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Journal

Social Neuroscience, 13(1)

ISSN

1747-0919

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Publication Date

2018-01-02

DOI

10.1080/17470919.2016.1248788

Peer reviewed



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To cite this article: Katherine K. M. Stavropoulos, Michaela Viktorinova, Adam Naples, Jennifer Foss-Feig & James C. McPartland (2016): Autistic traits modulate conscious and nonconscious face perception, *Social Neuroscience*, DOI: [10.1080/17470919.2016.1248788](https://doi.org/10.1080/17470919.2016.1248788)

To link to this article: <http://dx.doi.org/10.1080/17470919.2016.1248788>



Accepted author version posted online: 18 Oct 2016.
Published online: 10 Nov 2016.



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Autistic traits modulate conscious and nonconscious face perception

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ABSTRACT

Difficulty with emotion perception is a core feature of autism spectrum disorder (ASD) that is also associated with the broader autism phenotype. The current study explored the neural underpinnings of conscious and nonconscious perceptions of affect in typically developing individuals with varying levels of autistic-like traits, as measured by the Autism Quotient (AQ). We investigated the relationship between autistic traits and face processing efficiency using event-related potentials (ERPs). In 20 typically developing adults, we utilized ERPs (the P100, N170, and P300) to measure differences in face processing for emotional faces that were presented either (a) too quickly to reach conscious awareness (16 ms) or (b) slowly enough to be consciously observed (200 ms). All individuals evidenced increased P100 and P300 amplitude and shorter N170 latencies for nonconscious versus consciously presented faces. Individuals with high AQ scores evidenced delayed ERP components. Nonconsciously perceived emotional faces elicited enhanced neural responses regardless of AQ score. Higher levels of autistic traits were associated with inefficient face perception (i.e., longer latency of ERP components). This delay parallels processing delays observed in ASD. These data suggest that inefficient social perception is present in individuals with subclinical levels of social impairment.

ARTICLE HISTORY

Received 10 March 2016
Revised 8 August 2016
Published online
14 November 2016

KEYWORDS

Event-related potential;
autistic traits; face
perception

Introduction

Autism is a neurodevelopmental disorder encompassing a wide range of socio-emotional impairments, as well as the presence of restricted or repetitive interests and atypical sensory response. Subclinical traits of autism are observed in the general population, with clinical status (i.e., meeting a diagnosis of autism) representing extreme values on a continuous distribution (Constantino & Todd, 2003). Self-reported autistic traits vary across the general population with the continuous distribution approaching clinical significance at its upper extreme (Hoekstra, Bartels, Verweij, & Boomsma, 2007; Ronald, Happé, Price, Baron-Cohen, & Plomin, 2006; Skuse, Mandy, & Scourfield, 2005). These findings are consistent with the notion of a *broader autism phenotype* (BAP; Folstein & Rutter, 1977). Originally coined to describe autistic traits in relatives of children with autism spectrum disorder (ASD), the term “BAP” is also used to refer to any individual that displays a subclinical set of characteristics resembling ASD, presumably with overlapping genetic contributions as the full-blown ASD phenotype (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001).

Autistic traits in a typically developing (TD) population are reflected in neural functioning. Using temporal (event-related potentials (ERPs)) neuroimaging techniques, Cox et al. (2015) reported attenuated neural activity to social versus nonsocial incentives among TD adults with high autistic traits compared to those with low autistic traits. Similarly, Carter Leno, Naples, Cox, Rutherford, and McPartland (2015) demonstrated that individuals with lower scores on the Social Responsiveness Scale (SRS; Constantino & Gruber, 2005) had enhanced neural responses to social versus nonsocial feedback, whereas individuals with higher scores on the SRS evidenced the opposite pattern (e.g., larger neural response to nonsocial vs. social feedback). Further, Puzzo, Cooper, Vetter, and Russo (2010) reported differential activity of the mirror neuron system as revealed by electroencephalogram (EEG) in individuals with high and low AQ scores. These studies support the notion that variability in autistic traits within TD populations can be linked to brain function.

Difficulty with emotional processing are commonly evident in ASD. This includes orienting (Dawson,

Meltzoff, Osterling, Rinaldi, & Brown, 1998) to, scanning (Pelphrey et al., 2002; Sasson et al., 2007), and interpreting emotional expressions (Ashwin, Chapman, Colle, & Baron-Cohen, 2006; Lindner & Rosén, 2006; Philip et al., 2010; Wallace, Coleman, & Bailey, 2008), which are all closely related to the extraction of mental states and bonding with others (Basch, 1983). Individuals with ASD exhibit aberrant neural activity in response to emotional faces (Dawson, Webb, & McPartland, 2005; Monk et al., 2010), even when behavioral indicators of emotion matching are intact (Wang, Dapretto, Hariri, Sigman, & Bookheimer, 2004). Evidence from temporal (ERPs) neuroimaging techniques indicates that face processing is delayed in ASD; that is, individuals with ASD show longer latency ERP components when viewing faces (McPartland, Dawson, Webb, Panagiotides, & Carver, 2004; McPartland et al., 2011; O'Connor, Hamm, & Kirk, 2007). Given the previous findings that individuals with ASD process faces more slowly than their typically developing peers, studies manipulating length of stimulus presentation may be informative for better understanding the neural systems underpinning face-processing delays in ASD. For example, nonconscious stimulus presentation, i.e., presentation of a stimulus at a duration too brief for awareness of perception, has been applied to investigate differences in the neural correlates of automatic versus intentional processing. Nonconscious perception has also been demonstrated to influence behavior; for example, Winkielman, Berridge, and Wilbarger (2005) found that presentation of nonconscious affective faces influenced participants' consumption and value ratings of a beverage, even when the subjects reported no change in mood or awareness of the nonconscious stimulus.

Both spatial (functional magnetic resonance imaging (fMRI)) and temporal (ERPs) neuroimaging techniques have been employed to investigate the neural basis of nonconscious processing. Early fMRI evidence demonstrated that when emotional faces are presented quickly (<40 ms) and immediately followed by a neutral face (producing "backwards masking"), subjects reported no awareness of the emotional face but showed increased right amygdala activation (Morris, Öhman, & Dolan, 1998). ERPs have also been used to index nonconscious brain activity (e.g., Balconi & Lucchiari, 2007; Kiss & Eimer, 2008; Pegna, Landis, & Khateb, 2008; Williams, Morris, McGlone, Abbott, & Mattingley, 2004). Nonconsciously presented masked faces elicit early negative ERP components similar to those elicited by consciously presented nonmasked faces. However, later components, occurring after 200 ms, increase in magnitude with stimulus duration (i.e., as stimulus increasingly can be consciously perceived; Pegna et al., 2008). This suggests that early

face processing occurs similarly for both conscious and nonconscious stimuli, but components often thought to index processes related to stimulus awareness (e.g., P300) may be enhanced for consciously presented stimuli.

Few studies have investigated nonconscious emotion processing in individuals with ASD. Of the behavioral studies that have been conducted, findings suggest that individuals with ASD are less affected by nonconscious information compared to TD controls (Hall, West, & Szatmari, 2007; Kamio, Wolf, & Fein, 2006). Neural studies of nonconscious emotion processing in ASD are sparse and variable. Relative to TD controls, individuals with ASD show reduced reactivity in response to briefly presented emotional faces, as indexed by fMRI (Kleinhans et al., 2011), electrophysiology (Fujita et al., 2013), and pupillometry methods (Nuske, Vivanti, Hudry, & Dissanayake, 2014). However, other studies suggest that individuals with ASD may have similar activation in the amygdala (but reduced activation in the fusiform) in response to backwards-masked stimuli (Hall, Doyle, Goldberg, West, & Szatmari, 2010). To our knowledge, the relationship between nonconscious emotional perception and subclinical levels of autistic traits has not yet been investigated.

The current study investigated the neural correlates of conscious and nonconscious perception of emotional faces in relation to autistic traits. Harnessing the temporal sensitivity of ERPs, the present study tested the sensitivity of early ERP components (P100, N170) indexing rapid emotional processing in the absence of awareness, as well as later components (P300) marking attention allocation. We predicted that individuals with high levels of autistic traits would have longer N170 and P100 latencies than individuals with low autistic traits, and that this effect would be more pronounced for nonconscious relative to consciously perceived face stimuli. The current study was designed to investigate whether previous findings of reduced sensitivity to briefly presented emotional faces in ASD is limited to individuals with ASD, or whether these findings can be replicated in a sample of TD adults with high versus low levels of autistic traits.

Methods

Participants

The sample consisted of 29 typically developing right-handed adults from the New Haven community recruited through local advertisements. Three subjects were excluded because of unusable EEG data (see "EEG recording and data analysis" section), one was excluded due to being able to consciously perceive very short duration (intended to achieve nonconscious perception) stimuli, and four were excluded due to absence

of behavioral data (see “Behavioral measures” section). All participants had normal or corrected-to-normal visual acuity, were medication-free, and had no reported history of either psychiatric or neurological disorders. Informed consent was obtained from all participants, as per approval of the Human Investigation Committee at the Yale School of Medicine. Thus, our final sample consisted of 20 subjects (age: $M = 22.68$ years, $SD = 1.67$; sex: 13 females)

Autism-spectrum quotient (AQ)

The AQ (Baron-Cohen et al., 2001) is a 50-item forced choice self-report questionnaire for adults that identifies and quantifies autistic traits. It uses a four-point scale (*definitely agree* – *slightly agree* – *slightly disagree* – *definitely disagree*) across five domains: social skills, attention switching, attention to detail, communication, and imagination. The individual scores one point for each answer that reflects abnormal or autistic-like behavior. This measure is sensitive to autistic traits in non-clinical populations (Bishop et al., 2004; Puzzo et al., 2010). A median split procedure was used to divide participants into groups with high (High AQ, $n = 9$) and low (Low AQ, $n = 11$) autistic traits based on their AQ scores (overall median = 16, range = 7–35. Low AQ group, $M = 12.15$, $SD = 2.91$; High AQ group, $M = 22.08$, $SD = 5.40$). The overall mean and standard deviations of the AQ in the current sample are comparable to those observed in a recent large-scale sample of 3900 TD individuals (Baron-Cohen et al., 2014).

Stimuli

Stimuli were adapted from the MacArthur face database, a standardized and well-established resource for experiments testing emotional face perception (Tottenham et al., 2009).¹ Color photographs of 31 unique individuals (15 female, 16 male) displaying neutral, fearful, and sad faces were selected. Ethnicity of the selected individuals was as follows: 23 European-American, 1 African-American, 2 Latino-American, and 5 Asian-American. Selected pictures were transformed into gray scale and further adjusted in Adobe Photoshop CS3 so that the eyes, eyebrows, nose, and mouth were the only visible features (Pegna et al., 2008). All stimuli were equiluminant and presented against a black background.

The final stimulus set consisted of 93 expressions of neutral, sad, and fearful affect. In the nonconscious condition, each of these stimuli was paired with its corresponding scrambled mask to prevent the appearance of a negative afterimage and to block visual awareness of the stimulus. Masks had the same visual properties as face stimuli. We chose scrambled faces rather than neutral expressions as masks to ensure that neural responses could be attributed to the emotional faces themselves, rather than to the subsequent mask (Kleinhans et al., 2011; Nuske et al., 2014).

Experimental design

Neutral, sad, and fearful faces were presented in both nonconscious (16 ms presentation) and conscious (200 ms presentation) conditions. The stimulus durations for the conscious and nonconscious conditions followed Pegna et al. (2008). To prevent anticipation effects, each trial started with a fixation cross-presented for a randomly varied duration of 500–900 ms. All the stimuli were backward masked (e.g., the stimulus occurred first, followed immediately by the mask) with scrambled faces displayed for 284 ms in the nonconscious condition and 100 ms in the conscious condition, such that the total duration of a target and a mask altogether was always 300 ms. A blank screen was always presented for 500 ms following the target and mask, after which a probe stimulus asked participants to press “1” if they saw an emotional face and “2” if they did not see an emotional face (i.e., the face they saw displayed a neutral expression). Once a response was given, there was a blank screen for 500 ms prior to onset of the subsequent trial.

In total, there were 360 trials with 60 trials for each of the six categories (fearful nonconscious, fearful conscious, neutral nonconscious, neutral conscious, sad nonconscious, and sad conscious). The experiment was divided into three 120-trial blocks. To minimize priming effects, stimuli were presented in a pseudo-random sequence such that no two sequential trials contained the same emotion. Figure 1 shows the order and timing of each trial.

During the EEG experiment, participants were seated in a dimly lit room and introduced to the experiment by instructions presented on a computer screen. A CRT display along with a computer running E-Prime 2.0 software was used for stimulus presentation. Images appeared in the center of the screen, subtending a

¹Development of the MacBrain Face Stimulus Set was overseen by Nim Tottenham and supported by the John D. and Catherine T. MacArthur Foundation Research Network on Early Experience and Brain Development. Please contact Nim Tottenham at tott0006@tc.umn.edu for more information concerning the stimulus set.

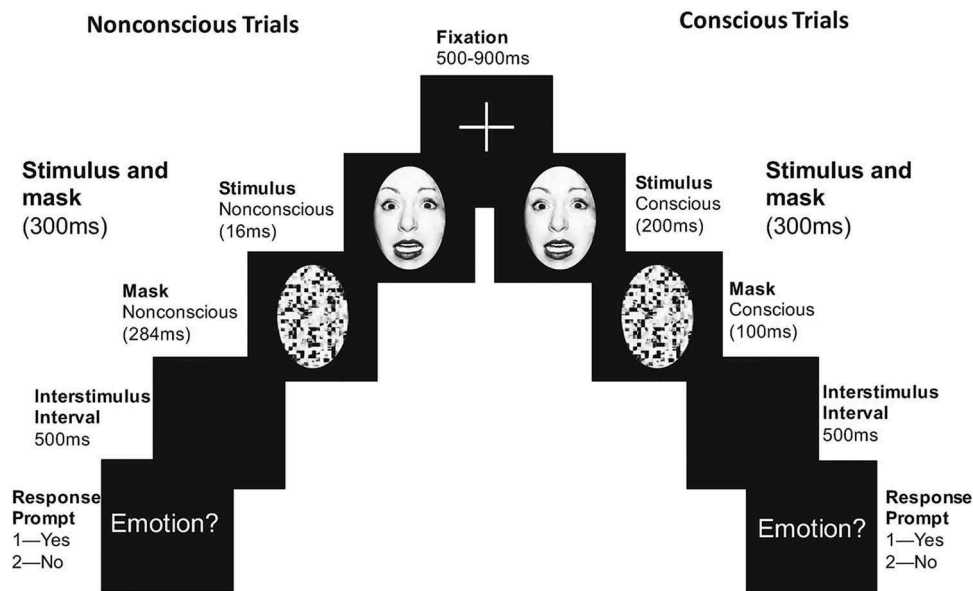


Figure 1. Order and timing of each trial. Conscious trial presentations are shown on the right, and nonconscious trial presentations are shown on the left.

horizontal angle of 6° and a vertical angle of 8.8° . The viewing distance was 75 cm. The total duration of the experiment was approximately 20 min. For each participant, the onset and offset times of all 360 trials were extracted from E-Prime and the stimulus display time was calculated to confirm that, as programmed, the nonconscious and conscious stimuli were presented consistently at 16 ms and 200 ms, respectively.

EEG recording and data analysis

Data were recorded using a 128 electrode Hydrocel Geodesic Sensor Net. During recording, electrodes were referenced to the vertex and impedances were kept below 40 k Ω . EEG was recorded with Netstation 4.4 software operated from an Apple Macintosh Computer (Powermac G5 running at 1.8 Ghz with 3GB of RAM) at 250 Hz. EEG signals recorded from Netstation were amplified (1000 \times) using an EGI System 200 amplifier.

EEG data were low-pass filtered off-line at 30 Hz. Filtered data were processed using ERPlab and EEGLab (Lopez-Calderon & Luck, 2014). Artifacts were removed via a four-step process. Data were inspected for large-scale drift, movement artifact, and high frequency noise exceeding ± 500 mV, and these artifacts were manually removed. Following this, data were epoched from -100 to 600 ms after stimulus presentation. Eye-blink artifacts were identified using

independent component analysis. Individual components were inspected alongside epoched data, and components responsible for blinks were removed. To remove any additional artifacts, we utilized a moving window peak-to-peak procedure in ERPlab (Lopez-Calderon & Luck, 2014) using a 200 ms moving window, 100 ms window step, and 150 mV voltage threshold. Prior to averaging, each subject's data were re-referenced to the average reference. Trial-by-trial data were averaged separately within each of the 6 conditions. Participants that had fewer than 15 trials in any condition were excluded from further analyses ($n = 3$). On average, participants had $M = 39.77$, $SD = 10.68$ trials in each condition, with no significant differences across conditions in number of trials retained ($p = .875$), or in number of trials across groups of high versus low AQ scores (all $ps > .5$).

Statistical analysis

Data were analyzed using repeated measures analyses of variance (ANOVAs) in SPSS (version 21), with follow-up t -tests to explore main effects and interactions detected in primary analyses. We used a significance threshold of .05 (corrected for multiple comparisons using Bonferroni correction when doing follow-up tests). Greenhouse Geisser corrected degrees of freedom were used when the assumption of sphericity was violated.

ERP measures

For the P100 and N170 components, $3 \times 2 \times 2 \times 2$ repeated measures ANOVAs were conducted with emotion (fear, neutral, sad), stimulus type (nonconscious, conscious), and hemisphere (right, left) as within-subjects variables. P100 amplitude was defined as the maximum amplitude between 90 and 150 ms after stimulus onset, and P100 latency was defined as the latency to the maximum amplitude between 90 and 150 ms after stimulus presentation. N170 amplitude was defined as the negative peak amplitude between 150 and 225 ms after stimulus presentation, and N170 latency was defined as the latency to the minimum amplitude between 150 and 225 ms after stimulus presentation. For the P300 component, $3 \times 2 \times 2$ repeated measures ANOVAs were conducted as above, without the hemisphere factor. P300 amplitude was defined as the maximum amplitude between 200 and 300 ms after stimulus onset, and P300 latency was defined as the latency to the maximum amplitude between 200 and 300 ms after stimulus presentation. P100 and N170 components were extracted for each participant by averaging over occipitotemporal electrodes. The P300 component was extracted for each participant by averaging over central-parietal electrodes. Electrode clusters for each component are shown in Figure 2. For all

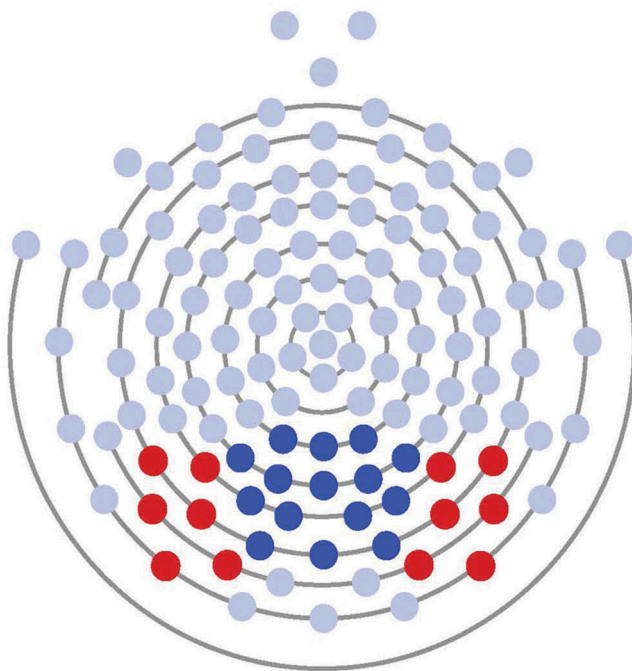


Figure 2. Electrode clusters for each component. The P100 and N170 components were extracted for each participant by averaging the activity over the occipitotemporal electrodes in red. The P300 component was extracted for each participant by averaging over the central-parietal electrodes in blue.

components, high versus low AQ was entered into the model as a between-subjects variable. When significant interactions were observed, follow-up pairwise comparison *t*-tests were run and corrected for multiple comparisons using the Bonferroni correction. If significant interactions between more than two variables were found, follow-up ANOVAs and (corrected) pairwise *t*-tests were run.

Results

Behavioral measures

Behavioral responses were analyzed for the 180 nonconscious trials in order to confirm that these trials were not consciously perceived. Proportions of “hits” (i.e., participants indicated they saw an emotional face when one was presented) and “false alarms” (i.e., participants indicated they saw an emotional face when the presented face was neutral) were computed. For a subset of participants ($n = 21$; behavioral data was unavailable for four participants), proportion of false alarms was subtracted from proportion of hits in order to determine behavioral accuracy for nonconscious trials. Participants with an accuracy rate of above 50% were excluded from ERP analysis ($n = 1$). For remaining participants with behavioral data ($n = 20$), a one-sample *t*-test was conducted on the behavioral accuracy proportion (proportion of hits minus proportion of false alarms), and compared against zero – which would be expected if participants were responding at chance levels for nonconscious trials. Behavioral accuracy proportions were not significantly different from zero, $t(19) = 1.78, p > .05$. Independent *t*-tests were conducted in order to compare accuracy between groups. No significant differences were observed between groups for either “hits” or “false alarms” for trials in the nonconscious condition (all $ps > .3$). The relationship between hits, false alarms, and AQ score was further explored using correlations. No significant relationship was observed between AQ score and hits or false alarms in the nonconscious condition ($r_s < .2$). Relationship between hits and false alarms and AQ score for both conscious and nonconscious conditions is displayed in Figure 3.

In order to confirm that subjects were able to successfully complete the behavioral task in the conscious condition, the 180 conscious trials were analyzed. Proportions of “hits” and “false alarms” were computed. Similarly to our method reported above for calculating behavioral accuracy during nonconscious trials, we subtracted false alarms from hits and conducted a one-sample *t*-test on the behavioral

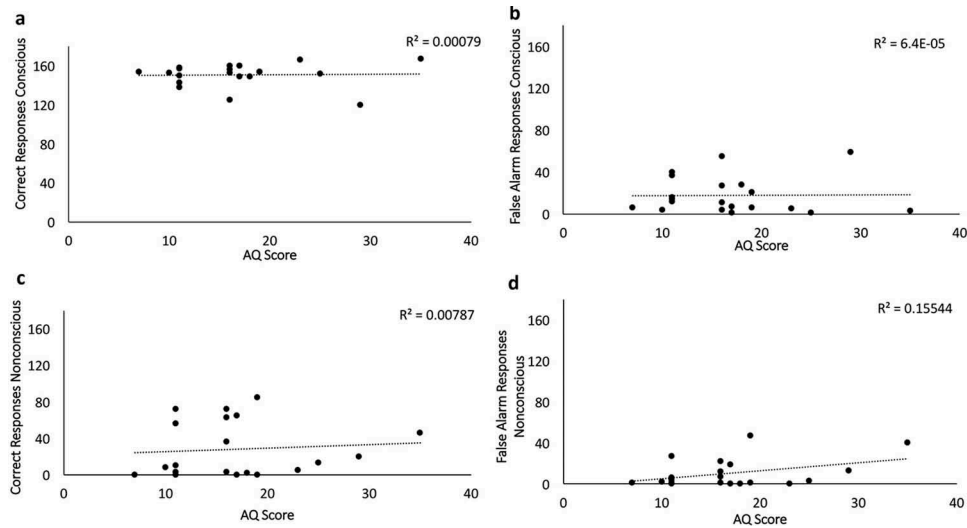


Figure 3. Scatter plots of participant behavioral performance. Panel A depicts the relationship between AQ score and correct responses in the conscious condition. Panel B depicts false alarm responses in the conscious condition. Panel C depicts correct responses in the nonconscious condition. Panel D depicts false alarm responses in the non-conscious condition.

accuracy proportion compared against zero. Participants' accuracy was significantly higher than zero on conscious trials, $t(19) = 20.69$, $p < .000$. Independent t -tests were conducted in order to compare accuracy between groups. No significant differences were observed between groups for either "hits" or "false alarms" for trials in the conscious condition ($ps > .3$). As with the nonconscious trials, the relationship between hits, false alarms, and AQ score was further explored using correlations. No significant relationship was observed between hits or false alarms and AQ score in the conscious condition ($rs < .1$). Detailed information about participant performance can be found in Table 1.

P100 amplitude

A significant main effect of stimulus type was found, $F(1, 18) = 10.72$, $p = .004$, $\eta^2 = .373$, such that nonconsciously presented faces elicited a larger P100 component than consciously presented faces. A significant emotion \times hemisphere interaction was observed, $F(2, 17) = 4.38$, $p = .029$, $\eta^2 = .340$. Pairwise comparisons revealed a marginal effect of hemisphere for fearful faces ($p = .086$, $\eta^2 = .155$) such that the P100 was larger

in the right versus left hemisphere for fearful faces regardless of AQ score. A significant interaction was found among emotion, stimulus type, hemisphere, and AQ score, $F(2, 17) = 5.27$, $p = .017$, $\eta^2 = .383$. To clarify this interaction, separate ANOVAs were conducted for each factor in the interaction. Subsequent ANOVAs comparing stimulus type revealed a significant effect of stimulus type for fearful faces in the right hemisphere for individuals with low AQ scores, such that nonconsciously presented fearful faces elicited a larger P100 in the right hemisphere versus consciously presented fearful faces ($p = .012$). Additionally, a significant effect of stimulus type in individuals with low AQ score for neutral faces in the left hemisphere was found, such that nonconsciously presented neutral faces elicited a larger P100 in the left hemisphere versus consciously presented neutral faces ($p = .019$). For individuals with high AQ scores, a significant effect of stimulus type was observed for neutral faces in the right hemisphere such that nonconsciously presented neutral faces elicited a larger P100 in the right hemisphere versus consciously presented neutral faces ($p = .026$). Figure 4 shows grand averaged waveforms from individuals with both high and low AQ scores in both conditions.

Table 1. Behavioral results for all subjects, subjects with Low AQ scores, and subjects with High AQ scores.

Group	Entire sample ($n = 20$)	Low AQ ($n = 11$)	High AQ ($n = 9$)	p -Value (between group differences)
Correct Conscious Mean (SD)	150.9 (11.8)	149.7 (10.4)	152.3 (13.8)	$p > .3$
False Alarm Conscious Mean (SD)	17.8 (17.7)	20.5 (16.9)	14.5 (19.1)	$p > .3$
Correct nonconscious Mean (SD)	27.9 (30.3)	29.3 (30.7)	26.2 (31.5)	$p > .3$
False Alarm nonconscious Mean (SD)	10.3 (13.9)	7.5 (9.1)	13.6 (18.2)	$p > .3$

Note that the maximum number of trials in each condition is 180. Presented as: Mean (Standard Deviation).

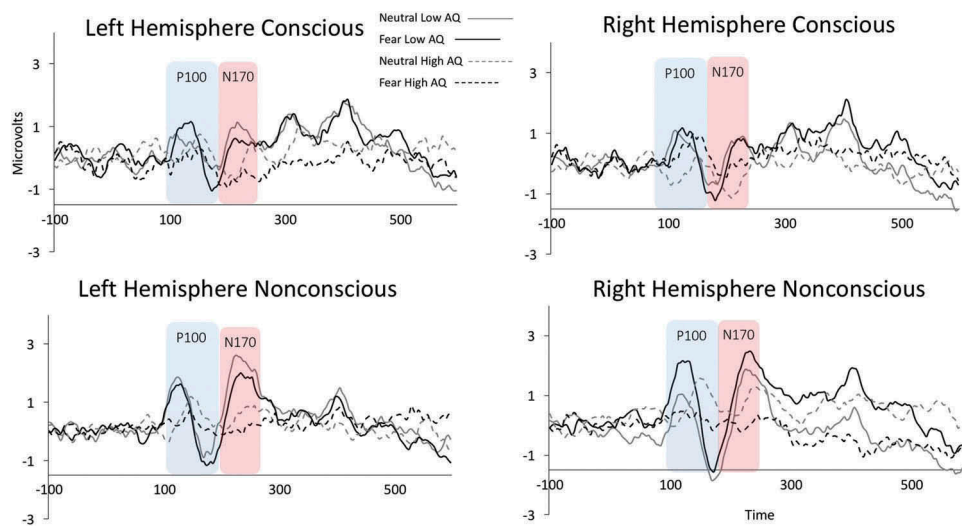


Figure 4. Grand averaged waveforms from individuals with both low and high AQ scores. Each hemisphere is shown separately, and is further separated by trial type (e.g., conscious versus nonconscious presentation). ERP response to neutral faces in individual with low AQ scores is shown in solid gray, response to fearful faces in individuals with low AQ scores are shown in solid black. ERP response to neutral faces in individuals with high AQ scores are shown in dashed gray, and response to fearful faces in individuals with high AQ scores in shown in dashed black.

P100 latency

A significant main effect of AQ score was found, $F(1, 18) = 9.36$, $p = .007$, $\eta^2 = .342$, wherein, across both conscious and nonconscious stimuli and all emotion conditions, individuals with high AQ scores had longer P100 latencies than did those with low AQ scores. No other pairwise comparisons were significant.

N170 amplitude

No significant main effects or interactions were observed.

N170 latency

A significant main effect of emotion was found, $F(2, 17) = 3.82$, $p = .043$, $\eta^2 = .31$. Pairwise comparisons revealed that sad faces elicited a marginally significantly faster N170 than neutral faces ($p = .065$). A significant main effect of stimulus type was found, $F(1, 18) = 5.42$, $p = .032$, $\eta^2 = .232$, such that nonconscious face presentations elicited a significantly faster N170 than conscious presentations. A significant main effect of AQ score was found, $F(1, 18) = 12.90$, $p = .002$, $\eta^2 = .418$, such that individuals with low AQ scores had a faster N170 than those with high AQ scores across all emotion and stimulus type conditions.

A significant interaction of emotion and AQ score was found, $F(2, 17) = 3.60$, $p = .05$, $\eta^2 = .298$. Follow-up pairwise comparisons revealed that, relative to

individuals with high AQ scores, individuals with low AQ scores had a significantly faster N170 to neutral faces ($p < .001$, $\eta^2 = .565$) and a significantly faster N170 response to fearful faces ($p = .011$, $\eta^2 = .310$). Individuals with low and high AQ scores did not differ in their N170 latency to sad faces. Figure 5 shows the interaction of emotion and AQ score. A significant interaction of stimulus type and AQ score was found, $F(1, 18) = 7.27$, $p = .015$, $\eta^2 = .288$. Follow-up pairwise

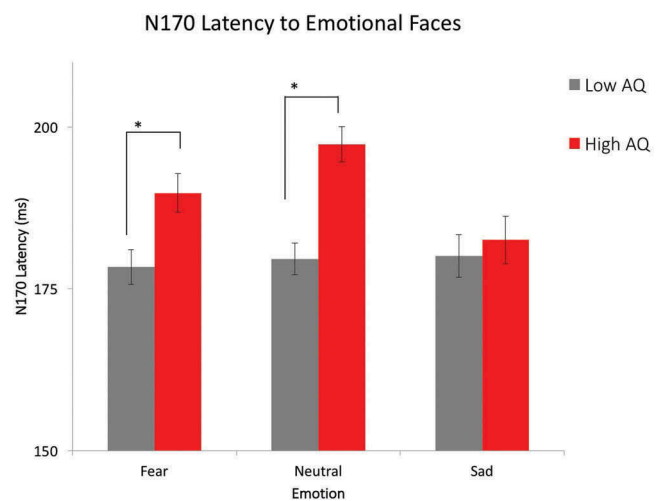


Figure 5. Latency to N170 in response to emotional faces (regardless of whether faces were presented consciously or nonconsciously) in individuals with high versus low AQ (Autism Quotient) scores. Individuals with low AQ scores are depicted in gray, and those with high AQ scores are depicted in red. * $< .05$.

comparisons revealed that, relative to individuals with high AQ scores, individuals with low AQ scores had a significantly faster N170 to both conscious ($p = .001$, $\eta^2 = .430$) and nonconscious ($p = .043$, $\eta^2 = .209$) stimulus presentations. Figure 3 shows grand averaged waveforms for individuals with both high and low AQ scores.

P300 amplitude

A marginal effect of stimulus type was observed, $F(1,18) = 3.19$, $p = .091$, $\eta^2 = .151$, such that nonconsciously presented faces elicited larger P300s compared to consciously presented faces across all emotion conditions and in both individuals with high and low AQ scores. No other significant main effects or interactions were found.

P300 latency

No significant main effects or interactions were observed.

Brain and behavior correlations

In order to explore relationship between AQ score and ERP components of interest in a quantitative manner, we conducted correlations between AQ score and amplitude and latency of P100, N170, and P300 components separately. In order to conduct meaningful correlations, we calculated the following five values for the amplitude and latency of each component: nonconscious (e.g., N170 latency for nonconscious stimulus

presentations collapsed across emotion and hemisphere), conscious (e.g., N170 latency for conscious stimulus presentations collapsed across emotion and hemisphere), fear (e.g., N170 latency for presentations of fearful faces collapsed across stimulus type and hemisphere), sad (e.g., N170 latency for presentations of sad faces collapsed across stimulus type and hemisphere), and neutral (e.g., N170 latency for presentations of neutral faces collapsed across stimulus type and hemisphere). We hypothesized that, similar to the ERP results reported above, significant correlations would be observed between AQ score and P100 and N170 latency.

P100

No significant correlations were observed between P100 amplitude and AQ score. Significant positive correlations were observed between P100 latency and nonconsciously presented trials ($r(18) = .505$, $p = .023$) and between P100 latency and neutral faces ($r(18) = .49$, $p = .027$). Significant correlations between ERP latency and AQ scores can be seen in Figure 6.

N170

No significant correlations were observed between N170 amplitude and AQ score. Significant positive correlations were observed between N170 latency for consciously presented trials and AQ score ($r = .572$, $p = .008$), as well as N170 latency in response to neutral faces and AQ score ($r = .582$, $p = .007$).

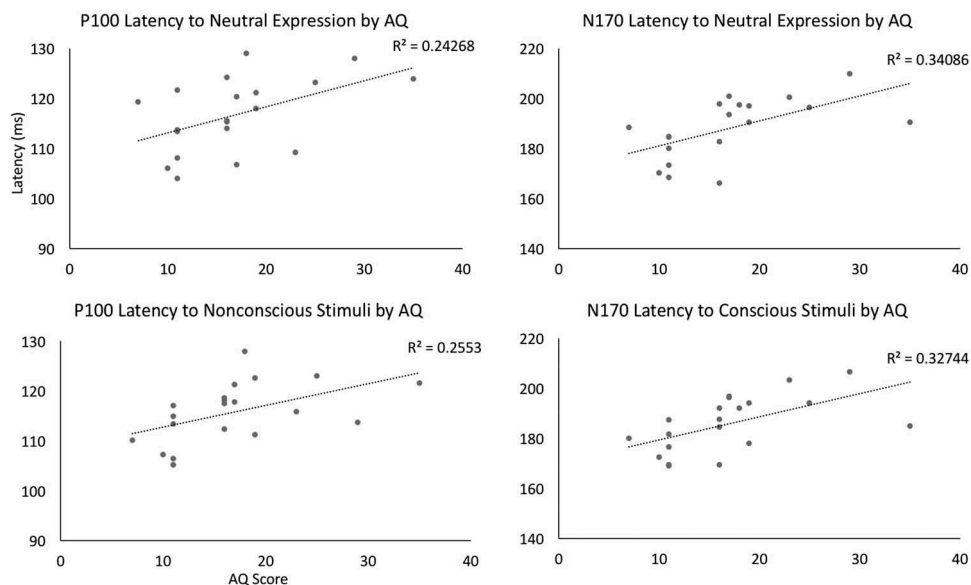


Figure 6. Scatter plots of the relationship between ERP components and Autism Quotient (AQ) score.

P300

No significant correlations were observed between P300 amplitude or latency and AQ score.

Discussion

This study investigated the electrophysiological correlates of emotional face processing in relation to subclinical autistic traits. By utilizing both consciously and nonconsciously presented stimuli, we hoped to gain understanding of the neural processes associated with rapid emotional processing and whether they are modulated by levels of autistic traits in typically developing individuals.

Results revealed enhanced P100 and marginally enhanced P300 amplitudes, as well as faster N170 latency during nonconscious versus conscious perception of face stimuli. This finding was independent of the emotion the face depicted or the participant's level of autistic traits. Although some previous investigations have not observed differences between conscious and nonconscious stimulus presentations (Genetti, Khateb, Heinzer, Michel, & Pegna, 2009), others have observed an enhanced P100 to nonconsciously presented stimuli (Smith, 2012). An enhanced P100 amplitude to nonconscious stimuli may reflect this component's sensitivity to rapid emotional processing, providing further evidence that the P100 is a marker of early stage emotional processing (Itier & Taylor, 2002; Utama, Takemoto, Koike, & Nakamura, 2009). Previous research suggests that the N170 is reliably elicited by nonconsciously presented faces, particularly those with fearful expressions (Kiss & Eimer, 2008; Pegna et al., 2008), but these studies have not found systematic differences in N170 latency for consciously versus unconsciously presented faces. While previous research has demonstrated that the P300 can be elicited reliably by nonconsciously presented stimuli (Bernat, Shevrin, & Snodgrass, 2001; Shevrin, 2001), whether consciously or nonconsciously presented emotional stimuli elicit more robust neural markers of attention and orienting remains unclear. Some previous studies have found attenuated P300 amplitudes for nonconsciously presented faces (Genetti et al., 2009), some have found equivalent P300 amplitudes (Balconi & Lucchiari, 2007), and others observe enhanced P300 amplitude for nonconsciously presented emotional faces (Balconi & Mazza, 2009; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004). Thus, our results are in agreement with some previous research, but inconsistent with others. One potential explanation for these discrepancies might be due to differences in stimulus presentation. Some previous studies utilized backwards masking with

neutral faces as the mask (Genetti et al., 2009; Liddell, Williams, Rathjen, Shevrin, & Gordon, 2004), while others used a variety of emotional expressions as the masking stimulus (Balconi & Mazza, 2009). It is important to note that the current study did not use faces as backwards masks but instead utilized scrambled faces. Thus, it is difficult to compare between previous P100 and P300 findings, as well as to directly compare them to the current study. However, further research should be undertaken on the role of the P100, N170, and P300 components in conscious versus nonconscious processing of emotional faces in order to clarify how changes in stimulus length affect neural correlates of both early emotion recognition and later attention and orienting.

Latencies for the P100 and N170 were delayed for individuals with higher levels of autistic traits relative to those with lower levels of autistic traits regardless of emotion or stimulus type. However, correlations suggest that this finding is most robust for presentations of neutral faces. Our correlations also suggest that the relationship between AQ score and ERP latency differs between ERP components. For the P100, a positive correlation was observed between AQ score and latency for nonconscious face presentations. That is, as AQ scores got higher (e.g., higher levels of autistic traits), P100 latency slowed for nonconscious trials. For N170, the same relationship was observed, but for conscious face presentations. This finding suggests that observed differences between individuals with high versus low AQ scores are most robust for nonconscious presentations during early components (P100), and most robust for conscious face presentations for later components (N170). These findings are consistent with those from clinical samples of individuals with ASD. Specifically, O'Connor, Hamm, and Kirk (2005) observed longer P100 and N170 latencies to emotional faces in individuals with Asperger's syndrome versus TD, and McPartland et al. (2004) found that compared to TD controls, individuals with ASD have longer N170 latencies to faces. Our results extend these findings to individuals with subclinical levels of autistic traits, adding to the body of evidence that N170 latency may represent a biomarker for social-communicative function spanning clinical and normative ranges of function (McPartland, Bernier, & South, 2015).

With regard to the effects of conscious versus nonconscious perception, no significant differences between groups were observed. That is, our finding that the P100 and P300 components are larger and N170 component occurs earlier in response to nonconscious versus consciously presented faces spans across both groups, and our findings that ERPs are generally slower in individuals with high versus low levels of

autistic traits span across both conscious and nonconscious stimulus presentations.

With respect to previous investigations of rapidly presented emotional faces in ASD, it is difficult to directly compare our results with those of either Kleinmans et al. (2011) or Nuske et al. (2014) due to inherent differences between fMRI, pupillometry, and electrophysiology. Broadly, however, our results extend previous findings by suggesting that differences in rapid face processing are observed not only when comparing individuals with ASD vs. TD but also within TD individuals separated by levels of autistic traits. The only previous study to use ERP to investigate rapidly presented faces in individuals with and without ASD found differences between groups for fearful faces versus objects (Fujita et al., 2013). The authors compared upright and inverted faces to upright and inverted objects and found that TD individuals had significantly larger N100 components in response to upright fearful faces vs. upright objects, while individuals with ASD did not have differences among stimuli. The authors did not find differences between or within groups for either the P100 or P300 components (Fujita et al., 2013). While our results differ those of Fujita et al. (2013), important differences were present between the two study designs and analysis, i.e., Fujita et al. (2013) were interested in differences in early evoked potentials for upright versus inverted faces versus objects, while the current study only investigated upright faces with different emotional expressions.

Limitations

The current study has some limitations that should be considered when interpreting our results. One potential limitation is that the current sample size was insufficient to investigate potential effects of sex on the current paradigm. Since ASD is a predominantly male disorder known to manifest sex differences in face perception (Coffman, Anderson, Naples, & McPartland, 2015), it is worthwhile for future investigations of AQ score on conscious versus nonconscious face processing to analyze male and female data separately. Another limitation of the current study is that we cannot be sure that differences between consciously and unconsciously presented trials observed in early visual components (e.g., P100) was not due to low-level visual differences between scrambled versus intact faces (Rainer, Augath, Trinath, & Logothetis, 2002). However, we note that visual ERP responses to earlier onset of scrambled faces would not account for differences observed between individuals with low versus high

AQ scores, nor would it account for effects observed in later ERP components (e.g., N170 and P300). Finally, due to the small number of “correct” responses during the nonconscious condition and “incorrect” responses during the conscious condition, we were unable to meaningfully compare ERP responses after correct versus incorrect responses.

Conclusion

This study investigates the influence of autistic traits on the neural processing of nonconsciously presented emotional faces. These findings provide novel evidence that inefficient neural processing of face stimuli (as reflected by longer latencies), which has been speculated to occur because of lack of neural specialization (McPartland et al., 2004; Tanaka & Curran, 2001), may not be restricted to individuals with a diagnosis of ASD but may extend to those with subclinical levels of social impairment. In this way, our findings suggest that common electrophysiological differences seen in individuals with ASD may be part of a broader autism phenotype rather than categorically present for individuals with ASD and absent for others. Future studies should consider additional experimental groups (e.g., TD individuals with high AQ scores, individuals with low AQ scores, and individuals diagnosed with ASD) in order to gain more specific information about how subclinical versus clinical levels of autistic traits affect neural correlates of both consciously and nonconsciously presented faces. Useful information could also be gained from adding measures of social behavior and competence by third-party raters (e.g., clinician ratings, SRS-2 filled out by spouses/friends) in order to relate electrophysiological measures with specific areas of social impairment such as reduced eye-contact and lack of initiating with peers.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by Autism Science Foundation Postdoctoral Fellowship (KKMS); National Institute of Mental Health [RO1 MH100173-01A1] (JM); National Institute of Mental Health [RO1 MH100173-02S1] (JM); National Institute of Mental Health [K23MH086785] (JM); NARSAD Young Investigator Award (JM); National Institute of Mental Health, Czech Republic [ED2.1.00/03.0078] (and the European Regional Development Fund) (MV); and Anna Freud Centre-University College London-Yale Child Study Center program (MV).

References

- Ashwin, C., Chapman, E., Colle, L., & Baron-Cohen, S. (2006). Impaired recognition of negative basic emotions in autism: A test of the amygdala theory. *Social Neuroscience*, 1(3–4), 349–363. doi:10.1080/17470910601040772
- Balconi, M., & Lucchiari, C. (2007). Consciousness and emotional facial expression recognition. *Journal of Psychophysiology*, 21(2), 100–108. doi:10.1027/0269-8803.21.2.100
- Balconi, M., & Mazza, G. (2009). Consciousness and emotion: ERP modulation and attentive vs. pre-attentive elaboration of emotional facial expressions by backward masking. *Motivation and Emotion*, 33(2), 113–124. doi:10.1007/s11031-009-9122-8
- Baron-Cohen, S., Cassidy, S., Auyeung, B., Allison, C., Achoukhi, M., Robertson, S., Pohl, A., & Lai, M.C. (2014). Attenuation of typical sex differences in 800 adults with autism vs. 3,900 controls. *PLoS ONE*, 9, e102251.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, 31(1), 5–17. doi:10.1023/A:1005653411471
- Basch, M. F. (1983). Empathic understanding: A review of the concept and some theoretical considerations. *Journal of the American Psychoanalytic Association*, 31(1), 101–126. doi:10.1177/000306518303100104
- Bernat, E., Shevrin, H., & Snodgrass, M. (2001). Subliminal visual oddball stimuli evoke a p300 component. *Clinical Neurophysiology*, 112, 159–171. doi:10.1016/S1388-2457(00)00445-4
- Bishop, D.V. M., Maybery, M., Maley, A., Wong, D., Hill, W., & Hallmayer, J. (2004). Using self-report to identify the broad phenotype in parents of children with autistic spectrum disorders: A study using the autism-spectrum quotient. *Journal Of Child Psychology And Psychiatry*, 45, 1431–1436. doi:10.1111/j.1469-7610.2004.00325.x
- Carter Leno, V., Naples, A., Cox, A., Rutherford, H., & McPartland, J. C. (2015). Common and distinct modulation of electrophysiological indices of feedback processing by autistic and psychopathic traits. *Social Neuroscience*, 1–12. doi:10.1080/17470919.2015.1108223
- Coffman, M. C., Anderson, L. C., Naples, A. J., & McPartland, J. C. (2015). Sex differences in social perception in children with ASD. *Journal of Autism and Developmental Disorders*, 45(2), 589–599. doi:10.1007/s10803-013-2006-5
- Constantino, J. N., & Gruber, C. P. (2005). *Social responsiveness scale*. Los Angeles, CA: Western Psychological Services.
- Constantino, J. N., & Todd, R. D. (2003). Autistic traits in the general population: A twin study. *Archives of General Psychiatry*, 60(5), 524–530. doi:10.1001/archpsyc.60.5.524
- Cox, A., Kohls, G., Naples, A. J., Mukerji, C. E., Coffman, M. C., Rutherford, H. J., ... McPartland, J. C. (2015). Diminished social reward anticipation in the broad autism phenotype as revealed by event-related brain potentials. *Social Cognitive and Affective Neuroscience*, 10(10), 1357–1364. doi:10.1093/scan/nsv024
- Dawson, G., Meltzoff, A. N., Osterling, J., Rinaldi, J., & Brown, E. (1998). Children with autism fail to orient to naturally occurring social stimuli. *Journal of Autism and Developmental Disorders*, 28, 479–485. doi:10.1023/A:1026043926488
- Dawson, G., Webb, S. J., & McPartland, J. (2005). Understanding the nature of face processing impairment in autism: Insights from behavioral and electrophysiological studies. *Developmental Neuropsychology*, 27(3), 403–424. doi:10.1207/s15326942dn2703_6
- Folstein, S., & Rutter, M. (1977). Infantile autism: A genetic study of 21 twin pairs. *Journal of Child Psychology and Psychiatry*, 18(4), 297–321. doi:10.1111/jcpp.1977.18.issue-4
- Fujita, T., Kamio, Y., Yamasaki, T., 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. doi:10.1016/j.rasd.2013.03.001
- Genetti, M., Khateb, A., Heinzer, S., Michel, C. M., & Pegna, A. J. (2009). Temporal dynamics of awareness for facial identity revealed with ERP. *Brain and Cognition*, 69(2), 296–305. doi:10.1016/j.bandc.2008.08.008
- Hall, G. B. C., Doyle, K. A. R., Goldberg, J., West, D., & Szatmari, P. (2010). Amygdala engagement in response to subthreshold presentations of anxious face stimuli in adults with autism spectrum disorders: Preliminary insights. *PLoS One*, 5(5), e10804. doi:10.1371/journal.pone.0010804
- Hall, G. B. C., West, C. D., & Szatmari, P. (2007). Backward masking: Evidence of reduced subcortical amygdala engagement in autism. *Brain and Cognition*, 65(1), 100–106. doi:10.1016/j.bandc.2007.01.010
- Hoekstra, R. A., Bartels, M., Verweij, C. J., & Boomsma, D. I. (2007). Heritability of autistic traits in the general population. *Archives of Pediatrics & Adolescent Medicine*, 161(4), 372–377. doi:10.1001/archpedi.161.4.372
- Itier, R. J., & Taylor, M. J. (2002). Inversion and contrast polarity reversal affect both encoding and recognition processes of unfamiliar faces: A repetition study using ERPs. *Neuroimage*, 15(2), 353–372. doi:10.1006/nimg.2001.0982
- Kamio, Y., Wolf, J., & Fein, D. (2006). Automatic processing of emotional faces in high-functioning pervasive developmental disorders: An affective priming study. *Journal of Autism and Developmental Disorders*, 36(2), 155–167. doi:10.1007/s10803-005-0056-z
- Kiss, M., & Eimer, M. (2008). ERPs reveal subliminal processing of fearful faces. *Psychophysiology*, 45(2), 318–326. doi:10.1111/j.1469-8986.2007.00634.x
- Kleinhaus, N. M., Richards, T., Johnson, L. C., Weaver, K. E., Greenson, J., Dawson, G., & Aylward, E. (2011). fMRI evidence of neural abnormalities in the subcortical face processing system in ASD. *Neuroimage*, 54(1), 697–704. doi:10.1016/j.neuroimage.2010.07.037
- Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: an event-related potential study. *Journal Of Cognitive Neuroscience*, 16, 479–486. doi:10.1111/j.1469-8986.1994.tb01028.x
- Liddell, B. J., Williams, L. M., Rathjen, J., Shevrin, H., & Gordon, E. (2004). A temporal dissociation of subliminal versus supraliminal fear perception: An event-related potential study. *Journal of Cognitive Neuroscience*, 16(3), 479–486. doi:10.1162/089892904322926809
- Lindner, J. L., & Rosén, L. A. (2006). Decoding of emotion through facial expression, prosody and verbal content in children and adolescents with Asperger's syndrome.

- Journal of Autism and Developmental Disorders*, 36(6), 769–777. doi:10.1007/s10803-006-0105-2
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8, 213. doi:10.3389/fnhum.2014.00213
- McPartland, J., 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. doi:10.1111/j.1469-7610.2004.00318.x
- McPartland, J. C., Bernier, R., & South, M. (2015). Realizing the translational promise of psychophysiological research in ASD. *Journal of Autism and Developmental Disorders*, 45(2), 277–282. doi:10.1007/s10803-014-2325-1
- 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(5–6), 436–451. doi:10.1080/17470919.2011.586880
- Monk, C. S., Weng, S.-J., Wiggins, J. L., Kurapati, N., Louro, H. M. C., Carrasco, M., ... Lord, C. (2010). Neural circuitry of emotional face processing in autism spectrum disorders. *Journal of Psychiatry & Neuroscience: JPN*, 35(2), 105–114. doi:10.1503/jpn.090085
- Morris, J. S., Öhman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393, 467–470. doi:10.1038/30976
- Nuske, H. J., Vivanti, G., Hudry, K., & Dissanayake, C. (2014). Pupillometry reveals reduced unconscious emotional reactivity in autism. *Biological Psychology*, 101, 24–35. doi:10.1016/j.biopsycho.2014.07.003
- O'Connor, K., Hamm, J. P., & Kirk, I. J. (2007). Neurophysiological responses to face, facial regions and objects in adults with Asperger's syndrome: An ERP investigation. *International Journal of Psychophysiology*, 63(3), 283–293. doi:10.1016/j.ijpsycho.2006.12.001
- 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 Cognition*, 59, 82–95. doi:10.1016/j.bandc.2005.05.004
- Pegna, A. J., Landis, T., & Khateb, A. (2008). Electrophysiological evidence for early non-conscious processing of fearful facial expressions. *International Journal of Psychophysiology*, 70(2), 127–136. doi:10.1016/j.ijpsycho.2008.08.007
- Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders*, 32(4), 249–261. doi:10.1023/A:1016374617369
- Philip, R. C., Whalley, H. C., Stanfield, A. C., Sprengelmeyer, R., Santos, I. M., Young, A. W., ... Hall, J. (2010). Deficits in facial, body movement and vocal emotional processing in autism spectrum disorders. *Psychological Medicine*, 40(11), 1919–1929. doi:10.1017/s0033291709992364
- Puzzo, I., Cooper, N. R., Vetter, P., & Russo, R. (2010). EEG activation differences in the pre-motor cortex and supplementary motor area between normal individuals with high and low traits of autism. *Brain Research*, 1342, 104–110. doi:10.1016/j.brainres.2010.04.060
- Rainer, G., Augath, M., Trinath, T., & Logothetis, N. K. (2002). The effect of image scrambling on visual cortical BOLD activity in the anesthetized monkey. *NeuroImage*, 16, 607–616. doi:10.1006/nimg.2002.1086
- Ronald, A., Happé, F., Price, T. S., Baron-Cohen, S., & Plomin, R. (2006). Phenotypic and genetic overlap between autistic traits at the extremes of the general population. *Journal of the American Academy of Child & Adolescent Psychiatry*, 45(10), 1206–1214. doi:10.1097/01.chi.0000230165.54117.41
- Sasson, N., Tsuchiya, N., Hurley, R., Couture, S. M., Penn, D. L., Adolphs, R., & Piven, J. (2007). Orienting to social stimuli differentiates social cognitive impairment in autism and schizophrenia. *Neuropsychologia*, 45(11), 2580–2588. doi:10.1016/j.neuropsychologia.2007.03.009
- Shevrin, H. (2001). Event-related markers of unconscious processes. *International Journal of Psychophysiology*, 42, 209–218. doi:10.1016/S0167-8760(01)00165-9
- Skuse, D. H., Mandy, W. P., & Scourfield, J. (2005). Measuring autistic traits: Heritability, reliability and validity of the social and communication disorders checklist. *The British Journal of Psychiatry*, 187, 568–572. doi:10.1192/bjp.187.6.568
- Smith, M. L. (2012). Rapid processing of emotional expressions without conscious awareness. *Cerebral Cortex*, 22(8), 1748–1760. doi:10.1093/cercor/bhr250
- Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science*, 12, 43–47. doi:10.1111/1467-9280.00308
- Tottenham, N., Tanaka, J. W., Leon, A. C., McCarry, T., Nurse, M., Hare, T. A., ... Nelson, C. (2009). The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Research*, 168(3), 242–249. doi:10.1016/j.psychres.2008.05.006
- Utama, N. P., Takemoto, A., Koike, Y., & Nakamura, K. (2009). Phased processing of facial emotion: An ERP study. *Neuroscience Research*, 64(1), 30–40. doi:10.1016/j.neures.2009.01.009
- Wallace, S., Coleman, M., & Bailey, A. (2008). Face and object processing in autism spectrum disorders. *Autism Research*, 1(1), 43–51. doi:10.1002/aur.7
- Wang, A. T., Dapretto, M., Hariri, A. R., Sigman, M., & Bookheimer, S. Y. (2004). Neural correlates of facial affect processing in children and adolescents with autism spectrum disorder. *Journal of the American Academy of Child & Adolescent Psychiatry*, 43(4), 481–490. doi:10.1097/00004583-200404000-00015
- Williams, M.A., Morris, A.P., McGlone, F., Abbott, D.F., & Mattingley, J.B. (2004). Amygdala responses to fearful and happy facial expressions under conditions of binocular suppression. *Journal Of Neuroscience*, 24, 2898–2904. doi:10.1523/JNEUROSCI.4977-03.2004
- Winkielman, P., Berridge, K. C., & Wilbarger, J. L. (2005). Unconscious affective reactions to masked happy versus angry faces influence consumption behavior and judgments of value. *Personality and Social Psychology Bulletin*, 31(1), 121–135. doi:10.1177/0146167204271309