition to the functional images we collected a high-resolution T1-weighted anatomical scan for each participant (182 slices, voxel size = $.98 \times .98 \times 1.2$ mm, TR = 9.6 ms, TE = 4.6 ms, 256×256 acquisition matrix). Stimuli were presented using Psychtoolbox 3 (Brainard, 1997). Visual stimuli were displayed via an NEC projector with a NP21LP lamp that projected the image on a screen the participant viewed through a mirror. Viewing distance was approximately 64 cm. Auditory stimuli were presented diotically at a comfortable hearing level using a customized air-conduction sound delivery system (MR Confon Audio Amplifier mkII). The headphones attenuated the surrounding scanning noise with about 30–40 dB SPL along the .1–10.0 kHz domain.

2.5. fMRI preprocessing

Imaging data were preprocessed and analyzed using the Statistical Parametrical Mapping software package (SPM 8, Wellcome Department of Cognitive Neurology, London, UK) and MATLAB. Functional images underwent slice timing

correction (ascending order; first image as reference), motion correction (3rd degree spline interpolation), co-registration (anatomical to functional images; mean functional image as reference), and spatial normalization to the standard MNI (Montreal Neurological Institute) brain space. Functional images were spatially smoothed by about twice the voxel size by convolution of a Gaussian kernel of 5 mm full-width at half-maximum (Op de Beeck, 2010).

2.6. General linear models (GLMs)

In our earlier work (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018) we determined using a pilot study the most appropriate statistical approach to analyze the data, the here described approach with three separate GLMs (visual, auditory, congruency), versus a “full-GLM” modeling approach with the 96 Audio-Visual (A-V) combinations of conditions, with each trial modeled as an event. Although both approaches provided a very similar pattern of results, the full-GLM approach seemed to result in less stable results with a lower Signal-to-Noise Ratio (SNR), possibly because each A-V combination only had a single presentation per run. Moreover, by creating separate GLMs we could use more precise onsets and durations of each processing involved (visual, auditory and social congruency processing). Based on these considerations, the main experiment was analyzed with three separate GLMs. The GLMs modeled the pre-processed data for each voxel and participant. The GLMs included regressors for each experimental condition per run, as well as the 6 motion correction parameters (translations and rotations). Each predictor's time course was convolved with the canonical hemodynamic response function (HRF) in SPM. The experimental conditions were different in the three GLMs. First, in the visual GLM, the 12 visual stimuli were included as conditions, with onsets and duration corresponding to the visual presentation time (i.e., from 0 to 2.5 s). Second, the auditory GLM contained the 8 auditory stimulus conditions, considering the auditory presentation time (from .6 to 1.3 s). Third, the social congruency GLM had two conditions (congruent vs incongruent) based on cross-modal valence congruency (e.g., a positive image combined with a negative utterance is considered ‘incongruent’). This approach guaranteed a perfect balance between ‘congruent’ and ‘incongruent’ conditions, while avoiding potential visual or auditory biases, because all visual and auditory stimuli occur an equal number of times for congruent and incongruent trials. As we used extreme ends of the valence continuum (very positive or very negative), both for the visual and auditory domains, this social congruency criterion reflected quite well the participants' responses. The two social congruency conditions were modeled in relation to the time-window during which social congruency judgements could be performed, i.e., from the beginning of the auditory presentation (6 s from trial onset) until the end of the trial (4.5 s).

2.7. Regions of interest (ROIs)

We included the same ROIs as in our previous studies with this paradigm (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018; Pegado, Hendriks, Amelynck,

Fig. 2 – Behavioral Results (left = TD group; right = HFA group). **A)** Similarity of *visual* valence ratings across participants. Visual valence ratings were performed with unisensory presentations, outside the scanner, using a 9 level scale. The visual ratings were highly similar (i.e., high correlation of dissimilarity matrices for pairwise visual stimuli) across participants both within and across groups, but a statistically group difference could be noticed with HFA participants showing more idiosyncrasy than TD participants ($T(42) = -2.83$; $p = .007$). **B)** Similarity of *auditory* valence ratings across participants. Same procedure as used previously for visual stimuli. A greater idiosyncrasy (lower between-participant correlations) in the auditory valence ratings was observed in the HFA group relative to TD group ($T(42) = -4.78$; $p < .0001$). **C)** Similarity of

Daniels, Bulthé, Masson, et al., 2018). These ROIs were selected based on the literature, restricted to key brain regions involved in visual, auditory and social inference processing. While considering the hierarchical organization of these three neural systems, we included low- and high-level visual and auditory areas, and the higher-order mentalizing network. In order to avoid the use of additional localizers runs, as recommended by a pilot study [briefly reported in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018)], we used independent ROI masks normalized to MNI space, using either the anatomical atlas WFU PickAtlas Toolbox (Wake Forrest University PickAtlas, <http://fmri.wfubmc.edu/cms/software>) or functional parcels from other laboratories (see below). These independent masks were combined (by means of a conjunction analysis) with individual functional data that specify voxels modulated by our task: the F-contrast of all task trials against fixation trials (implicitly modeled), at a threshold of .0001 (uncorrected for multiple comparisons), using a separate 'neutral GLM' where all task trials were modeled as a single condition. ROIs with at least 20 active voxels were included. If a given participant ROI did not meet this criterion, his data was not used in the group analysis for this ROI.

For sensory processing, a *low level visual ROI* (Early Visual Cortex-EVC) was defined based on Brodman's areas (BA) 17 and 18. As a *high-level visual ROI*, a functional parcel of the Lateral Occipital Complex (LOC) from the Kanwisher lab was used (Julian, Fedorenko, Webster, & Kanwisher, 2012). The *low-level auditory ROI* (Early Auditory Cortex- EAC) was composed by BA 41 and 42. The *high-level auditory ROI* was based upon the "Temporal Voice Area"- TVA probabilistic map from Belin's lab (Pernet et al., 2015) concerning more than 200 participants, available at neurovault (<http://neurovault.org/collections/33/>). For *higher-order cognition ROIs*, since we used a mentalizing task we targeted the mentalizing neural network: medial Prefrontal Cortex (mPFC) [anterior and posterior parts], Temporo-Parietal Junction (TPJ) and Precuneus (PC) (Schurz et al., 2014). The use of separate ROIs instead of a whole ToM network was preferred because it could reveal differences between groups in specific parts of this ToM network, e.g., anterior vs posterior mPFC. Note that these regions are also known to process representations of emotions and valence in both visual and auditory modalities (Klasen, Kenworthy, Mathiak, Kircher, & Mathiak, 2011; Peelen, Atkinson, & Vuilleumier, 2010). Following the same approach as a recent meta-analysis of different mentalizing tasks (Schurz et al., 2014), we used the same parcels that were obtained in previous functional connectivity studies, both for mPFC (Sallet et al., 2013) and TPJ (Mars et al., 2011). Note that only right hemisphere parcels are available and thus only right TPJ and mPFC ROIs were used, but as ToM studies tend to find effects on the right hemisphere or bilaterally, this should not be of great concern (see the ToM meta-analysis [1] and our

previous studies on general population [2, 3]). Further, as we did not have particular hypotheses for the two subdivisions of TPJ (anterior and posterior parcels) we grouped them together in a single ROI. In contrast, for the mPFC, we kept this distinction as the literature shows a clear functional dissociation between anterior vs posterior parts for self-related vs others-related mentalizing processes respectively (Denny, Kober, Wager, & Ochsner, 2012; Mitchell, Macrae, & Banaji, 2006; Saxe, Moran, Scholz, & Gabrieli, 2006; Sul et al., 2015), by integrating the four original parcels into two. Finally, for PC, we used the anatomical mask in WFU PickAtlas (SPM). Given its role in emotion processing, an amygdala ROI was initially included (using anatomical atlas) in the analysis of the pilot fMRI experiment. Yet, as it did not show detectable information in any dimension, it was not included here.

Two ROIs (EVC and EAC) presented very thin configurations. This would lead to unrealistic delimitations of early processing cortex given the spatial uncertainty involved when comparing brains across participants. We thus enlarged by 1 voxel in all three directions. Next, to ensure that no overlap occurs between ROIs, we visually inspected the ROI borders of each ROI pair. As a first measure, we restricted the TVA probabilistic map to the most significant voxels by imposing an arbitrary threshold of $t = 50$, which restricted the ROI to its classical temporal cortex disposition and reduced considerably its overlap with other regions (e.g., TPJ). The resulting map was then transformed in a binary mask. As an additional measure, for this and all the other ROIs (all binary masks), we excluded the remaining overlapping voxels from the largest ROI of each pair. Only the following ROI intersections presented some overlap: EVC x LOC, EVC x PC, EAC x TVA, EAC x TPJ and TVA x TPJ (the first of each pair being the largest one). This procedure ensured a complete separation of the ROIs, without impacting upon their original spatial configuration. Note that all these procedures to define ROIs were exactly the same in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018; Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018).

2.8. Data quality check

2.8.1. No group differences in head movement

In order to ensure data quality and to rule out a potential confounding in group differences, motion during scanning was carefully evaluated and runs with excessive motion were removed from all analyses. Two different motion criteria were used. Runs were discarded when a movement of more than one voxel size ($= 2.2$ mm) in either direction on two consecutive scans was noticed. Runs were also removed when the Euclidean distance measure (additive measure of the amount of motion in all directions from one time point to another) exceeded one voxel size. For two HFA participants we excluded 1 and 2 runs respectively. For the TD participants we

behavioral responses during the social norm inference task inside the scanner (congruency judgements), across participants and runs. The two groups show equivalent individual consistency of responses (i.e., within-participant correlations) across the six runs (squares on the diagonal): $T(42) = -.59$; $p = .56$. In contrast, for between-participant correlations, the HFA group show significantly higher idiosyncrasy across participants ($T(42) = -2.62$; $p = .01$; see Results for details).

did not have to exclude any run. For the remaining data, no group differences were found for head movements in the Euclidean distance (.287 mm vs .431 mm; $T(42) = -1.46$; $p = .153$). Note that the functional connectivity analysis, which has been shown to be particularly sensitive to even minor amounts of the participant motion, included the recommended analysis step of data scrubbing (Power, Barnes, Snyder, Schlaggar, & Petersen, 2012).

2.9. Univariate analysis

Correlations between activity patterns (MVPA) are not necessarily related to overall differences in activity level between conditions (univariate analysis). Nevertheless, it is relevant to know whether MVPA findings are found in the context of effects that can also be picked up by a univariate voxel-level difference in activity (FWE corrected at $p < .05$).

2.9.1. Neutral GLM

The contrast of all stimuli minus fixation broadly activates the visual, auditory and motor cortex, and parietal and posterior mPFC cortex. Importantly, no group differences were found, which reflects a lack of a general brain response differences. Thus, further differences cannot be attributed to a general response difference. The same result was found using visual and auditory GLMs in this general all minus fixation contrast.

2.9.2. Visual GLM

Negative > positive images increased activity in high-level visual cortex bilaterally (temporal ventral and occipital lateral cortex) in both groups, with no group differences, while the contrast in the opposite direction did not elicit significant activations. This pattern of results could be due to the relative arousal effect of negative images. Further, animate vs inanimate contrasts activate again the same visual temporo-occipital regions but with different topographical distribution: while the inanimate > animate contrast shows higher activity in more medial temporal cortex (encompassing the Parahippocampal place area), the animate > inanimate contrast shows more lateral fusiform gyrus activity (encompassing the Face Fusiform Area- FFA) in both groups (no group differences).

2.9.3. Audio GLM

For positive vs negative stimuli contrasts (both directions), no statistically significant effect was found in neither group. Female > male voices evoked very restricted activations (7 voxels in controls and 9 voxels in ASD) in the left auditory cortex (no group differences), but the opposite contrast did not show significant results.

2.9.4. Congruency GLM

The congruent > incongruent contrast elicits activations in a restricted area (37 voxels) on right parietal cortex for TD group only, but no group differences is found. In contrast, the incongruent > congruent contrast (i.e., unexpected vs. expected social responses) leads to increased activity in right caudate nucleus in both groups (no group differences), a region involved

in several aspects of motor and action planning, including inhibitory control.

The limited sensitivity of the univariate analyses is overcome by pursuing a correlational MVPA approach, which allows us to capture the richness of multiple neural representations.

2.10. Multivoxel pattern analysis

We used correlation-based multivoxel pattern analysis (MVPA) to explore how the spatial response pattern in individual ROIs differs between experimental conditions (Haxby et al., 2001), closely following the methodology used before (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018; Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018). For each GLM and participant, we extracted the parameter estimates (betas) for each condition (relative to baseline) in each voxel of the ROIs. These obtained values for each run were then normalized by subtracting the mean response across all conditions (for each voxel and run separately). The full dataset (6 runs) was randomly divided into two independent subsets of 3 runs (using 'randperm' function in matlab). The multivoxel patterns of activity associated with each condition in set 1 (runs averaged) were correlated pairwise with the activity patterns in set 2 (runs averaged) by using the 'corrcoef' function in matlab (Pearson's r correlation coefficient). This procedure of splitting the data in two parts followed by correlating the multi-voxel patterns was repeated 100 times. The final neural similarity matrix for each ROI was obtained by averaging these 100 matrices. Representational Similarity Analysis (RSA) (Kriegeskorte, Mur, & Bandettini, 2008) could then be used to estimate the informational content in the neural matrices. The matrix size varied as a function of the GLM: 12×12 for visual, 8×8 for auditory and 2×2 for social congruency GLMs.

2.11. Statistical analysis pipeline

We compared the data of the two groups (using two-sample t -tests) in a hierarchical step-by-step way: 1) Which regions contain information of a given dimension? 2) What kind of representation do they contain? 3) How is the connectivity between the brain regions? 4) How similar or idiosyncratic are the results across participants in each level of analysis (level of information, representation and connectivity)?

1) *Selection of informative ROIs.* To test whether a certain region contained information about a given dimension (visual, auditory, or social congruency), we applied the following procedure. First, we calculated for each ROI, the mean correlations in the diagonal (identical pairs) and non-diagonal cells (different pairs) of the neural similarity matrix. Then, we performed a two sample two-tailed t -test across participants for diagonal vs non-diagonal mean correlations. This procedure is based on the fact that the same condition will typically show higher similarity across runs with itself relative to different conditions [i.e., higher correlations for diagonal vs non-diagonal cells (Ritchie, Bracci, & Op de Beeck, 2017)]. Lastly, a Bonferroni

Fig. 3 – Visual neural representations. A) Structure of neural similarity matrices for the visual GLM. B) Quantity of visual information. For each ROI, the quantity of neural information was calculated by using the correlational MVPA results for the same condition (Pearson's r same) minus that for different conditions (r different). * $p < .05$; ** $p < .01$; *** $p < .001$ (Bonferroni-corrected). No group difference was found for none of the regions (see Results). C) Quality of visual information. To evaluate the kind of neural representation in each visually informative brain region (i.e., showing significant visual information), neural similarity matrices were compared with plausible explicit models (pix = pixel wise model; lux = luminance model; anim = animacy model; val = valence model [visual]) and partial correlations with models were performed. The two groups show equivalent neural representations in all ROIs but in PC where the HFA group data was more significantly explained by (partial correlations) a low level model (the pixel wise model). Error bars represent ± 1 Standard Error of the Mean. * $p < .05$; ** $p < .01$; *** $p < .001$ (Bonferroni-corrected). Dashed lines represent the averaged between-participant correlations of neural matrices for each group (same color code).

correction for multiple comparisons (i.e., the number of ROIs) was applied. Results from this analysis are shown in Figs. 3B and 4B.

- 2) Comparing neural representations with theoretical models or behavioral data. For each ROI containing information of a given dimension (i.e., significant t-test in the previous step) we compared the neural similarity matrices with similarity matrices of explicit models, to understand the kind of representational content that is hosted by each ROI. In order to avoid the influence of the correlation of each

stimulus with itself (diagonal cells) we only included the non-diagonal cells, averaging upper and lower triangles of the neural similarity matrix. This final vector was used in all further representational analyses. Each theoretically-relevant model targeted a specific parameter of the stimulus set, i.e., the visual, auditory and congruency aspect. These parameters were compared between all pairs of conditions, leading to 12×12 visual or 8×8 auditory similarity matrices for each model. As the social congruency dimension could only generate 2×2 matrices, we

Fig. 4 – Auditory neural representations. The same procedure as in Fig. 2 was used to evaluate the neural activity (quantity and quality) but here for the auditory modality. A) Structure of neural similarity matrices for the auditory GLM. B) Quantity of auditory information (see Fig. 2 caption). C) Quality of auditory information (see Fig. 2 caption). The two groups show equivalent neural activity in all ROIs. * $p < .05$ (Bonferroni-corrected). Error bars represent ± 1 Standard Error of the Mean. Dashed lines represent the averaged between-participant correlations of neural matrices (note the relatively higher between participant correlations for the TD group in TVA). FO = Fundamental Frequency model; val = valence model [auditory]; emo = emotion (of utterances) model; gen = gender (of the voice) model.

Fig. 5 – Similarity of neural representations across participants. Left: Visual Neural Representations; Right: Auditory Neural Representations. For each ROI, neural similarity matrices of each participant were compared with all of the other group peers and the average of these between-participant correlations was obtained as an index of neural similarity. Only TVA showed significant group differences in neural idiosyncrasy, with HFA exhibiting lower between-participants similarity (Pearson's correlations). Error bars represent ± 1 Standard Error of the Mean.

could not build models to investigate specific neural patterns.

2.11.1. Visual Models

Four visual models were included for the RSA in this study (Fig. 3B in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018) in open access <https://www.frontiersin.org/articles/10.3389/fnhum.2018.00153/full>). 1) a pixelwise model: based on pixel values of each visual stimulus; 2) a luminance model: based on mean luminance values; 3) a visual valence model: based on all participants' (across both groups) average ratings of valence (1–9 level) obtained outside the scanner; 4) an animacy model: a binary model based on animacy of the images (animate vs inanimate). Results from this analysis are shown in Fig. 3C. The models were built to test different information content in each ROI, some related to low-level aspects (e.g., luminance) others related to more high-level aspects (e.g., animacy). The choice of the four visual models was restricted by relevance and feasibility to build these models, i.e., based on features of the stimuli that could be measured/classified and on the sensitivity of the models observed in a previous pilot study (briefly reported in [2]).

2.11.2. Auditory Models

We also included four auditory models for RSA purposes [Fig. 4B in (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018)]. 1) a fundamental frequency (F0) model: based on the fundamental frequency of the audio stimuli; 2) an auditory valence model: based on all participants' (across both groups) average valence ratings obtained outside the scanner; 3) an utterance emotion model: based on the four emotions conveyed by the utterances (fear, disgust, admiration and cuteness-like expressions); 4) a voice gender model: based on the gender of the voice. Results from this analysis are shown in Fig. 4C. Again, the models included here were restricted by relevance and feasibility.

To capture the specific contribution of each model explaining the neural pattern, we used partial correlation analysis, instead of simple correlations. This is particularly important when some models correlate with each other.

3) *Functional Connectivity analysis.* In order to probe group differences as reported in the literature, Functional Connectivity (FC) analysis was performed on functional fMRI data during the task, while regressing out the task-based activity. We used the neutral GLM (all conditions vs. fixation) to analyze the functional connectivity between the ROIs. Two TD participants and 4 HFA participants were excluded from this analysis as they did not meet the criteria for at least one ROI, i.e., 20 active voxels (see previous method section). The following parameters were applied: (1) bandpass filtering between .004 and .15 Hz (Balsters, Mantini, Apps, Eickhoff, & Wenderoth, 2016; Baria et al., 2013); (2) regression of head motion parameters and their first derivatives; (3) regression of task-related BOLD fluctuations (all minus fixation) (Boets et al., 2013; Ebisch et al., 2013); (4) scrubbing of motion-affected functional volumes

(Power et al., 2012); and (5) no spatial smoothing. The eight ROI inclusive masks were included as seed ROIs for the functional connectivity analysis. We obtained a representative BOLD time course for each ROI by averaging the time courses of the voxels within the ROI. For each participant, we then created a functional connectivity matrix by calculating Pearson cross-correlations between the BOLD time courses of each pair of ROIs. After converting the single-participant matrices to Z-scores with the Fisher's r -to-Z transformation, we calculated a group level matrix by conducting a random effects analysis across participants ($pFDR < .001$). Group-level comparisons among functional connectivity scores were performed by calculating independent-sample t tests on the Z-score matrices ($pFDR < .05$). Results from this analysis are shown in Fig. 6A.

4) *Similarity across participants.* Finally, for each of the previous analysis, we complemented the group differences approach with a single-participant approach by testing the reproducibility of results across participants within each group. We investigated participants' similarity for information level, neural representations and functional connectivity. For this, we used the neural data (i.e., diagonal vs non-diagonal, neural similarity matrices and functional connectivity matrices respectively) of each participant and correlated it (pearson's r) with the neural data matrices of all other individuals from the same group to calculate an overall 'similarity' index. Then, to check if inter-participant similarity of neural data in one group was greater than in the other group, we compared the correlation coefficients of participants from the two groups using two sample t -test statistics. Results from these analyses are shown in Figs. 5 and 6B-C.

2.12. Outside the scanner

2.12.1. Visual and auditory valence ratings

Before scanning, participants performed valence rating judgments for the stimuli of each modality (visual and audio) separately, using a 9-level scale. Note that the behavioral ratings were performed in just a few minutes (one single rating per item, i.e., 12 items in the visual modality and 8 in the auditory modality). Thus, it is unlikely that we have introduced fatigue effects with 20 trials. Instead, this single presentation of each item helped the participants to be familiarized with the stimuli used during the fMRI runs, avoiding surprise and facilitating the accurate judgement between the visual and auditory stimuli, from the beginning of the 1st run. Further, it gave us the opportunity to build models of the participant's perceived valence.

2.12.2. Congruency ratings with a 9-level rating scale

Participants additionally performed two runs of the main task (as inside the scanning) but instead of binary responses (congruent vs incongruent) they used 9-level scale ratings for social norm inferences, one run before and one after the fMRI. Beyond the familiarization with the task, this was used to check the similarity of response patterns within and between participants, in a more fine-grained way.

A) Strength of the Functional Connectivity across ROIs

B) Similarity of the Global Pattern of Functional connectivity across subjects

C) Similarity of the TVA connectivity pattern across subjects

Fig. 6 – Functional Connectivity (Left = TD group; Right = HFA group). A) Strength of the Functional Connectivity across ROIs. B) Similarity of the Global Pattern of Functional connectivity across participants. C) Similarity of the TVA connectivity pattern across participants. Note that HFA exhibit more idiosyncratic connections than TD (i.e., lower between-participant correlations).

2.12.3. Questionnaires

The Social Responsiveness Scale (SRS) (Constantino et al., 2003) was applied as a measure of social skills. It comprises 64 items covering subscales for social communication and interaction and for restricted and repetitive patterns of behavior and interests. A higher total score indicates a higher presence of quantitative autism traits.

The Beck Depression Inventory (BDI) (Beck et al., 1961) was applied as a screening for major depression.

3. Results

3.1. Groups matching

Table 1 shows that the groups match for gender (all males), age and full-scale IQ (Intellectual Quotient). As expected, the two groups differ on the Social Responsiveness Scale (SRS). Nevertheless, the average SRS score of the HFA sample is not very high, which indicates not very high social difficulties. Further, most of the HFA participants were socially active, were studying or had a job. Our sample represents thus a population of people with autism presenting a high level of social functioning.

3.2. Behavioral results

3.2.1. Unisensory valence ratings

In separate runs prior to the scanning session, valence ratings (1–9) were attributed to each visual and auditory stimulus presented in isolation. In general, participants (from both groups) showed a higher degree of agreement (between-participants Pearson's correlations) for the rating of visual stimuli valence ($r = .78 \pm .02$) than for auditory stimuli valence ($r = .47 \pm .17$). This significant difference ($T(43) = -12.7$; $p < .0001$) indicates more ambiguity in the perception of auditory than visual valences. Comparing groups, for valence ratings, in the visual modality, both groups show high consistency in valence ratings, but HFA exhibit slightly more idiosyncrasies (i.e., lower between-participant correlations) than TD (respectively, $r = .771 \pm .03$ vs $r = .790 \pm .02$; $T(42) = -2.83$; $p = .007$; Fig. 2A). In the auditory modality, HFA show clearly more idiosyncrasy than matched TD (respectively, $r = .371 \pm .13$ vs $.569 \pm .14$; $T(42) = -4.78$; $p < .0001$; Fig. 2B).

3.2.2. Task inside the scanner

The task used during scanning was to estimate how most people would judge the congruency between the visual and auditory stimuli and respond accordingly. The agreement between participants indexed by the correlation of response patterns across participants, (i.e., correlation of individual dissimilarity response matrix for pairwise conditions) can be used as an indication of participants' capacity to infer the social norm (how their peers responded). This reasoning is supported by our earlier report showing higher between-participant correlations when participants are required to respond according to the social norm (i.e., as most people would; the current task) than when they are asked to follow their own personal congruence estimate (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018). Note also that for this task we have multiple measurements, one for

each run, and the within-participant correlation across runs reflects the internal consistency or SNR (Signal-to-Noise Ratio). Fig. 2C show the similarity of response patterns across runs, both within (diagonal squares; 6 lines [one for each run] for each participant) and between-participants for the TD (left) and HFA (right) participants. The two groups exhibited equivalent within-participant correlations across the six runs (TD: $r = .51 \pm .15$; ASD: $r = .54 \pm .19$; $T(42) = -.59$; $p = .56$), indicating a consistent within-participant test-retest reliability. In contrast, the two groups differ in between-participants correlations, i.e., the averaged correlation of response patterns of one participant with each other participant from the group (TD: $r = .26 \pm .07$; ASD: $r = .19 \pm .08$; $T(42) = 2.62$; $p = .01$), indicating a better agreement about the social norm among peers in the TD group.

3.2.3. Task outside the scanner

Very similar results were obtained for the equivalent task performed outside the scan (one block before and one block after scanning), when participants rated the congruency on a 9-level scale (instead of binary congruency decisions). Again, no group differences were found for within-participant correlations (TD: $r = .63 \pm .15$; ASD: $r = .58 \pm .15$; $T(36) = 1.15$; $p = .26$) but a significant group difference was noticed for between-participants correlations (TD: $r = .50 \pm .07$; ASD: $r = .42 \pm .08$; $T(42) = 3.90$; $p = .0003$) replicating the better agreement between TD participants about social norms found inside the scanner.

3.3. fMRI MVPA results

3.3.1. Quantity of neural information

As previously (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018; Pegado, Hendriks, Amelynck, Daniels, Bulthé, Masson, et al., 2018), we first investigated which brain regions host information in each of the three domains (visual, auditory and congruency). For this, we contrasted the correlation coefficients in diagonal vs non-diagonal cells of neural similarity matrices for each GLM (see methods).

For the visual dimension (Fig. 3A and B), results revealed that several regions contained significant visual information, both for the TD group (all Bonferroni-corrected: EVC = .68; $p < .0001$; LOC = .74; $p < .0001$; TVA = .05; $p = .004$ and PC = .27; $p < .0001$) and HFA group (EVC = .68; $p < .0001$; LOC = .76; $p < .0001$; TPJ = .08; $p = .006$ and PC = .27; $p < .0001$). Importantly, no differences between TD and HFA were observed for any of the regions ($p > .9$ for all).

For the auditory GLM (Fig. 4A and B), the following regions showed significant auditory information in TD group: EAC (.15; $p < .0001$), TVA (.17; $p < .0001$) and TPJ (.08; $p = .029$) and in the HFA group: EAC (.13; $p < .0001$) and TVA (.19; $p < .0001$). Again, no group difference was found ($p > .9$ for all).

For the congruency GLM, no region showed significant information in none of the groups using the same procedure as with the other GLMs. As we have previously found significant congruency information in expected regions of the ToM network (TPJ, PC and pMPFC) in a slightly larger dataset of typically developing participants (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018) we collapsed the three regions here to increase the sensitivity of our analyses. In this post-hoc

analysis, the ToM network showed significant congruency information for both TD ($T(21) = 2.69; p = .014$) and ASD ($T(20) = 2.60; p = .017$). Importantly however, here again, the groups did not differ ($T(41) = .54, p = .59$).

3.3.2. Quality of neural information

To understand the type of representations contained in each informative brain region (identified by the previous quantitative analysis), we compared the neural similarity matrices with plausible explicit models (see Methods). As we did in the past (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018), we used Pearson's partial correlations between neural and model matrices in ROIs that proved informative (see previous section) for at least one of the groups. Note that neural similarity matrices of congruency dimension only had two cells (one value and its mirror negative value) and could therefore not be related to models.

3.3.2.1. VISUAL REPRESENTATIONS. For the visual modality (see Fig. 3C), activity patterns in EVC data were similarly explained in both groups by the low-level feature models (models in Fig. 3 of (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018): <https://www.frontiersin.org/articles/10.3389/fnhum.2018.00153/full>), both the pixelwise model (TD: $r = .11; p < .0001$; HFA: $r = .12; p < .0001$; $T(42) = -.56; p = .58$) and the luminance model (TD: $r = .22; p < .0001$; HFA: $r = .25; p < .0001$; $T(42) = -.65; p = .52$). Further EVC data was also explained by the high-level animacy model (TD: $r = .13; p = .009$; HFA: $r = .15; p = .0004$; $T(42) = -.54; p = .59$), while no effect was found for the visual valence model (TD: $r = -.02; p > .9$; HFA: $r = .01; p > .9$; $T(42) = .32; p = .75$). All partial correlations described are Bonferroni-corrected for the number of models tested.

LOC data was most strongly explained by the animacy model in both groups (TD: $r = .84; p < .0001$; HFA: $r = .85; p < .0001$; $T(42) = -.29; p = .78$), confirming that high-level visual cortex (LOC) made a clear distinction between animate versus inanimate images. The luminance model showed non-significant results in LOC (TD: $r = -.006; p > .9$; HFA: $r = .06; p = .38$; $T(42) = -1.26; p = .21$). As it partially co-varied with the animacy model, the luminance model could have been overshadowed by the substantial amount of variance explained by the animacy model. Further, LOC also represented visual valence (TD: $r = .15; p < .0001$; HFA: $r = .13; p < .0001$; $T(42) = .61; p = .54$) and low level pixelwise features (TD: $r = .08; p < .0001$; HFA: $r = .12; p < .0001$; the latter model presenting a marginally significant group difference ($T(42) = -1.97; p = .06$).

In both groups, Precuneus (PC) exhibited positive partial correlations for luminance (TD: $r = .19; p < .0001$; HFA: $r = .26; p < .0001$; $T(42) = -1.29; p = .21$) and animacy (TD: $r = .18; p = .0002$; HFA: $r = .18; p = .0001$; $T(42) = -.15; p = .88$) but not for valence (TD: $r = .07; p = .10$; HFA: $r = .05; p = .25$; $T(42) = .56; p = .58$). Importantly, while the TD group show no partial correlations in PC with the pixelwise model, the HFA group did, with a significant group difference (TD: $r = -.01; p > .9$; HFA: $r = .06; p = .03$; $T(42) = -2.74; p = .009$). This result suggest more low-level pixelwise information for HFA participants in the higher order area of PC.

TPJ data was significantly explained by the animacy model (TD: $r = .12; p = .003$; HFA: $r = .18; p = .001$; $T(42) = -1.19; p = .24$)

and pixelwise model in HFA group (TD: $r = -.01; p > .9$; HFA: $r = -.04; p = .02$; $T(42) = 1.04; p = .30$). In contrast, luminance and valence models did not explain TPJ data (luminance, TD: $r = -.03; p > .9$; HFA: $r = -.02; p > .9$; $T(42) = .002; p > .9$; valence, TD: $r = .001; p > .9$; HFA: $r = .01; p > .9$; $T(42) = -.22; p > .8$).

Finally, none of our visual models captured the kind of visual information represented in TVA: pixelwise (TD: $r = -.006; p > .9$; HFA: $r = .004; p > .9$; $T(42) = -.30; p = .76$), luminance (TD: $r = .015; p > .9$; HFA: $r = -.03; p = .65$; $T(42) = 1.34; p = .19$); valence (TD: $r = .08; p = .13$; HFA: $r = .01; p > .9$; $T(42) = 1.64; p = .11$), animacy (TD: $r = .06; p = .59$; HFA: $r = .08; p = .21$; $T(42) = -.30; p = .77$). Note that for TVA, the between-participant correlations (horizontal dashed line in Fig. 3) for the visual dimension was very low in both groups. Note also that in some cases the dashed lines of both groups overlap.

3.3.2.2. AUDITORY REPRESENTATIONS. In the auditory modality, partial correlations with the explicit auditory models (see models in Fig. 4 of (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018): <https://www.frontiersin.org/articles/10.3389/fnhum.2018.00153/full>) revealed that none of the models significantly explain the EAC data in both groups: F0 model (TD: $r = .08; p = .25$; HFA: $r = .04; p > .9$; $T(42) = .83; p = .41$), valence model (TD: $r = -.04; p > .9$; HFA: $r = .07; p = .51$; $T(42) = -1.51; p = .13$), emotion model (TD: $r = .14; p = .07$; HFA: $r = .06; p = .49$; $T(42) = 1.1; p = .28$), voice gender model (TD: $r = .008; p > .9$; HFA: $r = .04; p > .9$; $T(42) = -.53; p = .6$). The emotion model was found to explain data in TVA, with a significant group difference (TD: $r = .21; p = .001$; HFA: $r = .11; p = .02$; $T(42) = 1.85; p = .07$). It is worth noting that we did quite some effort to equate stimuli on various low-level dimensions. We did not do this to the same extent in a previously reported pilot experiment (Pegado, Hendriks, Amelynck, Daniels, Bulthé, Lee Masson, et al., 2018), where stimuli varied in sound duration and RMS power, which resulted in much stronger auditory representations in EAC. All the other models did not demonstrate an effect in TVA: the F0 model (TD: $r = .07; p = .16$; HFA: $r = .04; p > .9$; $T(42) = .7; p = .47$), the auditory valence model (TD: $r = -.09; p = .4$; HFA: $r = -.04; T(42) = -.98; p = .33$) and the voice gender model (TD: $r = -.03; p > .9$; HFA: $r = .04; p > .9$; $T(42) = -1.30; p = .20$; Fig. 4C).

Also for TPJ, utterance emotion was the model explaining most of the variance but did not reach significance: F0 (TD: $r = .09; p = .13$; HFA: $r = -.01; p > .9$; however the groups show a difference here: $T(42) = 2.04; p = .04$), auditory valence (TD: $r = .03; p > .9$; HFA: $r = .02; p > .9$; $T(42) = -.16; p = .88$), utterance emotion (TD: $r = .03; p > .9$; HFA: $r = .01; p > .9$; $T(42) = .74; p = .46$), voice gender (TD: $r = -.05; p > .8$; HFA: $r = -.05; p > .9$; $T(42) = 1.0; p = .31$). Note the lower between-participant correlations (dashed horizontal lines) for both EAC and TPJ relative to TVA in Fig. 4.

Thus, in both modalities, the groups essentially show equivalent neural representations. The only clear exception being that PC shows a higher partial correlation with a low-level visual feature model (pixelwise) in HFA relative to TD.

3.3.3. Similarity of neural representations across participants

Beyond differences at the group level, we were also interested to evaluate how similar an individual neural representation is

relative to the neural representations of other participants. For this, we compared individual neural representations of each brain region (neural similarity matrices) with the averaged matrix of the group (equivalent results are found using individual pairwise comparisons). We evaluated neural similarity matrices across participants in the visual and auditory modalities (Fig. 5 left and right respectively). Neural matrices of the congruency GLM just had two cells (one value and its mirror negative value) and were thus not suited for this representational similarity analysis.

For both visual and auditory dimensions, significant similarity of neural representations across participants was found in the same regions containing respectively visual and auditory information (previous diagonal vs non-diagonal analysis) for each group. Group comparisons show that for the visual dimension, no differences in idiosyncrasy were found between the groups (EVC: $p > .9$; LOC: $p > .9$; EAC: $p = .53$; TVA: $p > .9$; PC: $p = .14$; TPJ: $p = .20$; pmPFC: $p > .9$; amPFC: $p > .9$). For the auditory dimension, results revealed significantly more idiosyncratic neural representations in TVA for HFA relative to TD ($T(42) = 3.03$; $p = .03$; note that this p -value is Bonferroni-corrected for multiple comparisons across ROIs). All the other regions did not show group differences (EVC: $T(42) = -1.19$; $p > .9$; LOC: $T(42) = -1.06$; $p > .9$; EAC: $T(42) = 1.10$; $p > .9$; PC: $T(42) = -.49$; $p > .9$; TPJ: $T(42) = -2.13$; $p = .31$; pmPFC: $T(41) = 1.05$; $p > .9$; amPFC: $T(36) = 1.99$; $p = .43$).

3.4. Functional connectivity analysis

In order to confirm abnormalities in functional connectivity in autism as recently reported in the literature (Hahamy et al., 2015; Nunes et al., 2018), we then analyzed the functional connectivity patterns among the eight ROIs in a pairwise manner. In both groups, high connectivity strength was observed within visual areas, auditory areas and higher order regions. However, several areas exhibit strong connectivity beyond their neural system (Fig. 6A and supplementary Tables 1 and 2). We did not find group differences on functional connectivity strength of any ROI pair (supplementary Table 3).

Then, we analyzed to what extent the global functional connectivity pattern was similar across participants for each group. The global connectivity pattern (across the eight ROIs) revealed a similar degree of idiosyncrasy for both groups (Fig. 6B), with no significant group differences ($T(36) = 1.73$; $p = .091$). However, as TVA has previously shown more idiosyncratic neural representations in HFA we checked whether this region would present a more unique pattern of connectivity with other regions in the HFA group as compared to the TD group. Indeed, this was exactly what we found ($T(36) = 2.76$; $p = .009$; Fig. 6C).

4. Discussion

In the present work, we investigated the ability of HFA adults to infer shared social norms. For this, we created a multisensory task where the appropriateness of emotional vocal reactions to different visual scenes was evaluated while fMRI

brain data was recorded. An orthogonal design and MVPA analysis enabled us to compare neural representations at different hierarchical levels of neural information processing.

At the behavioral level, participants of both groups show equivalent intra-participant consistency of responses across runs. In contrast, HFA participants exhibit more idiosyncratic responses, i.e., lower between-participant correlations. These results suggest a reduced capacity to access the *shared* representations of social appropriateness but a normal and consistent access to their *own* representations of appropriateness. This result is in good accordance with previous work that found that HFA participants can respond in a consistent manner in social judgements tasks (suggesting good access to their subjective representations) but show difficulties to access *shared* mental states (Loveland et al., 2001; Nah & Poon, 2011; Tine & Lucariello, 2012). Further, unisensory valence ratings revealed that idiosyncrasies in the HFA group were already present at a perceptual level in both sensory modalities but most prominently in the more ambiguous auditory domain. This pattern of results is compatible with the idea that idiosyncrasies in social perception in HFA may already emerge at the sensory perceptual level. It is plausible that these idiosyncrasies accumulate from sensory processing to higher order cognition, as previously suggested (Baranek, Little, Parham, Ausderau, & Sabatos-DeVito, 2014; Baum, Stevenson, & Wallace, 2015; Thye, Bednarz, Herringshaw, Sartin, & Kana, 2018). Potential interdependencies between different levels of processing underline the importance of multi-level approaches that allow access to these different levels, as we did in the current study.

Brain analysis at the *group level* revealed strikingly similar patterns of neural activity between the two groups, both in terms of quantity of neural information (reproducibility of individual patterns for the same condition across runs) and quality of neural information (the nature of neural representations relative to explicit content-related models). This is apparent at all hierarchical levels and among both sensory modalities. However, there was two exceptions. First, more low-level visual information represented in the Precuneus (a high-level cognition area) was present in the HFA group. This finding may be reminiscent of an earlier study by Just and colleagues using a related social mentalizing task and machine learning algorithms. These authors could distinguish very accurately between participants with and without HFA based on activity patterns in Precuneus, and they showed that discrimination was driven by a high-order cognition factor (i.e., self-representations) which was only present in the control group and near-absent in the HFA participants (Just, Cherkassky, Buchweitz, Keller, & Mitchell, 2014). It is possible that our finding of more low-level information in this same high-level area is related to the atypical neural organization underpinning the low-level sensory bias in autism (Koldewyn, Jiang, Weigelt, & Kanwisher, 2013; Van der Hallen, Evers, Brewaeys, Van den Noortgate, & Wagemans, 2015). The second exception was that HFA participants show less emotional information in the 'Temporal Voice Area' (TVA), an auditory region that respond preferentially to human voices (Belin, Zatorre, Lafaille, Ahad, & Pike, 2000) encompassing the

Superior Temporal Sulcus and the Superior Temporal Gyrus, where activations can be observed for both explicit and implicit emotional vocalizations (Frühholz, Ceravolo, & Grandjean, 2012; Frühholz & Grandjean, 2013).

Furthermore, single-participant analysis confirmed more idiosyncratic patterns of neural activity in HFA participants, as previously observed (Byrge, Dubois, Tyszka, Adolphs, & Kennedy, 2015; Hahamy et al., 2015; Nunes et al., 2018; Salmi et al., 2013; Uddin, 2015). This was only noticeable in one auditory processing area: the 'Temporal Voice Area' (TVA). No group difference in idiosyncrasy was found for visual processing.

In addition, functional connectivity analysis showed no group differences in the strength of the global connectivity between the eight ROIs. Moreover, the analysis of single-participant similarity of global connectivity also demonstrated equivalent degrees of idiosyncrasies in the two groups. However, a more targeted analysis focusing specifically on the connectivity patterns of the TVA with other brain regions, revealed more idiosyncrasies in the HFA group relative to the TD group. So both MVPa and functional connectivity analyses reveal more idiosyncrasy in TVA in the HFA group. These results suggest that the idiosyncrasy observed in the TVA representations and connectivity might underpin the behavioral idiosyncrasy in HFA pertaining to the perception of auditory stimuli and their congruency with visual scenarios. Interestingly, a recent study investigating variations of networks across individuals in large datasets found that this same broad region is one of the two most idiosyncratic brain areas (Seitzman et al., 2019). Convergingly with our results, it was further observed that network variants are related to functional variations during tasks, that typical adult individuals cluster into subgroups on the basis of these variants and that these subgroups demonstrate similarities in behavior.

Nevertheless, despite comparable activity in primary auditory cortex, we cannot rule out an alternative explanation: hyper-/hyposensitivity in HFA group, as this could be present not at the primary sensory level but at a superior hierarchical level (attention allocation), creating difficulties to filter out relevant information (e.g., auditory stimuli against MR noise). It is a strength of our paradigm that it allows to assess representations at multiple levels and systems.

Interestingly, the TVA encompasses the Superior Temporal Sulcus (STS) which has been considered a major "social hub", integrating socially-relevant information across three neural systems: social perception, action observation and ToM (Yang, Rosenblau, Keifer, & Pelphrey, 2015). Thus, due to the presence of very unique neural representations and connectivity in this social hub area, one can expect atypical processing of social information in HFA and, accordingly, a reduced access to the shared way of perceiving the social world (Byrge et al., 2015).

Contrary to previous reports of a more global reduction of connectivity (Uddin, Supekar, & Menon, 2013) or global idiosyncratic patterns of neural connectivity (Hahamy et al., 2015; Uddin, 2015) in adults with HFA, here we notice a more localized idiosyncratic pattern of connectivity and representations centered around the TVA, which is a task-related area processing socially relevant information. One possible

explanation for this discrepancy of results can be related to differences in task paradigms. In particular, the typically used resting state paradigms may induce more freely floating cognitive activity favoring a broader brain recruitment, while our task, requiring a systematic processing of vocalizations, may have targeted the TVA and highlighted the connectivity pattern (and its increased idiosyncrasy in HFA) of this more specific brain area.

5. Conclusions

In summary, at the behavioral level, HFA participants show more difficulty to agree with their peers about social appropriateness of vocal utterances in different social contexts (visual scenarios). This increased idiosyncrasy is already present at the (uni)sensory level, especially when processing the emotional valence of the vocal utterances. Further, brain analysis revealed striking equivalent levels of information, representation and connectivity between the two groups in essentially all brain regions at the group level. In contrast, individual level analysis shows more idiosyncrasies in TVA for the HFA group, both in terms of representational content and in terms of functional connectivity. Overall, the present work suggests that despite globally having equivalent types of neural information, adults with HFA can show more unique patterns (idiosyncrasy) of neural information and this can lead to a greater difficulty to grasp the common sense. This finding may also reverberate within the context of the more philosophical-ethical debate to what extent HFA should be characterized as a neurological disorder or as a manifestation of intrinsic neurodiversity among the human population.

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Q4

Authors' contribution

F.P.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, visualization, writing original draft, review and editing.
H.O.B.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, supervision, writing review and editing.
B.B.: conceptualization, funding acquisition, methodology, project administration, writing review and editing.
M.H.: data curation, project administration.
S.A.: data curation, project administration.
N.D.: data curation, project administration.
J.S.: conceptualization, project administration.

Ethics approval and consent to participate

The study was approved by the Medical Ethics Committee UZ/KU Leuven University. All participants provided written informed consent prior to scanning.

Consent for publication

Not applicable.

Q5 Open practices

The study in this article earned Open Materials and Open Data badges for transparent practices. Materials and data for the study are available at <https://osf.io/hgyzf/>.

Uncited reference

Q7 Dinstein et al., 2012, Dinstein et al., 2011.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2019.11.008>.

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