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Preserved neural specialization for non-social information in autism

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Abstract

Context: Aberrant neural response to human faces in autism has been attributed to atypical social development and consequently reduced developmental exposure. The specificity of this deficit in neural specialization remains unclear.

Objective: To contrast neural specialization for social information (human faces) and non-social information (letters) in individuals with autism and typical development.

Design: Event-related potentials elicited by faces, inverted faces, houses, letters, and pseudoletters were recorded, and an electrophysiological marker of neural specialization (N170) was extracted.

Setting: University medical setting.

Participants: 36 individuals with autism spectrum disorder and 18 typically developing individuals matched for age, race, sex, handedness, and cognitive ability.

Main Outcome Measures: N170 amplitude and latency, behavioral performance on standardized measures of face recognition and word reading/decoding.

Results: Individuals with autism displayed slowed face processing and decreased sensitivity to face inversion, despite comparable brain response to letters. Brain responses were associated with behavioral performance in both groups.

Conclusions: Individuals with autism display atypical neural specialization for social information but intact specialization for non-social information. Results concord with specific dysfunction in social brain systems rather than non-specific problems with information processing.

Preserved neural specialization for non-social information in autism

The ability to efficiently perceive the human face is a crucial and early-emerging social ability. Specialized processing for faces emerges in the first days of life [1-4] and is honed by developmental experience [5]. Faces come to be encoded using configural processing mechanisms [6], reflected in disproportionate impairments in recognizing both upside down faces (the inversion effect [7]) and facial features out of context [8]. Functional neuroimaging studies show that faces elicit selective, right-lateralized hemodynamic activity in a portion of occipitotemporal cortex, the fusiform gyrus [9-11], and intra-cranial electrophysiological recordings reveal face-related negative electrical activity originating from this portion of cortex [12]. Likewise, event-related potentials (ERPs) recorded from corresponding scalp regions show a negative-going electrical deflection approximately 170 milliseconds after viewing a face (N170) [13]. The N170 reflects structural encoding, an early stage of face processing preceding higher-order processes like recognition [14], and is sensitive to perturbations in face configuration, including inversion [15]. Neural generators of the N170 have been localized to occipitotemporal sites including the fusiform gyrus [16-18], as well as the superior temporal sulcus [19], lingual gyrus [18], and posterior inferotemporal gyrus [18, 20].

These processing strategies and brain regions are also observed in the processing of visual stimuli with which viewers have extensive experience, or *perceptual expertise* [21, 22]. Experts at perceiving and discriminating among exemplars within a visually homogenous class (e.g., Greebles, birds, or cars [23, 24]) develop face-like patterns of brain activity, both in terms of hemodynamic [25] and electrophysiological response, as indexed by the N170 [26]. According to this model, these brain regions subserve a processing style rather than specific content, and face-related brain activity reflects human beings' extensive experience processing human faces during development [27].

Analogous specialization through developmental experience occurs in brain mechanisms subserving letter and word processing. Perception of printed letters [28] and words [29] selectively activates left fusiform gyrus and elicits a left-lateralized N170 in literate children as young as eight years of age [30, 31]. A maturational course independent of higher-order phonological or semantic processes [32, 33] and an early time course suggest that the "letter N170" marks pre-linguistic processes related to visual perception of form [31] and, like the N170 elicited by faces, automatic perceptual categorization within a domain of expertise [34]. Perceptual expertise effects for letters are revealed by enhanced N170 amplitude to familiar alphabets but not foreign alphabets or nonsensical letter approximations (pseudoletters) [35]. Converging evidence from neuroimaging studies and source localization analyses suggest left-lateralized sources in the fusiform gyrus and the inferior occipitotemporal cortex [16, 34, 36]. Though letter-related brain activity is typically contralateral to face processing areas [16], there is some degree of functional overlap; under special circumstances, such as precocious reading ability, right fusiform gyrus is recruited for letter and word recognition [37].

Because face perception is a well-understood and socially important behavior, it is has been employed as an avenue to understand social development in autism spectrum disorder (ASD). In ASD, decreased attention to human faces is evident by 6 to 12 months [38, 39], and abnormalities in face perception and recognition have been observed throughout the lifespan [40-44]. Individuals with ASD often exhibit abnormal viewing patterns to faces [45, 46], and neuroimaging studies reveal hypoactivation of the fusiform gyrus during face viewing [42, 47]. Studies of electrophysiological correlates of face perception suggest delayed N170 to human faces and decreased sensitivity to face inversion in individuals with ASD, as well as first degree relatives [48-54].

One theoretical explanation for these observed differences in face perception in ASD focuses on the role of developmental exposure to faces. The social motivation hypothesis [55] posits that, due to abnormalities in social drive very early in childhood, children with ASD do not attend to faces during sensitive developmental periods. Consequently, people with ASD fail to develop face processing expertise and associated patterns of behavioral and brain specialization [56]. Because the social motivation hypothesis implicates social drive as the dysfunction from which face perception difficulties originate (and not atypical functioning of brain regions subserving perceptual expertise), it presumes that individuals with ASD, given appropriate exposure to and interest in a stimulus class, should develop perceptual expertise in terms of both behavioral and brain specialization [57]. This notion is supported by a single-case study revealing behavioral and neural indices of perceptual expertise in a child with ASD during perception of cartoon characters associated with a circumscribed interest [58]. Though others have attempted to investigate brain response associated with expertise in this population [59], research has been stymied by difficulty finding shared areas of expertise in ASD; whereas groups of study participants experienced in perceiving faces are common, groups of individuals with ASD who share a common non-face area of expertise are rare.

The current work circumvented this difficulty by examining brain activity reflecting perceptual expertise for letters of the alphabet. As described above, development of perceptual expertise for letters and words is well studied and elicits brain activity similar to faces in terms of temporal characteristics and scalp topography (despite lateralization differences). This is a novel and uniquely appropriate comparison because, despite developmental disinterest towards faces and characteristic weakness in language, facility with reading has been a noted strength in ASD since Kanner's original account [60]. High-functioning individuals on the autism spectrum display age-appropriate skills in single word-reading and word-decoding ability [61-63], and a subgroup possesses precocious interest and proficiency in reading, or *hyperlexia* [64-66]. In this study, electrophysiological and behavioral methods were applied to compare perceptual expertise for faces and letters in individuals with ASD. Experiments contrasted neural response to faces versus houses, faces versus inverted faces, and letters versus pseudoletters and compared these parameters to behavioral measures assessing proficiency in face recognition and letter and word perception. Consistent with previous work, it was hypothesized that individuals with ASD would exhibit impaired face recognition and delayed brain response to faces, as well as decreased sensitivity to face inversion. In keeping with the notion that these atypicalities reflect developmental sequelae of social deficits, it was predicted that similar anomalies would not be observed for non-social stimuli; individuals with ASD would show typical skills in terms of letter and word perception and comparably enhanced response to letter stimuli with respect to unfamiliar pseudoletters. As prior work has revealed relationships among neural correlates of face perception and behavioral measures of face recognition [49], exploratory analyses examined relationships among neural and behavioral measures of face and letter perception.

Methods

Participants

Two groups participated in the study: individuals with ASD and medically and neuropsychiatrically healthy individuals with typical development. Exclusionary criteria for participants with ASD included seizures, neurological disease, history of serious head injury, sensory or motor impairment that would impede completion of the study protocol, active psychiatric disorder (other than ASD; screened with the Child Symptom Inventory: Fourth Edition [67]), or medication known to affect brain electrophysiology. Additional exclusionary criteria for typical participants included the above plus learning/language disability or family history of ASD. From an existing pool of subjects involved in ongoing research at the Yale Child Study Center, participants were selected based on having a Full Scale IQ (Differential Ability Scales: Second Edition [68]; Wechsler Intelligence Scale for Children – Fourth Edition [69]; Wechsler Adult Intelligence Scale: Third Edition [70]) in the average range or higher (Standard Score of 80 or above). All individuals with ASD had a pre-existing diagnosis that was confirmed with gold standard diagnostic assessments for research: combination of parent interview (Autism Diagnostic Interview-Revised [71]; ADI-R), semi-structured social and communication assessment (Autism Diagnostic Observation Schedule [72]), and clinical diagnosis based on DSM-IV-TR [73] criteria by an expert clinician. The ADI was not administered to one subject because a parent was unavailable for interviewing. Two individuals were included in the sample who failed to meet ADI-R onset criteria; for both of these high-functioning, verbal individuals, problems were not detected until enrolled in school with peers. In addition to the aforementioned exclusionary criteria, typical participants were recruited to match the ASD sample in terms of sex, ethnicity (determined by self or parent report), handedness (Edinburgh Handedness Inventory [74]), chronological age, and Full Scale IQ (Wechsler Abbreviated Scale of Intelligence [75]), and groups did not significantly differ on any of these variables. Behavioral assessments could not be administered to one typical participant due to time limitations. All procedures were approved by the Human Investigation Committee at Yale School of Medicine and were carried out in accordance with the Declaration of Helsinki (1975/1983). Of an initial sample of 57 individuals with ASD and 25 typically developing participants, adequate artifact-free data was obtained from 36 and 18 participants, respectively, in Block 2, and 32 and 17, respectively, in Block 1. Table 1 displays demographic data for the larger sample; variation in sample between blocks did not introduce significant differences on matching factors.

[PLEASE INSERT TABLE 1 ABOUT HERE]

EEG procedures

Stimuli. Stimuli were administered in pseudorandom sequence in two counterbalanced blocks. The first block consisted of gray-scale digitized images of neutral faces, houses, inverted faces, and inverted houses (not included in current analyses), all displayed from a direct frontal perspective. The second block included letters and a confabulated alphabet of pseudoletters [35]. Example stimuli are displayed in the legends of Figures 1 and 2. Subjects were presented with 23 stimuli from each category four times, for a total of 92 stimuli per category. Stimuli were standardized in terms of size (subtended approximately five degrees of visual angle), background color (gray), and average luminance. To maximally engage participants with stimuli, participants completed a one-back task during administration, pressing a button when a stimulus repeated (9 times for each stimulus category). Because this behavioral task was confounded with face recognition, attention to task was monitored in real time through closed-circuit video, enabling pausing of data collection and redirection of attention to stimulus presentation if needed.

Data collection. Stimuli were presented on a Pentium-IV computer controlling a 51 cm color monitor (75-Hz, 1024x768 resolution) running E-Prime 2.0 software [76]. Displays were viewed at a distance of 90 cm in a sound attenuated room with low ambient illumination. EEG was recorded using NetStation 4.3. A 256 lead Geodesic sensor net (Electrical Geodesics Incorporated; [77] was dampened with potassium-chloride electrolyte solution, placed on the participant's head, and fitted according to the manufacturer's specifications. Impedances were kept below 40 kilo-ohms. ERP was recorded continuously throughout each stimulus presentation trial, consisting of a fixation cross (randomly varying from 250-750 ms), stimulus (500 ms), and blank screen (500 ms). The EEG signal was amplified (x1000) and filtered (0.1 Hz high-pass filter and 100 Hz elliptical low-pass filter) via a preamplifier system (Electrical Geodesics Incorporated). The conditioned signal was multiplexed and digitized at 250 Hz using an analog-to-digital converter (National Instruments PCI-1200) and a dedicated Macintosh computer. The vertex electrode was used as a reference, and data were re-referenced to an average reference after data collection.

Data editing and reduction. Data were averaged for each subject by stimulus type across trials. Averaged data were digitally filtered with a 30 Hz low-pass filter and transformed to correct for baseline shifts. The window for segmentation of the ERP was set from 100 ms before and 500 ms after stimulus onset. NetStation artifact detection settings were set to 200 μv for bad channels, 150 μv for eye blinks, and 150 μv for eye movements. Channels with artifacts on more than 50 percent of trials were marked as bad channels and replaced through spline interpolation. Segments that contained eye blinks, eye movement, and those with more than 20 bad channels were also excluded. Participants with less than 46 good trials for any stimulus category were excluded from analysis. Electrodes of interest were selected based on maximal observed amplitude of the N170 to faces and letters in grand averaged data and to conform to those used in previous research. Data were averaged across eight electrodes over the left (95, 96, 97, 106, 107, 108, 116, 117) and right lateral posterior scalp (151, 152, 153, 160, 161, 162, 170, 171). The time window for N170 analysis, extending from 108 ms to 327 ms post-stimulus onset, was chosen by visual inspection of grand averaged data and then customized for each subject to confirm that the component of interest was captured at each electrode. Peak amplitude and latency to peak were averaged across each electrode group within the specified time window and were extracted for each participant for each stimulus category.

Data analysis. N170 amplitudes and latencies to peak were separately analyzed using univariate repeated measures analyses of variance (ANOVA) with two within-subject factors, each with two levels: Condition (face/house; face/inverted face, letter/pseudoletter) and hemisphere (left/right). The between subjects factor was Group (ASD/Typical).

Behavioral procedures

Face perception. Face recognition was measured with the Benton Facial Recognition Test [78]. Participants viewed a grayscale image of a face and specified one or three matches from an array of six faces, varying in shadowing and orientation.

Letter perception. The Letter-Word Identification and Word Attack subtests of the Woodcock-Johnson Tests of Achievement – Third Edition [79] required the participant to read words aloud, with the former using genuine English words and the latter using novel words. Both subtests yielded a standard score (Mean = 100, SD = 15) derived from an age-based standardization sample.

Data analysis. Between-group differences in behavioral measures were analyzed with independent samples t-tests. Interrelationships among behavioral measures and ERP parameters (N170 latency, amplitude) were computed using Pearson Product-Moment Correlations.

Results

<u>Electrophysiological measures</u>

Faces versus houses. Tables 2 and 3 display N170 latency and amplitude, respectively, in all conditions for both groups and in both hemispheres. Figure 1 displays waveforms depicting ERPs to faces and houses. Faces elicited N170s with shorter latencies (main effect of Condition; $F(1,47) = 30.10$, $p \leq .01$) and larger amplitudes (main effect of Condition; $F(1,47) = 49.77$, $p \leq .01$) across hemispheres for both groups. Right-lateralization was evident only in typically developing individuals (Hemisphere by Group interaction; $F(1,47) = 7.22$, $p \leq .01$). N170 amplitude to houses was reduced in the left hemisphere across groups (Hemisphere by Condition interaction; $F(1,47) = 6.80$, $p \leq .01$), and, relative to typical individuals, bilaterally in the ASD group (Condition by Group interaction; $F(1,47) = 25.02$, $p \leq .05$). Predicted differences in latency between groups were reflected in a three-way interaction (Group by Hemisphere by Condition interaction; $F(1,47) = 3.09$, $p \leq .10$); in the right hemisphere, N170 latency to faces was significantly faster (a differences of approximately 20.4 milliseconds) in typically developing individuals than those with ASD ($F(1, 47) = 5.57$; $p \leq .05$). Figure 2 displays N170 amplitudes for faces and houses, highlighting this difference.

[PLEASE INSERT TABLE 2 ABOUT HERE]

[PLEASE INSERT TABLE 3 ABOUT HERE]

[PLEASE INSERT FIGURE 1 ABOUT HERE]

[PLEASE INSERT FIGURE 2 ABOUT HERE]

Face versus inverted faces. Waveforms depicting ERPs to faces and inverted faces are displayed in Figure 1. Inverted faces elicited N170s with longer latencies than upright faces (main effect of Condition; $F(1,47) = 4.66$, $p \leq .05$) across hemispheres for both groups. Across faces and inverted faces, typically developing individuals displayed enhanced amplitude in the right hemisphere, while those with ASD exhibited equivalent amplitude in both hemispheres (Hemisphere by Group interaction; $F(1,47) = 7.70$, $p \leq .01$). Across hemisphere, typically developing individuals displayed an inversion effect in the expected direction, with larger amplitude to inverted relative to upright faces, whereas individuals with ASD displayed attenuated N170 amplitudes to inverted faces relative to upright faces (Condition by Group interaction; $F(1,47) = 5.84$, $p \leq .05$).

Letters versus pseudoletters. Figure 3 displays waveforms depicting ERPs to letters and pseudoletters. For both groups, letters elicited N170s with larger amplitudes than pseudoletters across hemispheres (main effect of Condition; $F(1, 52) = 14.67$, $p \leq .01$). As displayed in Figure 4, paired samples t-tests revealed that this effect was carried by significantly enhanced amplitude to letters versus pseudoletters in the typical group in the left hemisphere ($t(1,17) = 2.12$, $p \leq .05$) and in the ASD group in both left ($t(1,35) = 2.90$, $p \leq .01$) and right hemispheres ($t(1,35) = 3.34$, $p \leq .01$). No other significant between group differences were detected.

[PLEASE INSERT FIGURE 3 ABOUT HERE]

[PLEASE INSERT FIGURE 4 ABOUT HERE]

<u>Behavioral measures</u>

Face perception. Table 4 displays mean score and standard deviation on behavioral measures for both groups. Individuals with ASD obtained significantly lower face recognition scores than typically developing individuals ($t(1,51)=3.29$, $p \leq .01$). For both groups, N170 latency to faces in the right hemisphere was correlated with face recognition skill; individuals with faster N170s displayed better face recognition performance (ASD: $r = -.39$, $p \leq .05$; Typical: $r = -.53$, $p \leq .05$). Among individuals with ASD, N170 amplitude to inverted faces was correlated with face recognition performance; those with better face recognition abilities were more likely to display an enhanced N170 associated with inversion ($r = -.47$, $p \leq .01$).

Letter perception. Groups performed comparably and in the average range on word reading and decoding tasks. Among typically developing individuals, longer N170 latency to letters in the right hemisphere was correlated with word reading score; those with longer latencies tended to perform better on the measure of single word reading ($r = .64$, $p \leq .01$).

[PLEASE INSERT TABLE 4 ABOUT HERE]

Comment

The current study contrasted neural specialization for social and non-social information in individuals with ASD and a cohort of typically developing individuals of comparable age, ethnicity, sex, handedness, and cognitive ability. A critical social stimulus with which most adults possess great experience, the human face, was contrasted with a comparably complex visual stimulus with minimal social relevance, houses. Consistent with predictions and with prior research [49], individuals with ASD displayed a selective processing delay for human faces relative to typical counterparts. This was reflected in a substantial (~20 milliseconds, approximately10% of total response time) difference in peak latency of the N170 ERP component between groups that was specific to faces and evident in the right hemisphere, the hemisphere in which face processing typically takes place. Individuals with ASD showed reduced hemispheric specialization compared to typical counterparts, who showed a marked right lateralization effect for faces. A second analysis contrasted brain response to upright and inverted human faces. This manipulation disrupts configural processing strategies typically applied to human faces and other expert stimuli and, in typically developing samples, perturbs neural response, resulting in an enhanced N170. In the current experiment, this inversion effect was evident in typically developing individuals; however, those with ASD showed attenuated, rather than enhanced, brain response to inverted faces. Finally, on a behavioral measure of face recognition, individuals with ASD, despite comparable intellectual ability, performed significantly worse than typically developing counterparts. Face recognition performance was associated with processing efficiency for faces; in both groups, individuals with better face recognition abilities displayed faster N170 response. Among individuals with ASD, increased inversion effects, as reflected by a stronger response to inverted faces, was associated with better face recognition performance. This pattern of anomalies, i.e., decreased efficiency of processing, insensitivity to inversion, and impaired face recognition, is hypothesized to reflect underdeveloped expertise for faces, a downstream effect of decreased attention to faces during childhood secondary to reduced social drive from infancy [55]. Indeed, the observed correlation between neural response to face inversion and recognition performance suggests that, in this case, development of expertise and processing proficiency are related.

These findings concord with prior work describing deviant social development in ASD. However, scant evidence to-date informs the specificity of the observed neural processing anomalies to social information. By measuring responses to non-social expert stimuli, the current study sought to demonstrate such selectivity in perceptual deficits in ASD. Following up on work showing N170-related expertise effects for letters, ERP response to letters of Roman alphabet were compared to a confabulated alphabet of pseudoletters [35]. In contrast to the discrepancies observed during perception of social stimuli, individuals with ASD displayed neural responses comparable to typical counterparts; both groups showed enhanced N170 to familiar letters. Similar results were obtained on behavioral measures, with individuals with ASD obtaining word reading and decoding scores that were comparable to the typical participants in this study and within the average range. These results suggest intact specialization, both behavioral and neural, associated with perceptual expertise for letters in individuals with ASD.

The current findings have significant implications for understanding the neuropathology of autism spectrum disorders. Two prevailing classes of theories attribute autistic impairments to (a) dysfunctional brain structures supporting social information processing [55] or (b) altered connectivity among distributed brain regions [80]; the former bespeaks the import of content and the latter bespeaks the import of process. Social information processing theories posit that social information is qualitatively unique and that specific brain systems have evolved to support this type of information processing. Connectivity theories, in contrast, have traditionally argued that social information is relevant only insofar as it relies on complex or cortically distributed processing mechanisms. The current work demonstrates, for the first time in a substantial sample of children with ASD, preserved specialization for a cognitive process subserved by distributed cortical regions. Development of letter expertise is an intricate process accruing over time and requiring elaborate communication of anterior and posterior cortical regions [81]. The demonstration of capacity for development of perceptual expertise in ASD reveals an example of intact functioning of such brain systems that is not consistent with non-specific, brain-wide dysfunction. Taking into consideration considerable evidence for atypical patterns of connectivity in ASD [80], current findings emphasize the potential value of studying connectivity *within* *specific brain systems in a developmental context*. In this way, scientists may also extricate atypical connectivity as potential cause or consequence of autistic dysfunction; it is likely that origins of dysfunction in functionally specific brain systems would, through developmental maturation, lead to broader connectivity problems. Such research may also serve to clarify to what degree problems with connectivity uniquely differentiate autism from the diversity of developmental and psychiatric disorders also manifesting atypical connectivity, e.g. obsessive-compulsive disorder, [82], schizophrenia [83], ADHD [84], and intellectual impairment [85].

This work yields clinically relevant implications for the detection and treatment of ASD. Results are supportive of the broad class of interventions designed to direct the attention of children with ASD to relevant social information. When children are appropriately engaged and attuned to information, in this case, letters, typical patterns of neural specialization develop; given the right input, the brain of a person with autism can function like that a of a typical peer, without ostensible reliance on compensatory mechanisms or alternative processing strategies. Findings add to a body of evidence that electrophysiological brain activity to faces represents a viable bio-behavioral risk marker for ASD, as temporal anomalies in neural correlates of face perception have been observed in children with ASD [53] and infants at-risk for ASD [54].

Though the current work replicates initial findings of temporal anomalies to faces [49], these findings have not fully replicated in all samples [86-88]. These varied results most likely reflect the phenotypic heterogeneity evident in ASD. Despite the unifying characteristic of social impairment, ASD presents in a remarkable diversity of manifestations, likely representing multiple etiologic pathways and variability in developmental experience [89]. Considering the manner in which face processing (especially in older children and adults) has been actively shaped by experience, it is intuitive that anomalies might emerge in a variety of ways or might not emerge universally [90]. In this regard, like any of the symptoms characterizing autism, anomalous face perception is neither necessary nor specific. It is one potential manifestation of atypical social development that, by virtue of a deep understanding of behavioral and brain bases in typical social development, is a viable avenue for investigating social disability. Variability in electrophysiological studies of face perception may also relate to differences in visual attention [86], a trend observed in hemodynamic studies [91, 92]. Our employment of a pre-stimulus fixation crosshair reduces the likelihood that between-group differences are attributable to differences in visual attention; resolution of this matter will ultimately require co-registration of eye-tracking and EEG. Finally, as is the case in all clinical research, variability in results is likely to mirror variability in clinical characterization. Application of gold standard diagnostic criteria has been inconsistent in ERP research; moving forward, adoption of clinically rigorous methods of characterization will be vital to derive directly comparable results.

There are several aspects of the current work that are being revisited and improved upon in ongoing research. Limiting the sample to high-functioning individuals was a necessary first step towards addressing the research questions posed in this study, but it limits generalizability to the broader range of individuals with ASD. Given that even many nonverbal children with ASD are capable of reading, these types of experiments offer a window into domains of strength and preserved neural functions of children on the autism spectrum, important goals for tailoring interventions and proscribing specific treatments. The sample in the current study focused on pre-adolescence, a time of rapid maturation of brain systems subserving face perception. Additional research in younger and older children and adults will elucidate the protracted maturational course of specialization for face perception in ASD and of letter expertise in both typical and atypical development. Of note, many participants in the current study displayed the bifid waveform morphology characteristic of pre-adult face responses [93]; however, this was not evident for letter N170s. Exploiting the dense spatial sampling afforded by the 256 lead net, analyses in progress are using individual-specific three-dimensional head models (computed with sensor registration images acquired with the Geodesic Photogrammetry System) to localize potentially distinct neural sources for these facets of the developing N170.

Understanding developmental factors is particularly important in the current context in that perceptual expertise for letters is clearly a distinct phenomenon from face expertise, occurring over a relatively compressed period of time rather than from birth. It will thus be essential to examine perceptual expertise for a greater variety of stimuli. Though it has been proposed that, like faces, letters are encoded using a holistic processing strategy [94], unlike faces, letters are processed at a basic rather than subordinate level of identification [28]. The

N170 has been posited to denote perceptual expertise at this basic level of identification, while later components, such as the N250, index expertise at the subordinate level of identification [95]. Similar mechanisms underlying perceptual expertise for both faces and letters exist at early processing stages as indexed by the N170, but study of a broader range of electrophysiological components and expert stimuli will paint a clearer picture of perceptual expertise development in ASD.

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Figure Legends

Figure 1. Grand averaged waveforms across entire scalp for faces, houses, and inverted faces for typical participants and those with ASD. Electrodes of interest in right and left hemisphere are highlighted. Subpanels display the averaged waveform across the eight specified electrodes in each hemisphere for both groups.

Figure 2. Mean latency of the N170 component (in milliseconds) elicited by faces and houses for both groups in both hemispheres. Error bars represent +/- 1 S.E. Significance at the $p \leq .05$ level is indicated by *.

Figure 3. Grand averaged waveforms across entire scalp for letters and pseudoletters for typical participants and those with ASD. Electrodes of interest in right and left hemisphere are highlighted. Subpanels display the averaged waveform across the eight specified electrodes in each hemisphere for both groups.

Figure 4. Amplitude of the N170 component (in microVolts) elicited by letters and pseudoletters for both groups in both hemispheres. Error bars represent +/- 1 S.E. Significance at the $p \leq .05$ level is indicated by *, and significance at the $p \leq .01$ level is indicated by **.

Tables

Table 1

Participant Characteristics

	Typical (N=18)	ASD (N=36)
Number male (Percent)	15 (83.3)	32 (88.9)
Number White (Percent)	15 (83.3)	34 (94.4)
Number right handed (Percent)	16 (88.9)	31 (86.1)
Mean age (SD)	12.6 (2.4)	11.2 (3.4)
Mean Full Scale IQ (SD)	112.9 (13.4)	105.2 (17.3)

Table 2

N170 Latency

Hemisphere	Condition	*M* (milliseconds)	*SD*
Typical group			
Left	Faces	193.24	37.3
	Houses	215.59	43.4
	Inverted faces	194.82	35.3
	Letters	177.25	26.9
	Pseudoletters	179.56	26.8
Right	Faces	181.38	31.6
	Houses	217.50	36.4
	Inverted faces	188.85	32.7
	Letters	181.19	25.9
	Pseudoletters	176.03	28.5
ASD group			
Left	Faces	200.13	24.3
	Houses	221.67	31.2
	Inverted faces	205.42	27.7
	Letters	189.21	26.7
	Pseudoletters	178.83	19.3
Right	Faces	201.78	27.2
	Houses	219.38	27.8
	Inverted faces	204.66	31.3
	Letters	188.42	28.0
	Pseudoletters	183.51	23.6

Table 3

N170 amplitude

Hemisphere	Condition	*M* (microVolts)	*SD*
Typical group			
Left	Faces	0.39	1.7
	Houses	2.49	3.5
	Inverted faces	0.24	2.8
	Letters	-2.27	3.0
	Pseudoletters	-1.51	3.1
Right	Faces	-0.16	2.0
	Houses	0.89	2.6
	Inverted faces	-0.58	2.8
	Letters	-3.03	4.2
	Pseudoletters	-2.53	3.9
ASD group			
Left	Faces	-0.32	3.4
	Houses	3.16	4.0
	Inverted faces	0.59	3.6
	Letters	-3.09	3.6
	Pseudoletters	-2.22	3.3
Right	Faces	0.76	3.6
	Houses	3.44	4.2
	Inverted faces	1.52	3.5
	Letters	-3.57	3.1
	Pseudoletters	-2.29	2.9

Table 4

Performance on behavioral measures

Measure	Typical (N = 17) *M*	Typical (N = 17) *SD*	ASD (N = 36) *M*	ASD (N = 36) *SD*
Benton Face Recognition Score	41.41	3.6	37.11	4.8
Letter-Word Identification	108.41	9.9	105.67	15.0
Word Attack	101.41	9.7	103.86	11.6

Figure 1 TOP

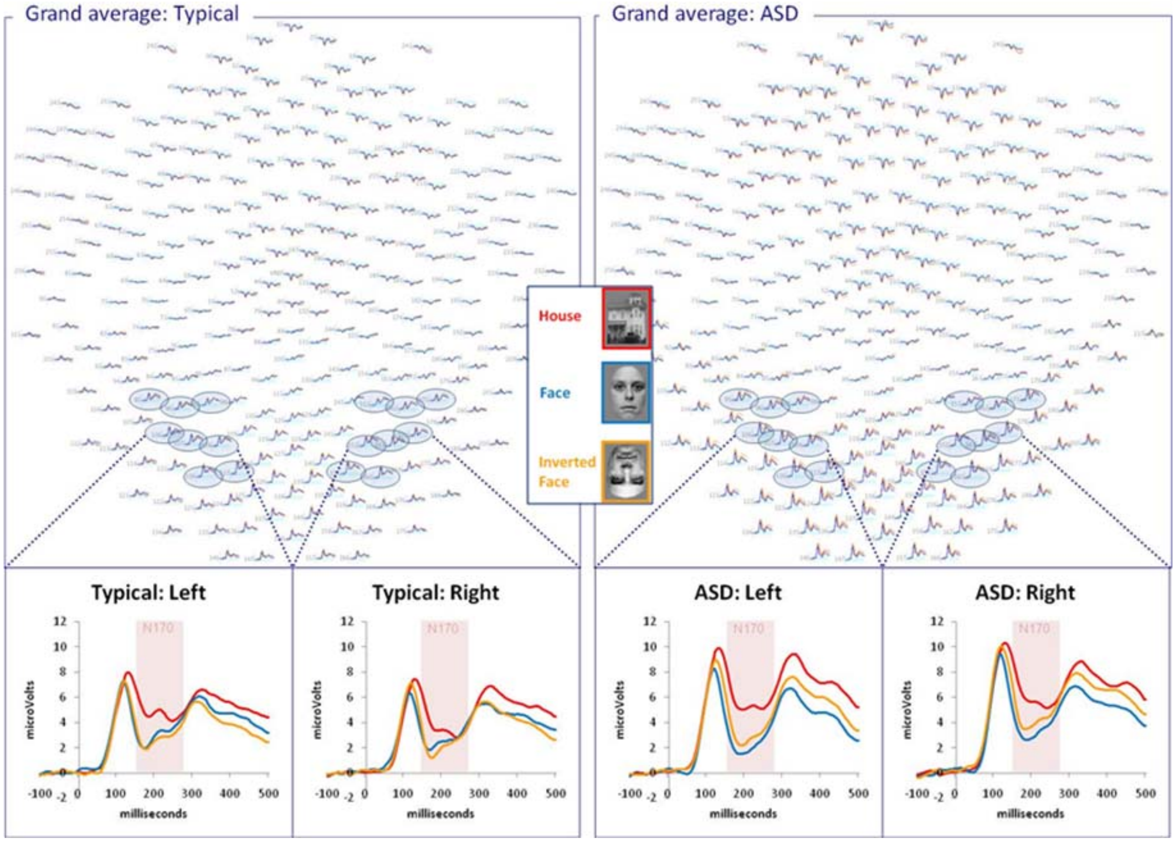

Grand average: Typical
Grand average: ASD
House
Face
Inverted Face
Typical: Left
Typical: Right
ASD: Left
ASD: Right
N170
microVolts
milliseconds

Figure 2 TOP

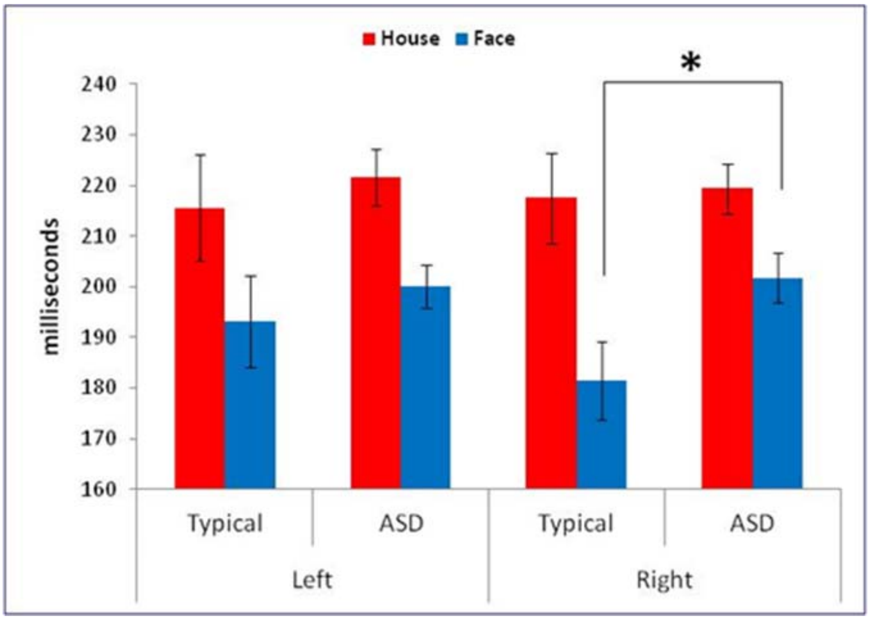

House
Face
*
240
230
220
210
200
190
180
170
160
milliseconds
Typical
ASD
Typical
ASD
Left
Right

Figure 3 TOP

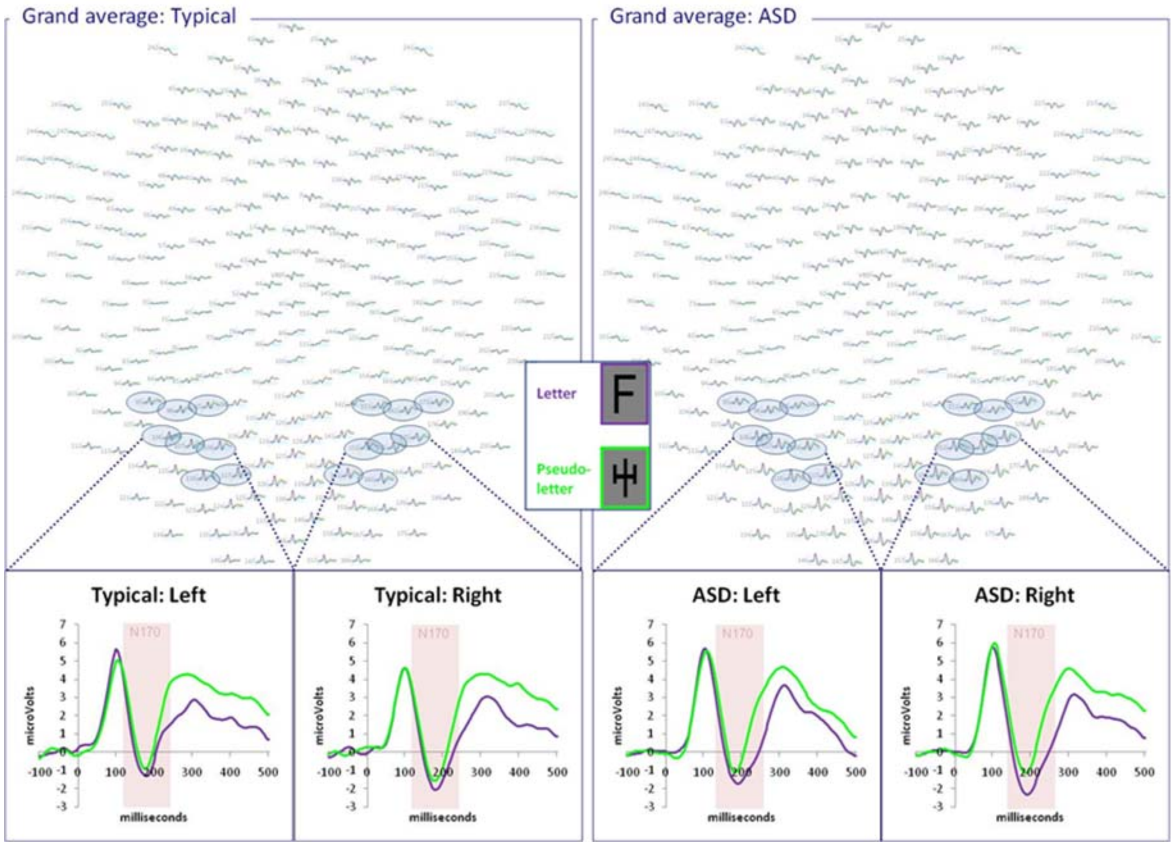
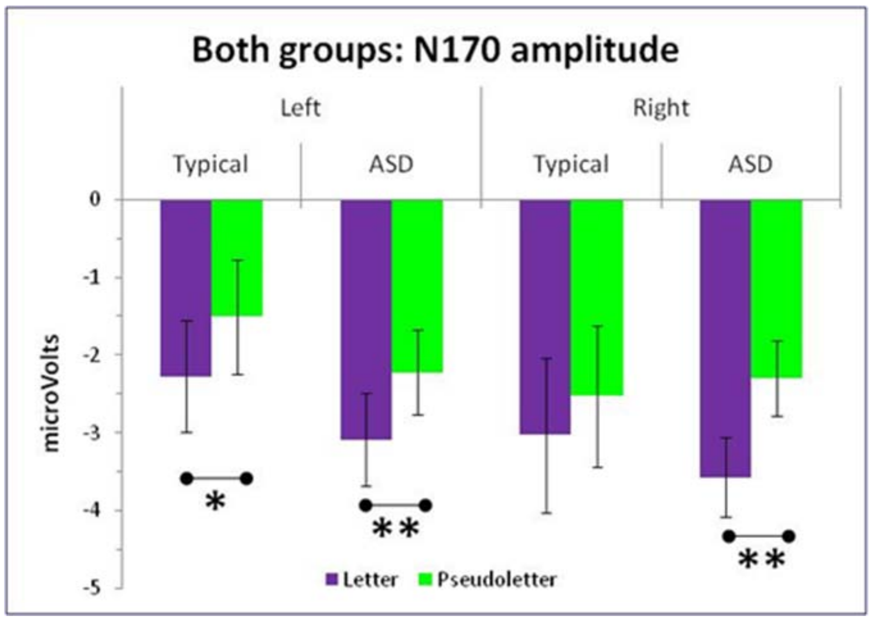

Grand average: Typical
Grand average: ASD
Letter
Pseudo-letter
Typical: Left
Typical: Right
ASD: Left
ASD: Right
N170
microVolts
milliseconds

Figure 4 TOP


Both groups: N170 amplitude
Left
Right
Typical
ASD
Typical
ASD
0
-1
-2
-3
-4
-5
microVolts
*
**
**
Letter
Pseudoletter