



# Investigating the perception of face identity in adults on the autism spectrum using behavioural and electrophysiological measures



Patrick Dwyer, Buyun Xu, James W. Tanaka\*

Department of Psychology, University of Victoria, Canada

## ARTICLE INFO

### Keywords:

Autism  
Fast periodic visual stimulation  
Face perception  
Holistic processing  
Face inversion effect

## ABSTRACT

In the present study, we investigated face processing in individuals with self-reported Autism Spectrum Disorder (ASD,  $n = 16$ ) and typically developing control participants ( $n = 16$ ) using behavioural and electrophysiological measures. As a measure of their face memory, we administered the Cambridge Face Memory Test to participants in the ASD group. The results showed that the scores of the ASD participants were reliably below the age- and gender-matched norms of neurotypical individuals. To measure brain responses to faces, we used the fast periodic visual stimulation method, presenting photographs of a same-identity face (i.e., base face) at a constant frequency of 6 Hz (F) interleaved with different-identity faces (i.e., the oddball faces) presented at 1.2 Hz. The 6 Hz presentation of the base face and 1.2 Hz presentation of the oddball face elicited periodic brain responses corresponding to face detection and face individuation processes, respectively. Participants viewed four blocks of upright faces and four blocks of inverted faces. The results showed an enhanced EEG response to upright base faces at 6 Hz frequency and its harmonics compared to inverted faces, and the response was most focal over medial occipital channels. An enhanced response was found to upright oddball faces at 1.2 Hz and its harmonics compared to the inverted faces, and the response was centred over occipito-temporal channels in the right hemisphere. Critically, no differences or interactions were found between the ASD and typically developing groups in the responses to either the 6 Hz base faces or the 1.2 Hz oddball faces. These results suggest that in individuals with ASD, the earlier stage of face perception, as measured by the fast periodic visual stimulation paradigm, can be dissociated from the later memory stage of face processing, as assessed by the Cambridge Face Memory Test.

## 1. Introduction

Most humans have remarkable face recognition abilities. Even newborn infants can discriminate between different face identities (Bushnell, 2001; Turati, Macchi Cassia, Simion, & Leo, 2006). These face recognition skills are invaluable in day-to-day life. Identifying a conversational partner can provide vital information about their past behaviour and their relationship to one's self, which might help one predict their behaviour in the interaction. However, if one fails to quickly identify another person, one might be forced to devote cognitive resources to the task of recognizing the individual instead of focussing on the conversation itself. Such a diversion of mental resources could be particularly problematic for individuals with prior impairments in social skills, including people with Autism Spectrum Disorder (ASD).

### 1.1. Autism and behavioural measures of face processing

A growing body of evidence indicates that individuals with ASD often have difficulty recognizing facial identities. Autism Spectrum Disorder (ASD) is a neurodevelopmental difference characterized by impairments in social interaction and communication and restricted and repetitive patterns of behaviour, interests, or activities (American Psychiatric Association, 2013). The Cambridge Face Memory Test (CFMT, Duchaine & Nakayama, 2006) has been used to investigate face recognition in individuals with ASD. Numerous studies using the CFMT (or CFMT for Children where appropriate) have found that performance was reduced in adults and children (Croydon, Pimperton, Ewing, Duchaine, & Pellicano, 2014; Ewbank et al., 2017; Ewing, Pellicano, & Rhodes, 2013; Hedley, Brewer, & Young, 2011; Kirchner, Hatri, Heekeren, & Dziobek, 2011; Lynn et al., 2016; O'Hearn, Schroer, Minshew, & Luna, 2010; Rhodes, Ewing, Jeffery, Avard, & Taylor, 2014; Rhodes, Neumann, Ewing, & Palermo, 2015; Schelinski, Roswandowitz,

\* Corresponding author at: Department of Psychology, University of Victoria, BC, Canada.  
E-mail addresses: [xubuyun@uvic.ca](mailto:xubuyun@uvic.ca) (B. Xu), [jtanaka@uvic.ca](mailto:jtanaka@uvic.ca) (J.W. Tanaka).

& von Kriegstein, 2017; Scherf, Elbich, Minshew, & Behrmann, 2015) as compared to typically-developing controls (but see Whyte, Behrmann, Minshew, Garcia, & Scherf, 2015).

Although face recognition impairments may be common in autism, it is not always the case that individuals are impaired in their face recognition abilities. Hedley et al. (2011) found considerable variability in the CFMT performance of individuals with autism: some participants with autism performed above the average for the typically-developing (TD) control group. Indeed, a variety of studies have found heterogeneity in the face processing ability of individuals on the autism spectrum (e.g., Annaz, Karmiloff-Smith, Johnson, & Thomas, 2009; Davies, Bishop, Manstead, & Tantam, 1994; Dimitriou, Leonard, Karmiloff-Smith, Johnson, & Thomas, 2015; Klin et al., 1999; Rutherford, Clements, & Sekuler, 2007). Furthermore, while people on the autism spectrum experience impairments when face identity information must be held in memory, they may not have such great difficulties with tasks requiring discrimination of simultaneously-presented faces (Weigelt, Koldewyn, & Kanwisher, 2012, pp. 1070–1078; Wolf et al., 2008).

As a plausible explanation of their face recognition impairments, it has been hypothesized that individuals on the autism spectrum are impaired in their holistic face processing abilities. Face recognition relies upon holistic processing where the features of a face (e.g., eyes, nose, mouth, etc.) are not processed independently, but seen as an integrated whole (e.g., Rossion, 2008, 2013; Sergent, 1984; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). One of the gold standards of holistic face processing is the inversion effect: due to the disruption of whole-face processing, face recognition is disproportionately impaired by inversion relative to the recognition of other objects (Yin, 1969). However, the research is unclear as to whether individuals with ASD lack holistic face processing as measured by the inversion effect. Whereas some researchers have found that people with ASD demonstrate a reduced or absent face inversion effect (Bookheimer, Wang, Scott, Sigman, & Dapretto, 2008; Hobson, Ouston, & Lee, 1988; O'Brien, Spencer, Girges, Johnston, & Hill, 2014; Rose et al., 2007; Rosset et al., 2008; Scherf et al., 2015; Tantam, Monaghan, Nicholson, & Stirling, 1989; van der Geest, Kemner, Verbaten, & van Engeland, 2002), other studies have shown the normal inversion effect in individuals with ASD (Barton, Hefter, Cherkasova, & Manoach, 2007; Falck-Ytter, 2008; Guillon et al., 2016; Hedley, Brewer, & Young, 2015; Lahaie et al., 2006; Reed et al., 2007; Scherf, Behrmann, Minshew, & Luna, 2008; Teunisse & de Gelder, 2003).

### 1.2. Electrophysiological measures of face processing

Event-related potentials (ERPs) have been applied to investigate the brain activity associated with face processing in autism. Many of these studies have focused on the N170 component, which, in typical development, primarily reflects the detection of a face stimulus (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000), as well as the individuation of face stimuli (Rossion & Jacques, 2011). Studies have shown that N170 amplitudes were reduced and latencies delayed in individuals with autism relative to control participants (e.g., McPartland, Dawson, Webb, Panagiotides, & Carver, 2004; McPartland et al., 2011; O'Connor, Hamm, & Kirk, 2005).

Experiments have investigated holistic processing in ASD by examining whether early ERP components, including the N170, differ in response to upright and inverted faces. Such a difference between face orientations would constitute an electrophysiological variety of face inversion effect, and the presence of such a face inversion effect would generally indicate that holistic processing is intact. However, a number of empirical studies suggest that early ERP components do not differ between upright and inverted orientations in autistic subjects, but do differ in controls, suggesting that holistic processing in ASD is impaired (Fujita et al., 2013; McPartland et al., 2004; McPartland et al., 2011; Tye et al., 2015; Webb et al., 2012). Nevertheless, other studies of this

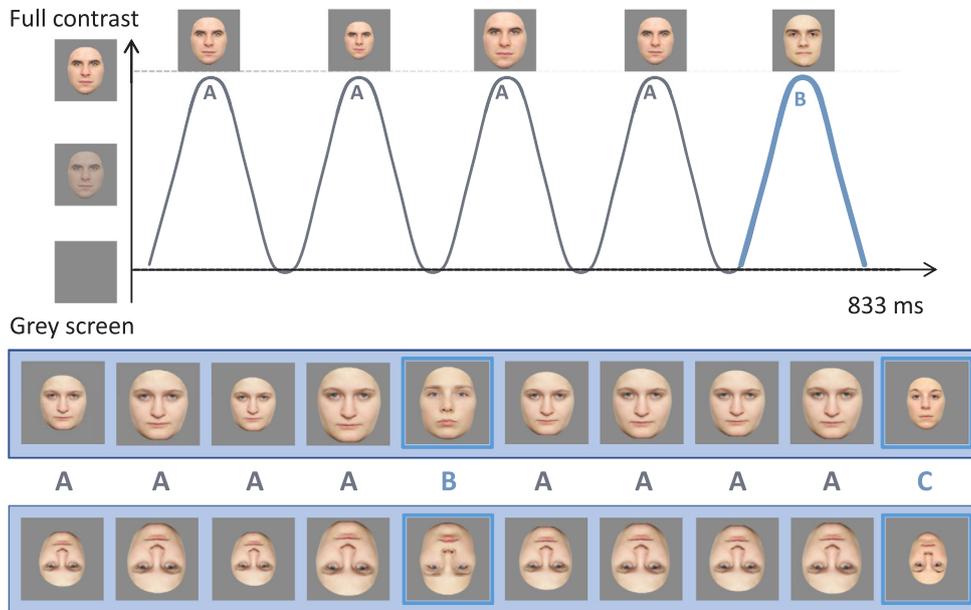
type have yielded evidence of electrophysiological face inversion effects in autistic participants, suggesting that holistic processing is intact (Neuhaus, Kresse, Faja, Bernier, & Webb, 2016; Tavares, Mouga, Oliveira, & Castelo-Branco, 2016; Tye et al., 2013).

ERP studies investigating sensitivity to face identity in autism have generally focused on later components. For example, Churches, Damiano, Baron-Cohen, and Ring (2012) report that N250 amplitudes towards a learned target face differed between TD and autistic subjects, but that no such difference was found for nontarget faces, suggesting that autistic subjects may have failed to identify the target face. Key and Stone (2012) examined the N290 (infant N170) and P400 components in infants at risk for autism, and while amplitudes in response to familiar and unfamiliar faces showed similar patterns of differences in at-risk and control groups, only the control group showed greater P400 latency to unfamiliar faces. However, other electrophysiological studies have obtained results more suggestive of intact individuation. Webb et al. (2010) found similar patterns of differences in ASD and TD participants in P2, N250, and FN400 responses to familiar, repeated, and unfamiliar faces. Anomalous findings from Key and Corbett (2014) complicate the picture further. Although the experimenters did observe the expected pattern of greater sensitivity to face repetition in TD subjects in the P600 component, Key and Corbett also found that the FN400 response was sensitive to face repetition in autistic but not TD subjects, perhaps due to group differences in sensitivity to perceptual features. Thus, conventional ERP studies offer mixed evidence with regard to the presence or absence of face identification responses in ASD. Both the heterogeneity of the autism spectrum and the number of different ERP components under investigation might be partly responsible for the confused state of this literature.

In the current study, we employ a relatively new technique in high level vision to study the brain activity of individuals with and without autism. Fast periodic visual stimulation (FPVS), a research method using steady-state visual evoked potentials (SSVEP) in EEG, may offer a more objective means of studying face processing with EEG (Rossion, 2014, p. 1604). In FPVS studies, stimuli are presented repeatedly at a fixed frequency, so that any periodic change in amplitude uniquely associated with that frequency and its harmonics can reasonably be assumed to constitute a response to the stimulus. Rapid presentation frequencies are ordinarily used in FPVS studies, resulting in very swift replacement of successive images, which suggests that paradigm may be most suitable for investigations of early perceptual processing. However, FPVS has a number of advantages. For example, because signal is confined to the relatively narrow range defined by the frequencies of interest, and because these frequencies can in turn be deliberately selected to avoid overlap with ranges characterized by high spontaneous activity, responses are generally robust compared to noise (Alonso-Prieto, 2011, p. 3; Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015, p. 4; Rossion, 2014, p. 1604). Furthermore, the method can be used to “tag” multiple stimuli if they are presented at different frequencies, as there will be separate responses to each presentation frequency (Norcia et al., 2015).

The greater objectivity of the FPVS response may make it a particularly suitable approach to investigate face perception in autism. While there are many potential explanations for the mixed results of previous EEG studies, it is possible that the subjectivity of ERP may have contributed. Not only do stimulus events generally produce a number of different ERP components, but defining and measuring the components underlying surface waveforms can be challenging (see Luck, 2014, pp. 52–55). Furthermore, in conventional ERP studies, researchers may be forced to make many decisions related to data processing and artifact rejection, which can affect results and conclusions. In contrast, FPVS responses occur at exact frequencies defined by experimenters, can be easily quantified, and are largely preserved from artifacts (Rossion, 2014, p. 1604).

FPVS can be used to investigate brain responses reflecting sensitivity to changes in face identities (Liu-Shuang, Norcia, & Rossion,



**Fig. 1.** Schematic illustration of the FPVS oddball paradigm employed by the present study (adapted from Liu-Shuang et al., 2014; Xu et al., 2017). Above: faces were presented with sinusoidal contrast modulation at a rate of 6 cycles per second ( $=6$  Hz), with display alternating between face presentation and monochromatic grey screen. Cycle duration was 167 ms. Every fifth face ( $6/5 = 1.2$  Hz) was a different-identity oddball. To avoid pixel-wise overlap of features, image size randomly varied between 80% and 120%. Below: four blocks of upright faces and four blocks of inverted faces were presented (60 s each); an inversion effect would suggest that faces are processed holistically.

2014). The FPVS oddball paradigm directly separates the response to the detection of face identity changes (the individuation response) from the generic response to the presentation of a face. Images of a single face identity can be repeatedly presented at a higher frequency, and the presentation of these images can then be periodically interrupted by the presentation of an oddball, a different-identity face associated with a unique, lower frequency (Fig. 1). The generic response to faces will be associated with the higher, same-identity frequency and its harmonics, while the individuation response will be associated with the lower, oddball frequency and its harmonics. It is important to recall that the response to the detection of the oddball face as a face stimulus will be included within the rest of the generic response; only activation associated with sensitivity to the separate identity of the oddball will be included within the individuation response. The FPVS oddball paradigm has been used to study the face inversion effect (Liu-Shuang et al., 2014) and is sensitive to the individual differences in face processing (Xu, Liu-Shuang, Rossion, & Tanaka, 2017).

The present study used the FPVS oddball paradigm to examine the generic response to the presentation of face stimuli and the individuation response reflecting perceptual sensitivity to changes in face identity in samples of ASD and control participants. To the best of our knowledge, the present study is the first to examine face perception using FPVS with adults with ASD. While two previous studies have used FPVS to investigate face processing in a special population, with a single participant with prosopagnosia (Alonso-Prieto, 2011; Liu-Shuang, Torfs, and Rossion, 2016), the current study tested a larger sample ( $n = 16$ ) of individuals with ASD to compare with an age and gender matched control sample ( $n = 16$ ). The current study also included both upright and inverted face blocks, allowing for the examination of responses associated with holistic face processing. In line with the results of previous studies (e.g., Liu-Shuang et al., 2014; Xu et al., 2017), we expected to observe a robust generic response centred over medial occipital areas and a robust individuation response centred over occipito-temporal areas in TD participants. We also expected to find an effect of orientation on the occipito-temporal individuation response of TD participants, indicating that TD participants process face identities holistically. Given the face recognition impairments that have often been found in studies of individuals on the autism spectrum, we anticipated finding that the occipito-temporal individuation response to upright faces would be smaller in participants with ASD than in TD participants. Finally, in line with those studies indicating that holistic processing may be reduced in individuals with ASD, we did not expect

to find an effect of orientation on the occipito-temporal individuation response of participants with ASD.

## 2. Methods

### 2.1. Participants

Participants included sixteen high-functioning adults who declared themselves to have diagnoses of Autism Spectrum Disorder or equivalent pervasive developmental disorders (13 male, 3 female,  $M_{Age} = 30.13$ ,  $SD_{Age} = 11.58$ ). Nine participants reported that they were diagnosed with Asperger Syndrome, three participants reported diagnoses of Autism Spectrum Disorder, two participants reported diagnoses of High-Functioning Autism, and one participant reported a diagnosis of Pervasive Developmental Disorder – Not Otherwise Specified. One participant reported an autism spectrum diagnosis but declined to provide further detail. All participants on the autism spectrum were Caucasian in ethnicity. Participants with autism were recruited through a combination of advertising with local service providers and community groups in Victoria, British Columbia and emails to individuals listed in the University of Victoria Centre for Autism Research, Technology, and Education (CARTE) participant database.

In the sample of adults recruited for this study, it was not always possible to obtain reports of autistic symptoms from a suitable individual, such as a parent. Therefore, following their initial visit to the lab for the fast periodic visual stimulation task, participants with autism were later asked to return to complete the Ritvo Autism Asperger Diagnostic Scale-Revised (RAADS-R), a self-report measure designed as a tool to aid in the process of diagnosing autism in adults. It consists of 80 questions, with a maximum possible score is 240; scores of 65 or higher are consistent with the presence of autism. A large, multi-site validation study indicates that the RAADS-R has sensitivity of 97% and specificity of 100% when used to discriminate between individuals with autism and typically-developing (TD) individuals or individuals with other psychiatric diagnoses (Ritvo et al., 2011). The measure also shows high concurrent validity with the Social Responsiveness Scale-Adult (SRS-A) and Module 4 of the Autism Diagnostic Observation Schedule (ADOS) (Ritvo et al., 2011; Ritvo, 2013). The RAADS-R has been employed as a confirmation of autism diagnosis in previous research (e.g., Brosnan, Lewton, & Ashwin, 2016; Dunlop, Enticott, & Rajan, 2016; Libero et al., 2016; Zimmerman, Ownsworth, O'Donovan, Roberts, & Gullo, 2016, 2017). Fifteen of the 16 participants with autism<sup>1</sup>

completed the RAADS-R. Three participants were not in Victoria and completed the questionnaire online. Scores ranged from 88 to 194 ( $M = 126.53$ ,  $SD = 34.79$ ), exceeding the cut-off score of 65.<sup>2</sup>

For comparison, a sample of typically-developing (TD) controls was recruited through a combination of the University of Victoria Department of Psychology's Sona research participation system and emails to past participants in studies conducted by the University of Victoria's Different Minds Lab. Controls were matched to participants with autism on gender (13 male, 3 female) and selected for age equivalence ( $M_{\text{Age}} = 29.00$ ,  $SD_{\text{Age}} = 11.74$ ). 15 control participants were Caucasian, and the remaining control participant was a natural-born citizen of a Caucasian-majority country. Participants recruited through the Sona research participation system were compensated with bonus credit towards course grades, while participants recruited from the community were compensated with \$20 gift certificates from a bookstore.

## 2.2. Stimuli

The stimuli shown to participants in the EEG experiment were 50 full-colour photographs (25 male, 25 female) of different human faces. All images displayed a neutral facial expression. All photographs were generated under standardized conditions with regard to lighting, background, and distance from the camera. Adobe Photoshop was used to remove external features, including hair and ears, from the final images (Liu-Shuang et al., 2014). Each face was resized to a final height of 250 pixels (with random size variation from that base height, as described below); width varied between 175 and 197 pixels. Images were displayed against a neutral gray background with a display resolution of 1280 x 1024 pixels at a distance of 58 cm from participants. The average visual angle of the stimuli was 7.1 degrees in height by 5.2 degrees in width.

## 2.3. Procedure

The procedure of this study was approved by the Human Research Ethics Board of University of Victoria, and was carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Participants were first brought to the lab and signed the consent form. Participants viewed eight 60-second blocks of faces. Blocks differed with regard to stimulus orientation (upright vs. inverted) and gender (male vs. female), with two blocks for each of four conditions (upright male, upright female, inverted male, inverted female). Order of gender and orientation was counterbalanced, with same-gender faces being grouped together within each half of the experiment. The order of the first half (first four blocks) mirrored the second half (last four blocks). For example, a block of upright male

<sup>1</sup> One participant was not available when invited to complete the RAADS-R. Because there is no reason to suppose that this participant differed from the rest of the sample, their FPVS and CFMT data were retained.

<sup>2</sup> Participants with autism were also asked to disclose any co-occurring diagnoses. 15 participants provided responses, while one participant declined to answer. Of the respondents, seven reported that they were not diagnosed with any additional conditions. The additional diagnoses of the remaining eight participants included Non-Verbal Learning Disability (3 participants), Bipolar Disorder (2 participants), Major Depression (2 participants), Obsessive-Compulsive Disorder (2 participants), Social Anxiety Disorder (2 participants), Attention-Deficit Hyperactivity Disorder (1 participant), Developmental Coordination Disorder (1 participant), Dysthymia (1 participant), Generalized Anxiety Disorder (1 participant), Post-Traumatic Stress Disorder (1 participant), and Sensory Processing (Integration) Disorder (1 participant). Two of the eight participants reported being diagnosed with more than one additional disorder. One participant believed that their diagnoses of Obsessive Compulsive Disorder, Major Depression, and Bipolar Disorder were made in error; however, the diagnoses are nevertheless included in the figures provided above.

faces would be followed by inverted male (same gender, different orientation), upright female (same orientation, different gender), and inverted female (different gender and orientation) blocks. In the second half of the experiment, blocks would be presented in the reverse order (i.e., inverted female, upright female, inverted male, upright male).

Within each block, face images were presented at a frequency of exactly 6 Hz (the *generic frequency*, F), or a rate of six faces per second. This frequency is recommended for use in studies with FPVS of faces (Alonso-Prieto, 2011, pp. 129-163; Alonso-Prieto, Van Belle, Liu-Shuang, Norcia, & Rossion, 2013). Face images were presented in the sequence AAAABAAAACAAAADAAAAEA..., where each letter represents a different facial identity. Thus, every fifth face was a different identity, and these different-identity faces were presented at a frequency of 1.2 Hz (the *individuation frequency*, F/5). Responses at the generic frequency and its harmonics were assumed to reflect detection and generic visual processing of the stimuli, while responses at the individuation frequency and its harmonics were assumed to reflect processing of face identity information. The selection of the base face (A) in each block was random with replacement, while the oddball faces (B, C, D, E...) were randomly selected in each block from the remaining same-gender face images.

Stimuli were presented through sinusoidal contrast modulation using a custom script based on Psychtoolbox in MATLAB (Liu-Shuang et al., 2014). Cycles began with a uniform grey background, after which a face appeared with increasing contrast. Full contrast was reached at 83.3 ms, after which contrast decreased at the same rate. Cycle offset occurred at 166.7 ms. Face size varied randomly between 80% and 120% in each cycle, corresponding to heights of 200 to 300 pixels. Increments of 2%, or 5 pixels, were used. This variation in image size minimized the degree to which any individual face feature overlapped, or continued to occupy the same pixels across two successive presentations. If images had overlapped excessively, it is possible that sensitivity to facial identity would be conflated with neural responses to low-level changes in individual face features (Dzhelyova & Rossion, 2014).

Participants were not explicitly instructed to view the face images, nor were participants asked to respond to the presentation of the face images. However, to ensure that participants directed gaze towards the stimuli, participants performed a task orthogonal to the experimental manipulation. A fixation cross was displayed in the center of the face images, immediately below the eyes, throughout each block. On eight occasions during each block, at random intervals, this cross briefly (200 ms) changed colour from red to blue. Participants were instructed to press a key when they detected a colour change.

## 2.4. EEG data acquisition

EEG was recorded from 36 Ag/AgCl ring electrodes in a nylon cap (EASY CAP GmbH, Herrsching-Breitbrunn, Germany) mounted in accordance with the extended international 10–20 system. Impedance was reduced below 20k $\Omega$  through the application of an abrasive, conductive gel to electrode sites. Low-noise electrode differential amplifiers with a frequency response of DC 0.17–67.5 Hz (90 dB/octave roll off) were used to amplify signals, which were recorded to disk using Brain Vision Recorded software (Brain Products GmbH, Munich).

## 2.5. EEG preprocessing

EEG signal was processed using Letswave 6 (<http://www.nocions.org/letswave/>) and MATLAB (MathWorks). A Butterworth filter with a slope of 24 dB/octet was used to digitally band-pass filter EEG data; high-pass cut-off was 0.1 Hz and low-pass cut-off was 100 Hz. Filtered data were then re-referenced to an average reference. EEG recordings for each block were subsequently cropped to create 60-second segments time-locked to the onset and offset of the first and last cycles, respectively, in each block. In order to reduce noise, each participant's EEG

data were then averaged in the time domain separately for each level of orientation (upright vs. inverted) for each individual participant. Averaged data were then subjected to a Fast Fourier Transform (FFT) and frequency amplitude was extracted at a fine resolution of  $1/60 = 0.017$  Hz.

## 2.6. ROI selection

To avoid commission of nonindependence error, regions of interest (ROIs) were initially selected based on the previous results obtained by Xu et al. (2017), who found that the generic response was centred over medial occipital channels (Oz and POz), while the individuation response was centred over lateral occipito-temporal channels (left hemisphere: P7, PO7, TP9; right hemisphere: P8, PO8, TP10). Liu-Shuang et al. (2014) obtained similar results, but those authors also subjected the generic response over occipito-temporal channels to additional analyses. Therefore, the present study analyzed the individuation response over occipito-temporal channels and the generic response over occipital channels. The generic response over occipito-temporal channels was analyzed, but it is not reported here due to length.

## 2.7. Harmonic selection

To identify frequency harmonics for further analysis, EEG data were then grand-averaged for each condition, producing a total of four averaged data files (ASD upright, ASD inverted, TD upright, TD inverted). The most central channels of interest for the generic response (occipital channels; Oz and POz) and for the individuation response (occipito-temporal channels; P7, P8, PO7, PO8, TP9, and TP10) were then pooled separately. Next, Z-scores for these pooled channels were computed, reflecting the difference between amplitude at each frequency and mean amplitude of 18 adjacent frequency bins (9 of the 11 adjacent frequency bins on each side, excluding the immediately adjacent bins and the most extreme of the 10 bins thereafter), divided by the standard deviation of the adjacent bins. Frequencies of interest (1.2 Hz, 6 Hz, and their respective harmonics) were then scanned for the presence of Z-scores above 2.57, corresponding to a probability level of  $p = .005$ , over the appropriate channels of interest, in any of the four conditions (e.g., a Z-score above 2.57 in any occipito-temporal frequency bin between 2.3 and 2.5 Hz). The presence of a Z-score exceeding 2.57 in any condition of orientation and group was deemed sufficient for inclusion of the corresponding harmonic in all conditions. This relatively liberal criterion was chosen to facilitate fair comparison of groups and conditions. Frequencies for further analysis for the generic response were 6 Hz and its harmonics up to and including 36 Hz, while frequencies for further analysis for the individuation response were 1.2 Hz and its harmonics up to and including 8.4 Hz. The fifth harmonic of 1.2 Hz, 6 Hz, was excluded from analyses of the individuation response due to the confounding of the generic and individuation responses at that frequency.

## 2.8. Baseline-Corrected amplitudes

Fourier-transformed response amplitudes for each level of orientation (upright vs. inverted) and for each participant were converted into baseline-corrected amplitudes. Baseline-corrected amplitude was calculated as the subtractive difference between amplitudes at each frequency and mean amplitudes of 18 adjacent frequency bins (9 frequency bins on each side, excluding the immediately adjacent bins and the most extreme of the 10 bins thereafter). Baseline-corrected amplitudes at each harmonic of the 1.2 Hz and 6 Hz responses up to and including 8.4 Hz and 36 Hz, respectively, were then summed separately within each participant, response, and orientation condition to produce separate baseline-corrected amplitude values for the generic and individuation responses for each participant, orientation condition, and channel. The values corresponding to the different occipital (Oz, POz),

left occipito-temporal (P7, P8, PO7), and right occipito-temporal (PO8, TP9, TP10) channels of interest were then added separately. This produced separate baseline-corrected amplitude values for each of the 32 participants, for each orientation condition, and for each response and the corresponding ROIs.

## 2.9. Cambridge face memory Test (CFMT)

Following completion of the FPVS EEG task, but prior to the administration of the RAADS-R, participants with autism were invited to return to lab to complete the upright version of the CFMT, a measure of face memory (Duchaine & Nakayama, 2006). All sixteen participants with autism completed the measure.

In the introductory phase of the CFMT, participants with autism memorized study faces presented in three different profile views for a total of 3 s per profile. The memorization of each study face was followed by three three-alternative forced-choice trials, with one trial for each profile. Participants were instructed to select the target which they had previously studied, with selections indicated by pressing the key corresponding to the position of the face on the screen. Each trial contained one target item identical to the study items. Following the final trial corresponding to each study item, a new study item was presented until participants had seen a total of six study items and completed eighteen trials.

The introductory phase was followed by the no-noise phase, which began with the presentation of an array of frontal images of six study faces for a total of 20 s. The study face identities were the same as the study and target faces presented in the introductory phase. After the review array had been studied, participants on the autism spectrum completed 30 three-alternative forced-choice trials, each of which contained one of the six target faces alongside two distractors. Target face images in these trials were not strictly identical to the study faces; the faces were of the same identities as study faces, but differed in lighting and/or pose.

Finally, participants with autism completed the noise phase of the CFMT. Participants began by reviewing the previously-presented array of six study faces for 20 s. After the review, participants completed 24 three-alternative forced-choice trials, each of which contained one of the six target faces alongside two distractors. Gaussian noise was added to target and distractor images in this phase.

For the purpose of comparison, a large normative dataset ( $n = 1471$ ) was made freely available online by Wilmer et al. (2012). The final normative value is the average of sixteen normative values for individuals of the same sex and age as the autistic participants. Because the normative dataset included a disproportionate number of younger individuals, normative values for individuals < 20 years of age are the average response for same-sex individuals of the exact same age in years. However, five- and ten-year intervals, respectively, were used for individuals aged 20–29 (e.g., same-sex individuals aged 25–29) and > 30 (e.g., same-sex individuals aged 40–49).

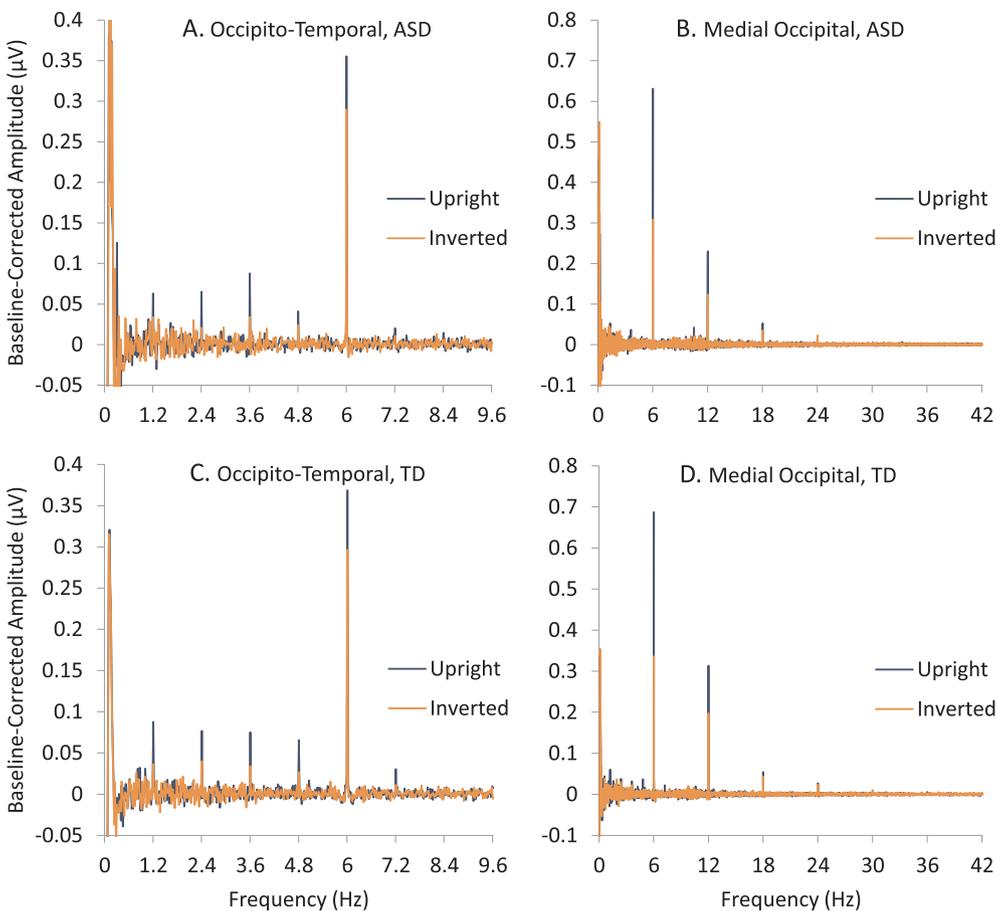
## 3. Results

### 3.1. Cambridge face memory Test

The average total score out of 72 for participants on the autism spectrum was 48.31 ( $SD = 10.40$ ), 95% CI [42.77, 53.85]. Normative responses for age and gender were calculated from this dataset, producing a total normative score of 54.26, exceeding the upper bound of the confidence interval for ASD responses.

### 3.2. Orthogonal fixation cross task

Performance on the orthogonal fixation cross task was at levels approaching ceiling in all conditions of group and orientation, without any significant differences between conditions.<sup>3</sup>



**Fig. 2.** Above: Frequency spectra of the baseline-corrected response over occipito-temporal channels P7, P8, PO7, PO8, TP9, and TP10 (A) and over medial occipital channels Oz and POz (B) for participants with autism. Below: Frequency spectra of the baseline-corrected response over occipito-temporal channels (C) and over medial occipital channels (D) for TD participants.

A two-way ANOVA examining the effects of group and orientation on accuracy yielded no main effect of group,  $F(1, 29) = 1.19, p = 0.28, \eta_p^2 = .04$ . TD participants ( $M = 0.99, SD = 0.02$ ) were no more accurate than autistic participants ( $M = 0.98, SD = 0.05$ ). There was also no main effect of orientation,  $F(1, 29) = 0.40, p = 0.53, \eta_p^2 = .01$ . Participants were no more accurate in the upright condition ( $M = 0.99, SD = 0.02$ ) than in the inverted condition ( $M = 0.98, SD = 0.05$ ). Finally, there was no interaction between orientation and group,  $F(1, 29) = 1.71, p = 0.20, \eta_p^2 = .06$ .

A two-way ANOVA examining the effects of group and orientation on response time yielded no main effect of group,  $F(1, 29) = 0.37, p = 0.55, \eta_p^2 = .01$ . Autistic participants ( $M = 526$  ms,  $SD = 165$  ms) were no faster than TD participants ( $M = 561$  ms,  $SD = 261$  ms). There was also no main effect of orientation,  $F(1, 29) = 0.26, p = 0.61, \eta_p^2 = .01$ . Response times in the upright condition ( $M = 530$  ms,  $SD = 211$  ms) were no faster than response times in the inverted condition ( $M = 556$  ms,  $SD = 222$  ms). Finally, there was no interaction of orientation and group,  $F(1, 29) = 1.45, p = 0.24, \eta_p^2 = .05$ .

### 3.3. Frequency domain analysis

The generic response was centred over medial occipital channels (Fig. 2). A two-way ANOVA examining effects of group and orientation on this medial occipital generic response yielded a large main effect of orientation,  $F(1, 30) = 60.51, p < .0001, \eta_p^2 = .67$  (Fig. 3). Responses in upright blocks ( $M = 1.99, SD = 0.92$ ) were much larger than responses in inverted blocks ( $M = 1.06, SD = 0.54$ ). There was no main

effect of group,  $F(1, 30) = 1.16, p = .29, \eta_p^2 = .04$ . TD responses ( $M = 1.66, SD = 0.87$ ) did not differ from ASD responses ( $M = 1.40, SD = 0.89$ ). There was no interaction between orientation and group,  $F(1, 30) = 0.09, p = .76, \eta_p^2 = .003$ .

A robust individuation response was found over the lateral occipito-temporal channels (Fig. 2). A three-way ANOVA examining the effects of group, orientation, and hemispheric lateralization on this occipito-temporal individuation response yielded a large main effect of orientation,  $F(1, 30) = 23.41, p < .0001, \eta_p^2 = .44$  (Fig. 4). Responses in the upright blocks ( $M = 0.95, SD = 0.80$ ) were much larger than responses in the inverted blocks ( $M = 0.42, SD = 0.50$ ). A main effect was also found for hemisphere,  $F(1, 30) = 11.96, p = .002, \eta_p^2 = .29$ . Responses over the right hemisphere ( $M = 0.81, SD = 0.73$ ) were much larger than responses over the left hemisphere ( $M = 0.56, SD = 0.67$ ). There was no main effect of group,  $F(1, 30) = 0.42, p = .52, \eta_p^2 = .01$ . TD responses ( $M = 0.75, SD = 0.66$ ) did not significantly differ from ASD responses ( $M = 0.63, SD = 0.77$ ). Finally, there was also no interaction between orientation and group,  $F(1, 30) = 0.06, p = .80, \eta_p^2 = .002$ ; no interaction between orientation and hemisphere,  $F(1, 30) = 2.42, p = .13, \eta_p^2 = .08$ ; no interaction between group and hemisphere,  $F(1, 30) = 1.06, p = .31, \eta_p^2 = .03$ ; and no interaction between group, orientation, and hemisphere,  $F(1, 30) = 1.27, p = .27, \eta_p^2 = .04$ .

Large individual differences were found in the magnitude of the individuation response at 1.2 Hz and its harmonics. The baseline-corrected amplitudes of participants' individuation responses in the upright condition ranged from  $-0.13$  to  $6.60$   $\mu\text{V}$ , while responses in the inverted condition ranged from  $-0.41$  to  $3.53$   $\mu\text{V}$  (Fig. 5).

In the group of participants with autism, no correlation was found between occipito-temporal individuation responses to upright faces and CFMT scores,  $r(15) = .13, p = .62$ .

<sup>3</sup> Accuracy was defined as the proportion of fixation crosses to which participants correctly pressed a key. Due to technical issues, it was not possible to retrieve fixation cross data from one TD participant.

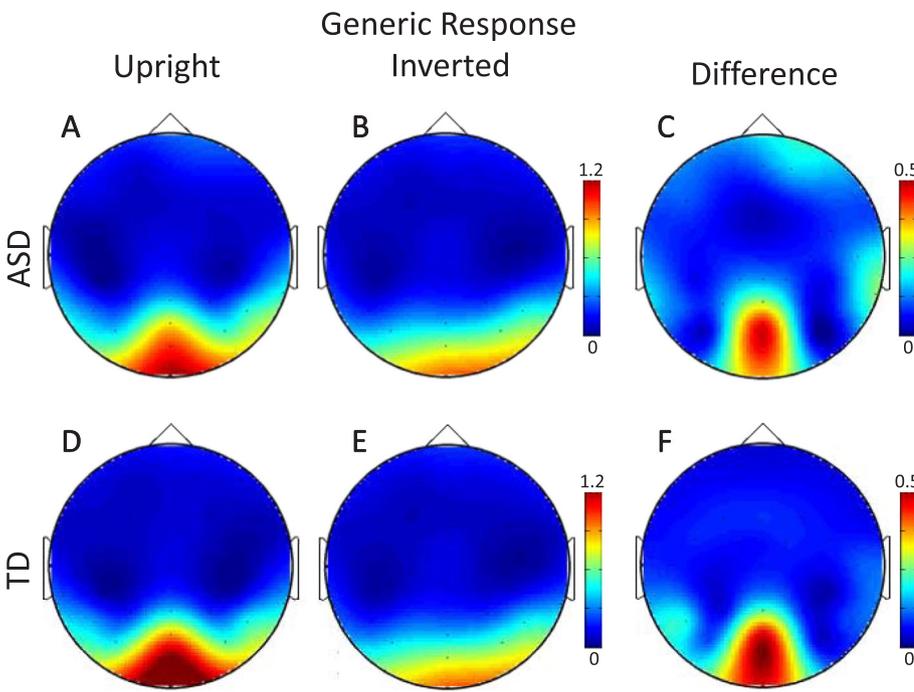


Fig. 3. Above: scalp plots depicting the distribution of the baseline-corrected generic (6 Hz + harmonics) response in participants with autism. Plots represent the upright (A) and inverted (B) conditions and the difference between orientation conditions (C), reflecting holistic processing. Below: scalp plots depicting the distribution of the generic response in TD participants. Plots represent the upright (D) and inverted (E) conditions and the difference between orientation conditions (F).

#### 4. Discussion

In this study, participants with autism scored lower than the age- and gender-appropriate norm for the CFMT, a behavioural face memory test, which replicates previous reports that participants with autism exhibit impairments on the CFMT. To evaluate the electrophysiological correlates of face processing, we applied the fast periodic visual stimulation (FPVS) oddball paradigm, presenting upright and inverted faces to ASD and TD adults. Both groups showed equivalent face inversion effects in the generic response at the 6 Hz frequency, which reflects the generic detection of the face stimulus, as well as in the individuation response at the 1.2 Hz frequency, which reflects sensitivity to face identity. Surprisingly, there was no evidence that participants with autism were less sensitive to the changes in face identity than TD

participants. Altogether, these results may suggest that face recognition impairments in autism are more pronounced in face memory, rather than face perception.

For the generic response at 6 Hz and harmonics, which peaked at the medical occipital scalp locations, a large effect of orientation was found in both groups: upright faces elicited larger responses than inverted faces. This finding was consistent with Liu-Shuang et al. (2014, p. 64), indicating that holistic processing may even play a role in lower-level processing of faces. Moreover, for the face individuation response at 1.2 Hz and its harmonics, a significant inversion effect was also present, replicating previous studies (Liu-Shuang et al., 2014; Liu-Shuang et al. 2016).

However, contrary to our hypothesis, the present study found no interactions of group and orientation in the individuation response.

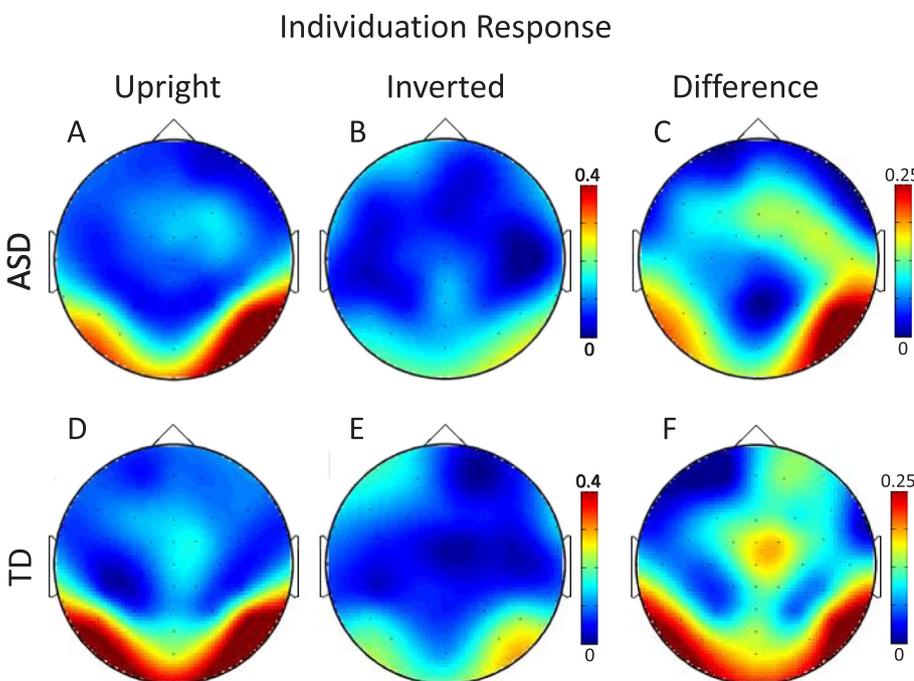
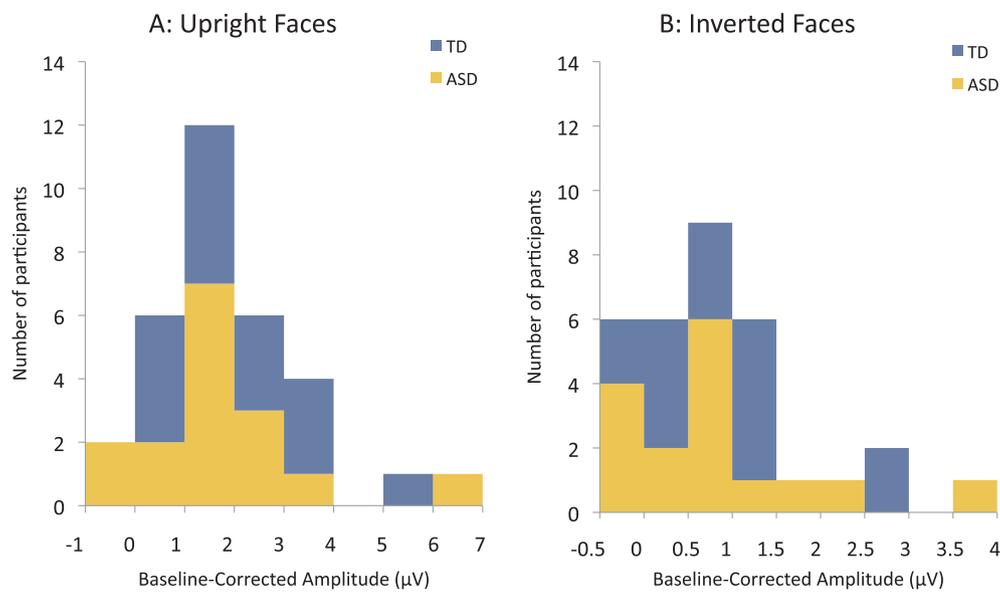


Fig. 4. Above: scalp plots depicting the distribution of the baseline-corrected individuation (1.2 Hz + harmonics) response in participants with autism. Plots represent the upright (A) and inverted (B) conditions and the difference between orientation conditions (C), reflecting holistic processing. Below: scalp plots depicting the distribution of the individuation response in TD participants. Plots represent the upright (D) and inverted (E) conditions and the difference between orientation conditions (F).



**Fig. 5.** Left, A: Histogram depicting the distribution of the occipito-temporal individuation (1.2 Hz + harmonics) responses to upright faces. Right, B: Histogram depicting the distribution of the occipito-temporal individuation responses to inverted faces.

Instead, the large magnitude of the inversion effects in the individuation response suggests that holistic processing is intact in participants with autism at the perceptual level. The lack of any interaction of group and orientation in the present study appears to be inconsistent with the results of ERP studies suggesting that, as evinced by abnormal amplitudes, holistic processing is disrupted in individuals on the autism spectrum (McPartland et al., 2004; McPartland et al., 2011). On the other hand, the lack of a group-orientation interaction appears to buttress the conclusions of a recent review of behavioural studies by Weigelt et al. (2012), who argue against the existence of qualitative differences in face processing in autism. While ASD may still be associated with weaknesses in the areas of integrative and holistic processing (see Frith, 2003; Just, Cherkassy, Keller, & Minshew, 2004; Vermeulen, 2012), such impairments might be restricted to higher cognitive functions, rather than face perception. However, it should be noted that some electrophysiological studies suggestive of abnormal holistic processing in ASD found differences in ERP latency, rather than amplitude (McPartland et al., 2004; Tye et al., 2015). In order to investigate the inversion effects in the latency, the EEG data was analyzed in the time domain (see Supplementary Materials) following the procedures in Dzhelyova & Rossion (2014) and Retter & Rossion (2016). No group by orientation interaction was found in the latency of N170 elicited by oddball faces, consolidating the finding that both the ASD and TD groups had comparable face inversion effect in EEG. However, it should be noted that, given the heterogeneity of the autism spectrum, it is also possible that the ASD sample from the present study is not representative of the entire ASD population with regards to holistic face processing.

Statistical comparison of the occipito-temporal individuation responses in ASD and TD individuals yielded neither a main effect of group nor any interactions with group. This implies that individuals on the autism spectrum were no less sensitive to changes in face identities than TD controls, which appears to be inconsistent with behavioural studies demonstrating that individuals on the autism spectrum often show impairments in face recognition. There are several possible explanations for this unanticipated result. Given the heterogeneity of the autism spectrum, it is possible that the particular sample of individuals tested in the present study were unusually skilled at recognizing faces. However, participants on the autism spectrum performed poorly on the CFMT, suggesting that this is unlikely to be the case. Alternatively, given the high inter-individual variability in response amplitudes, the

present study may have lacked sufficient power to detect a real group difference in perceptual discrimination of faces. However, the apparent lack of any substantial tendency towards group differences in the FPVS individuation response may be inconsistent with this interpretation. Instead, recalling that the FPVS individuation response may primarily reflect perceptual discrimination of face identities rather than memory for face identities, it is possible that the lack of group differences in the FPVS individuation response indicates that perceptual sensitivity to face identity is intact in ASD, and that face recognition impairments in ASD are instead located in the domain of face memory.

The interpretation of this study's results as being consistent with the existence of impairments in face memory, but intact face perception, in ASD appears to be supported by the low scores obtained by participants with autism on the CFMT. Despite the lack of group differences in the FPVS individuation response, the CFMT scores of participants with ASD appeared to be lower than norms for TD people. This poor CFMT performance is consistent with the results of a number of previous studies which used the CFMT to investigate face perception in individuals on the autism spectrum (Ewbank et al., 2017; Hedley et al., 2011; Kirchner et al., 2011; Lynn et al., 2016; O'Hearn et al., 2010; Schelinski et al., 2017; Scherf et al., 2015).

Evidence does suggest that face perception and face memory can be dissociated from one another. When a previous study examined the relationship between the FPVS individuation response and scores on the CFMT, the relatively weak correlation between the measures suggested they examine different aspects of face processing (Xu et al., 2017). The present study offers further support to this idea. While the small size of the group of participants with autism suggests that considerable caution should be exercised in interpreting correlations, no association was found between CFMT scores and FPVS individuation responses in the present study. Research with typically-developing individuals also indicates that face memory, but not face perception, shows a domain-specific developmental trajectory (Weigelt et al., 2014). While face memory shows greater age-related improvements than non-face memory, face perceptual discrimination appears to develop similarly to non-face perceptual discrimination.

Furthermore, the idea that people with ASD have impairments in face memory, but not face perception, appears to be consistent with previous research. A review of behavioural studies suggests that individuals with autism have particular difficulty with face memory, over and above the perceptual discrimination of faces (Weigelt et al., 2012,

pp. 1070–1078).

In summary, this study investigated the face inversion effect in ASD as compared to the TD controls using the FPVS method. The EEG results showed that both groups exhibited face inversion effects of similar size in both the generic and individuation responses, suggesting that individuals with ASD had intact holistic processing in face perception. However, participants with ASD performed below normative levels in the behavior face memory test measured by the CFMT, suggesting that face recognition impairments in autism are located outside the domain of immediate perception, possibly but within the domain of face memory.

The current study is not without limitations. Although inclusion criteria included high-functioning autism (i.e., lack of intellectual disability), it is possible that there were differences in cognitive ability between the ASD and control groups. Future research could determine whether these results can be replicated when IQ is controlled for. Future research could also subject the relationships between the FPVS individuation response and behavioural tasks to further examination. Previous studies have found only a modest correlation between the FPVS individuation response and the CFMT (Xu et al., 2017), and this correlation was not found in the sample of participants with autism in the present study. If the FPVS individuation response is, indeed, primarily a measure of face discrimination at a perceptual level, the correlation between the individuation response and performance on a behavioural face discrimination task might be more robust.

## Acknowledgments

This work was supported by the Natural Sciences and Engineering Research Council of Canada and the Temporal Dynamics of Learning Center (NSF grant no. SBE-0542013) awarded to James Tanaka. We would also like to thank Authors with Autism for their support in participant recruitment.

## References

- Alonso-Prieto, E. (2011). Studying face individualization through event related potentials and steady state techniques in healthy and prosopagnosic individuals (Doctoral dissertation). Retrieved from DIAL.pr. <http://dx.doi.org/2078.1/110135>.
- Alonso-Prieto, E., Van Belle, G., Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2013). The 6 Hz fundamental stimulation frequency rate for individual face discrimination in the right occipito-temporal cortex. *Neuropsychologia*, *51*, 2863–2875. <https://doi.org/10.1016/j.neuropsychologia.2013.08.018>.
- Annaz, D., Karmiloff-Smith, A., Johnson, M. H., & Thomas, M. S. C. (2009). A cross-syndrome study of the development of holistic face recognition in children with autism, down syndrome, and Williams syndrome. *Journal of Experimental Child Psychology*, *102*(4), 456–486. <https://doi.org/10.1016/j.jecp.2008.11.005>.
- Barton, J. J. S., Hefter, R. L., Cherkasova, M. V., & Manoach, D. S. (2007). Investigations of face expertise in the social developmental disorders. *Neurology*, *69*(9), 860–870. <https://doi.org/10.1212/01.wnl.0000267842.85646.f2>.
- Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, *8*(6), 551–565. <https://doi.org/10.1162/jocn.1996.8.6.551>.
- Bookheimer, S. Y., Wang, A. T., Scott, A., Sigman, M., & Dapretto, M. (2008). Frontal contributions to face processing differences in autism: Evidence from fMRI of inverted face processing. *Journal of the International Neuropsychological Society*, *14*(6), 922–932. <https://doi.org/10.1017/S135561770808140X>.
- Brosnan, M., Lewton, M., & Ashwin, C. (2016). Reasoning on the autism spectrum: A dual process theory account. *Journal of Autism and Developmental Disorders*, *46*(6), 2115–2125. <https://doi.org/10.1007/s10803-016-2742-4>.
- Bushnell, I. W. R. (2001). Mother's face recognition in newborn infants: Learning and memory. *Infant and Child Development*, *10*, 67–74. <https://doi.org/10.1002/icd.248>.
- Churches, O., Damiano, C., Baron-Cohen, S., & Ring, H. (2012). Getting to know you: The acquisition of new face representations in autism spectrum conditions. *NeuroReport*, *23*(11), 668–672. <https://doi.org/10.1097/WNR.0b013e3283556658>.
- Croydon, A., Pimperton, H., Ewing, L., Duchaine, B. C., & Pellicano, E. (2014). The Cambridge Face Memory Test for Children (CFMT-C): A new tool for measuring face recognition skills in childhood. *Neuropsychologia*, *62*, 60–67. <https://doi.org/10.1016/j.neuropsychologia.2014.07.008>.
- Davies, S., Bishop, D., Manstead, A. S. R., & Tantam, D. (1994). Face perception in children with autism and Asperger's Syndrome. *Journal of Child Psychology and Psychiatry*, *35*(6), 1033–1057. <https://doi.org/10.1111/j.1469-7610.1994.tb01808.x>.
- Dimitriou, D., Leonard, H. C., Karmiloff-Smith, A., Johnson, M. H., & Thomas, M. S. C. (2015). Atypical development of configural face recognition in children with autism, Down syndrome and Williams syndrome. *Journal of Intellectual Disability Research*, *59*(5), 422–438. <https://doi.org/10.1111/jir.12141>.
- Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, *44*, 576–585. <https://doi.org/10.1016/j.neuropsychologia.2005.07.001>.
- Dunlop, W. A., Enticott, P. G., & Rajan, R. (2016). Speech discrimination difficulties in high-functioning autism spectrum disorder are likely independent of auditory hypersensitivity. *Frontiers in Human Neuroscience*, *10*, 401. <https://doi.org/10.3389/fnhum.2016.00401>.
- Dzhelyova, M., & Rossion, B. (2014). The effect of parametric size variation on individual face discrimination indexed by fast periodic visual stimulation. *BMC Neuroscience*, *15*, 87. <https://doi.org/10.1186/1471-2202-15-87>.
- Ewbank, M. P., Pell, P. J., Powell, T. E., von dem Hagen, E. A. H., Baron-Cohen, S., & Calder, A. J. (2017). Repetition suppression and memory for faces is reduced in adults with autism spectrum conditions. *Cerebral Cortex*, *27*(1), 92–103. <https://doi.org/10.1093/cercor/bhw373>.
- Ewing, L., Pellicano, E., & Rhodes, G. (2013). Using effort to measure reward value of faces in children with autism. *PLoS One*, *8*(11), e79493. <https://doi.org/10.1371/journal.pone.0079493>.
- Falck-Ytter, T. (2008). Face inversion effects in autism: A combined looking time and pupillometric study. *Autism Research*, *1*(5), 297–306. <https://doi.org/10.1002/aur.45>.
- Frith, U. (2003). *Autism: Explaining the enigma* (2nd ed.). Malden, MA: Blackwell Publishing.
- Fujita, T., Kamio, Y., Yamasaki, K., Yasumoto, S., Hirose, S., & Tobimatsu, S. (2013). Altered automatic face processing in individuals with high-functioning autism spectrum disorders: Evidence from visual evoked potentials. *Research in Autism Spectrum Disorders*, *7*(6), 710–720. <https://doi.org/10.1016/j.rasd.2013.03.001>.
- Guillon, Q., Rogé, B., Afzali, M. H., Baduel, S., Kruck, J., & Hadjikhani, N. (2016). Intact perception but abnormal orientation towards face-like objects in young children with ASD. *Scientific Reports*, *6*, 22119. <https://doi.org/10.1038/srep22119>.
- Hedley, D., Brewer, N., & Young, R. (2011). Face recognition performance of individuals with Asperger syndrome on the Cambridge face memory test. *Autism Research*, *4*(6), 449–455. <https://doi.org/10.1002/aur.214>.
- Hedley, D., Brewer, N., & Young, R. (2015). The effect of inversion on face recognition in adults with autism spectrum disorder. *Journal of Autism and Developmental Disorders*, *45*(5), 1368–1379. <https://doi.org/10.1007/s10803-014-2297-1>.
- Hobson, R. P., Ouston, J., & Lee, A. (1988). What's in a face? The case of autism. *British Journal of Psychology*, *79*(4), 441–453. <https://doi.org/10.1111/j.2044-8295.1988.tb02745.x>.
- Just, M. A., Cherkassy, V. L., Keller, T. A., & Minshew, N. J. (2004). Cortical activation and synchronization during sentence comprehension in high-functioning autism: Evidence of underconnectivity. *Brain*, *127*(8), 1811–1821. <https://doi.org/10.1093/brain/awh199>.
- Key, A. P., & Corbett, B. A. (2014). ERP responses to face repetition during passive viewing: A nonverbal measure of social motivation in children with autism and typical development. *Developmental Neuropsychology*, *39*(6), 474–495. <https://doi.org/10.1080/87565641.2014.940620>.
- Key, A. P. F., & Stone, W. L. (2012). Processing of novel and familiar faces in children at average and high risk for autism. *Developmental Cognitive Neuroscience*, *2*(2), 244–255. <https://doi.org/10.1016/j.dcn.2011.12.003>.
- Kirchner, J. C., Hatiri, A., Heekeren, H. R., & Dziobek, I. (2011). Autistic symptomatology, face processing abilities, and eye fixation patterns. *Journal of Autism and Developmental Disorders*, *41*(2), 158–167. <https://doi.org/10.1007/s10803-010-1032-9>.
- Klin, A., Sparrow, S. S., de Bildt, A., Cicchetti, D. V., Cohen, D. J., & Volkmar, F. R. (1999). A normed study of face recognition in autism and related disorders. *Journal of Autism and Developmental Disorders*, *29*(6), 499–508. <https://doi.org/10.1023/A:1022299920240>.
- Lahaie, A., Mottron, L., Arguin, M., Berthiaume, C., Jemel, B., & Saumier, D. (2006). Face perception in high-functioning autistic adults: Evidence for superior processing of face parts, not for a configural face-processing deficit. *Neuropsychology*, *20*(1), 30–41. <https://doi.org/10.1037/0894-4105.20.1.30>.
- Libero, L. E., Reid, M. A., White, D. M., Salibi, N., Lahti, A. C., & Kana, R. K. (2016). Biochemistry of the cingulate cortex in autism: An MR spectroscopy study. *Autism Research*, *9*(6), 643–657. <https://doi.org/10.1002/aur.1562>.
- Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, *52*, 57–72. <https://doi.org/10.1016/j.neuropsychologia.2013.10.022>.
- Liu-Shuang, J., Torfs, K., & Rossion, B. (2016). An objective electrophysiological marker of face individualisation impairment in acquired prosopagnosia with fast periodic visual stimulation. *Neuropsychologia*, *83*, 100–113. <https://doi.org/10.1016/j.neuropsychologia.2015.08.023>.
- Lynn, A. C., Padmanabhan, A., Simmonds, D., Foran, W., Hallquist, M. N., Luna, B., & O'Hearn, K. (2016). Functional connectivity differences in autism during face and car recognition: Underconnectivity and atypical age-related changes. Advance online publication *Developmental Science*. <https://doi.org/10.1111/desc.12508>.
- Luck, S. (2014). *An introduction to the event-related potential technique* [PDF] (2nd ed.). Cambridge, MA: MIT Press Retrieved from <http://ebookcentral.proquest.com>.
- McPartland, J. C., Dawson, G., Webb, S. J., Panagiotides, H., & Carver, L. J. (2004). Event-related brain potentials reveal anomalies in temporal processing of faces in autism spectrum disorder. *Journal of Child Psychology and Psychiatry*, *45*(7), 1235–1245. <https://doi.org/10.1111/j.1469-7610.2004.00318.x>.
- McPartland, J. C., Wu, J., Bailey, C. A., Mayes, L. C., Schultz, R. T., & Klin, A. (2011).

- Atypical neural specialization for social percepts in autism spectrum disorder. *Social Neuroscience*, 6, 436–451. <https://doi.org/10.1080/17470919.2011.586880>.
- Neuhauser, E., Kresse, A., Faja, S., Bernier, R. A., & Webb, S. J. (2016). Face processing among twins with and without autism: Social correlates and twin concordance. *Social Cognitive and Affective Neuroscience*, 11(1), 44–54. <https://doi.org/10.1093/scan/nsv085>.
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottareau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision*, 15(6): 4, 1–46. <https://doi.org/10.1167/15.6.4>.
- O'Brien, J., Spencer, J., Girges, C., Johnston, A., & Hill, H. (2014). Impaired perception of facial motion in autism spectrum disorder. *PLoS One*, 9(7), e102173. <https://doi.org/10.1371/journal.pone.0102173>.
- O'Connor, K., Hamm, J. P., & Kirk, I. J. (2005). The neurophysiological correlates of face processing in adults and children with Asperger's syndrome. *Brain and Cognition*, 59(1), 82–95. <https://doi.org/10.1016/j.bandc.2005.05.004>.
- O'Hearn, K., Schroer, E., Minshew, N., & Luna, B. (2010). Lack of developmental improvement on a face memory task during adolescence in autism. *Neuropsychologia*, 48, 3955–3960. <https://doi.org/10.1016/j.neuropsychologia.2010.08.024>.
- Reed, C. L., Beall, P. M., Stone, V. E., Kopeloff, L., Pulham, D. J., & Hepburn, S. L. (2007). Brief report: Perception of body posture – what individuals with autism spectrum disorder might be missing. *Journal of Autism and Developmental Disorders*, 37(8), 1576–1584. <https://doi.org/10.1007/s10803-006-0220-0>.
- Rhodes, G., Ewing, L., Jeffery, L., Avard, E., & Taylor, L. (2014). Reduced adaptability, but no fundamental disruption, of norm-based face-coding mechanisms in cognitively able children and adolescents with autism. *Neuropsychologia*, 62, 262–268. <https://doi.org/10.1016/j.neuropsychologia.2014.07.030>.
- Rhodes, G., Neumann, M. F., Ewing, L., & Palermo, R. (2015). Reduced set averaging of face identity in children and adolescents with autism. *The Quarterly Journal of Experimental Psychology*, 68(7), 1391–1403. <https://doi.org/10.1080/17470218.2014.981554>.
- Ritvo, A. R. (2013). RAADS-R. In F. Volkmar (Ed.), *Encyclopedia of autism spectrum disorders* (pp. 2489–2491). New York: Springer. [https://doi.org/10.1007/978-1-4419-1698-3\\_1993](https://doi.org/10.1007/978-1-4419-1698-3_1993).
- Ritvo, R. A., Ritvo, E. R., Guthrie, D., Ritvo, M. J., Hufnagel, D. H., McMahon, W., ... Eloff, J. (2011). The Ritvo Autism Asperger Diagnostic Scale-Revised (RAADS-R): A scale to assist the diagnosis of autism spectrum disorder in adults: An international validation study. *Journal of Autism and Developmental Disorders*, 41(8), 1076–1089. <https://doi.org/10.1007/s10803-010-1133-5>.
- Rose, F. E., Lincoln, A. J., Lai, Z., Ene, M., Searcy, Y. M., & Bellugi, U. (2007). Orientation and affective expression effects on face recognition in Williams syndrome and autism. *Journal of Autism and Developmental Disorders*, 37(3), 513–522. <https://doi.org/10.1007/s10803-006-0200-4>.
- Rosset, D. B., Rondan, C., Da Fonseca, D., Santos, A., Assouline, B., & Deruelle, C. (2008). Typical emotion processing for cartoon but not for real faces in children with autism spectrum disorders. *Journal of Autism and Developmental Disorders*, 38(5), 919–925. <https://doi.org/10.1007/s10803-007-0465-2>.
- Rossion, B. (2008). Picture-plane inversion leads to qualitative changes of face perception. *Acta Psychologica*, 128(2), 274–289. <https://doi.org/10.1016/j.actpsy.2008.02.003>.
- Rossion, B. (2013). The composite face illusion: A whole window into our understanding of holistic face perception. *Visual Cognition*, 21(2), 139–253. <https://doi.org/10.1080/13506285.2013.772929>.
- Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. *Experimental Brain Research*, 232(6), 1599–1621. <https://doi.org/10.1007/s00221-014-3934-9>.
- Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *NeuroReport*, 11(1), 69–74. <https://doi.org/10.1097/00001756-200001170-00014>.
- Rossion, B., & Jacques, C. (2011). The N170: Understanding the time-course of face perception in the human brain. In E. S. Kappenman, & S. J. Luck (Eds.), *The Oxford handbook of event-related potential components* (pp. 115–142). Oxford, UK: Oxford University Press.
- Rutherford, M. D., Clements, K. A., & Sekuler, A. B. (2007). Differences in discrimination of eye and mouth displacement in autism spectrum disorders. *Vision Research*, 47(15), 2099–2110. <https://doi.org/10.1016/j.visres.2007.01.029>.
- Schelinski, S., Roswandowitz, C., & von Kriegstein, K. (2017). Voice identity processing in autism spectrum disorder. *Autism Research*, 10(1), 155–168. <https://doi.org/10.1002/aur.1639>.
- Scherf, K. S., Behrmann, M., Minshew, N., & Luna, B. (2008). Atypical development of face and greeble recognition in autism. *Journal of Child Psychology and Psychiatry*, 49(8), 838–847. <https://doi.org/10.1111/j.1469-7610.2008.01903.x>.
- Scherf, K. S., Elbich, D., Minshew, N., & Behrmann, M. (2015). Individual differences in symptom severity and behavior predict neural activation during face processing in adolescents with autism. *NeuroImage*, 7, 53–67. <https://doi.org/10.1016/j.neuroimage.2014.11.003>.
- Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology*, 75(2), 329–340. <https://doi.org/10.1002/aur.56>.
- Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *The Quarterly Journal of Experimental Psychology: Section A*, 46(2), 225–245. <https://doi.org/10.1080/14640749308401045>.
- Tantam, D., Monaghan, L., Nicholson, H., & Stirling, J. (1989). Autistic children's ability to interpret faces: A research note. *Journal of Child Psychology and Psychiatry*, 30(4), 623–630. <https://doi.org/10.1111/j.1469-7610.1989.tb00274.x>.
- Tavares, P. P., Mouga, S. S., Oliveira, G. G., & Castelo-Branco, M. (2016). Preserved face inversion effects in adults with autism spectrum disorder: An event-related potential study. *NeuroReport*, 27(8), 587–592. <https://doi.org/10.1097/WNR.0000000000000576>.
- Teunisse, J.-P., & de Gelder, B. (2003). Face processing in adolescents with autistic disorder: The inversion and composite effects. *Brain and Cognition*, 52(3), 285–294. [https://doi.org/10.1016/S0278-2626\(03\)00042-3](https://doi.org/10.1016/S0278-2626(03)00042-3).
- Turati, C., Macchi Cassia, V., Simion, F., & Leo, I. (2006). Newborns' face recognition: Role of inner and outer facial features. *Child Development*, 77(2), 297–311. <https://doi.org/10.1111/j.1467-8624.2006.00871.x>.
- Tye, C., Farroni, T., Volein, A., Mercure, E., Tucker, L., Johnson, M. H., & Bolton, P. F. (2015). Autism diagnosis differentiates neurophysiological responses to faces in adults with tuberous sclerosis complex. *Journal of Neurodevelopmental Disorders*, 7, 33. <https://doi.org/10.1186/s11689-015-9129-2>.
- Tye, C., Mercure, E., Ashwood, K. L., Azadi, B., Asherson, P., Johnson, M. H., ... McLoughlin, G. (2013). Neurophysiological responses to faces and gaze direction differentiate children with ASD, ADHD and ASD + ADHD. *Developmental Cognitive Neuroscience*, 5, 71–85. <https://doi.org/10.1016/j.dcn.2013.01.001>.
- Van der Geest, J. N., Kemner, C., Verbaten, M. N., & van Engeland, H. (2002). Gaze behavior of children with pervasive developmental disorder toward human faces: A fixation time study. *Journal of Child Psychology and Psychiatry*, 43(5), 669–678. <https://doi.org/10.1111/1469-7610.00055>.
- Vermeulen, P. (2012). *Autism as context blindness*. Shawnee Mission, KS: AAPC Publishing.
- Webb, S. J., Jones, E. J. H., Merkle, K., Murias, M., Greenson, J., Richards, T., ... Dawson, G. (2010). Response to familiar faces, newly familiar faces, and novel faces as assessed by ERPs is intact in adults with autism spectrum disorders. *International Journal of Psychophysiology*, 77(2), 106–117. <https://doi.org/10.1016/j.ijpsycho.2010.04.011>.
- Webb, S. J., Merkle, K., Murias, M., Richards, T., Aylward, E., & Dawson, G. (2012). ERP responses differentiate inverted but not upright face processing in adults with ASD. *Social Cognitive and Affective Neuroscience*, 7(5), 578–587. <https://doi.org/10.1093/scan/nsq002>.
- Weigelt, S., Koldewyn, K., Dilks, D. D., Balas, B., McKone, E., & Kanwisher, N. (2014). Domain-specific development of face memory but not face perception. *Developmental Science*, 17(1), 47–58. <https://doi.org/10.1111/desc.12089>.
- Weigelt, S., Koldewyn, K., & Kanwisher, N. (2012). Face identity recognition in autism spectrum disorders: A review of behavioural studies. *Neuroscience and Biobehavioral Reviews*, 36(3), 1060–1084. <https://doi.org/10.1016/j.neubiorev.2011.12.008>.
- Whyte, E. M., Behrmann, M., Minshew, N. J., Garcia, N. V., & Scherf, K. S. (2015). Animal, but not human, faces engage the distributed face network in adolescents with autism. *Developmental Science*, 19(2), 306–317. <https://doi.org/10.1111/desc.12305>.
- Wilmer, J. B., Germine, L., Chabris, C. F., Chatterjee, G., Gerbasi, M., & Nakayama, K. (2012). Capturing specific abilities as a window into human individuality: The example of face recognition. *Cognitive Neuropsychology*, 29(5–6), 360–392. <https://doi.org/10.1080/02643294.2012.753433>.
- Wolf, J. M., Tanaka, J. W., Klaiman, C., Cockburn, J., Herlihy, L., Brown, C., ... Schultz, R. T. (2008). Specific impairment of face-processing abilities in children with autism spectrum disorder using the *Let's Face It!* skills battery. *Autism Research*, 1(6), 329–340. <https://doi.org/10.1002/aur.56>.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81(1), 141–145. <https://doi.org/10.1037/h0027474>.
- Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configural information in face perception. *Perception*, 16(6), 747–759. <https://doi.org/10.1068/p160747>.
- Xu, B., Liu-Shuang, J., Rossion, B., & Tanaka, J. W. (2017). Individual differences in face identity processing with fast periodic visual stimulation. *Journal of Cognitive Neuroscience*, 29(8), 1368–1377. [https://doi.org/10.1162/jocn\\_a\\_01126](https://doi.org/10.1162/jocn_a_01126).
- Zimmerman, D. L., Ownsworth, T., O'Donovan, A., Roberts, J., & Gullo, M. J. (2016). Independence of hot and cold executive function deficits in high-functioning adults with autism spectrum disorder. *Frontiers in Human Neuroscience*, 10, 24. <https://doi.org/10.3389/fnhum.2016.00024>.
- Zimmerman, D. L., Ownsworth, T., O'Donovan, A., Roberts, J., & Gullo, M. J. (2017). Associations between executive functions and mental health outcomes for adults with autism spectrum disorder. *Psychiatry Research*, 253, 360–363. <https://doi.org/10.1016/j.psychres.2017.04.023>.