

Linguistic and Non-Linguistic Semantic Processing in Individuals with Autism Spectrum Disorders: An ERP Study

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Abstract Individuals with autism spectrum disorders (ASD) experience difficulties with language, particularly higher-level functions like semantic integration. Yet some studies indicate that semantic processing of non-linguistic stimuli is not impaired, suggesting a language-specific deficit in semantic processing. Using a semantic priming task, we compared event-related potentials (ERPs) in response to lexico-semantic processing (written words) and visuo-semantic processing (pictures) in adults with ASD and adults with typical development (TD). The ASD group showed successful lexico-semantic and visuo-semantic processing, indicated by similar N400 effects between groups for word and picture stimuli. However, differences in N400 latency and topography in word conditions suggested different lexico-semantic processing mechanisms: an expectancy-based strategy for the TD group but a controlled post-lexical integration strategy for the ASD group.

Keywords Autism spectrum disorders · Semantic processing · ERP · Language · Pictures

Introduction

Semantic Processing Deficits in Autism

Autism spectrum disorder (ASD) is defined by deficits in social communication and interaction as well as restricted and repetitive behaviors or interests (American Psychiatric Association 2013). In practice, ASD often presents with a wide constellation of deficits in motor, sensory, cognitive, and social domains. One characteristic feature of ASD is the presence of widespread language impairments, especially in higher-level functions such as semantics (see reviews in Groen et al. 2008; Tager-Flusberg et al. 2005). Semantic processing, for the purposes of the current study, refers to the understanding of the meaning of a stimulus, be it a word, picture, sentence, or sound. In the present study, we hypothesize that specific impairments in semantic processing of linguistic stimuli may underlie many of the difficulties with language processing that individuals with ASD often face.

In typically developing (TD) populations, one way of exploring semantic processing is through the use of event-related potentials (ERPs). ERPs are derived from the electroencephalogram (EEG) and are taken to reflect cognitive functioning following the presentation of a stimulus. In particular, the N400 ERP component has been established as an index of semantic processing and integration (Kutas and Hillyard 1980; Lau et al. 2008), although a number of other functional interpretations exist (e.g. Brouwer et al. 2012; see Kutas and Federmeier 2011 for a broader discussion). (Note that for the purposes of the current discussion, we use the term “semantic integration” to refer to the process of assimilating the meanings of different pieces of information to arrive at a holistic understanding or a “gist”. We use the term “semantic processing” as a larger umbrella

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term for various subfunctions such as semantic access or semantic integration).

The amplitude of the N400 is reduced when stimuli are easier to integrate with their preceding semantic context, as in the case of a semantically congruent word at the end of a sentence (e.g. “He spread butter on his *toast*”) compared to stimuli that are difficult to integrate, as in the case of a semantically incongruent sentence-final word (e.g. “He spread butter on his *socks*”). Reduced N400 amplitude is also taken as a measure of semantic priming in paradigms using single words. For example, the N400 amplitude is reduced in response to a target word that is semantically related to a prime word (e.g. dog-CAT) compared to an unrelated prime word (e.g. rock-CAT). In a semantic priming paradigm with single words, the prime can act as the “context” for the target word, leading to a reduction in the N400 amplitude when the two words are related compared to when they are unrelated.

In studies of semantic processing of language, individuals with ASD do not always show an N400 effect (i.e. the difference in amplitude of the N400 elicited by contexts with higher congruency or semantic relatedness versus those with lower congruency or semantic relatedness), suggesting impairments in semantic processing (Braeutigam et al. 2008; Dunn et al. 1999; Dunn and Bates 2005; McCleery et al. 2010; Pijnacker et al. 2010; Strandburg et al. 1993; Verbaten et al. 1991). For example, when performing a semantic priming task in which pairs of pictures and spoken words were presented that either matched (e.g. a picture of a car followed by the spoken word “car”) or mismatched (e.g. a picture of a car followed by the spoken word “ball”), McCleery et al. (2010) observed an N400 effect in TD children but not in children with ASD, suggesting that children with ASD were not as sensitive to the semantic relationship between the stimuli. Individuals with ASD have also shown reduced N400 effects when reading sentences ending with either a semantically congruous or incongruous word (Braeutigam et al. 2008; Pijnacker et al. 2010), suggesting deficits in semantic processing and the ability to use sentence context.

Functional magnetic resonance imaging (fMRI) research demonstrates that brain areas important for semantic integration, such as Broca’s area and specifically the left inferior frontal gyrus (LIFG; Hagoort 2005), show reduced activation during language processing in individuals with ASD compared to TD controls (Gaffrey et al. 2008; Harris et al. 2006; Just et al. 2004). For example, Harris et al. (2006) and Gaffrey et al. (2008) both asked participants to make semantic decisions about written words, and reported greater activation during semantic decision in the LIFG/Broca’s area for the TD group compared to the ASD group. These results may suggest an atypical organization of the lexico-semantic system in autism. Just et al. (2004) have

provided evidence of deficits in semantic processing at the sentence level in individuals with ASD. This study asked participants to read actively and passively constructed sentences (e.g. “The cook thanked the father”; “The editor was saved by the secretary”) and judge the agent or the recipient of the action. Just et al. (2004) reported that during sentence processing (compared to a fixation condition), individuals with ASD showed greater activation in the left superior temporal gyrus (broadly corresponding to Wernicke’s area). Because this area has been associated with lexical processing, the authors interpreted this finding as indicative of more extensive processing of the meaning of single words in the ASD group (although this study did not include a condition with single words to corroborate this interpretation). In contrast, the ASD group showed less activation in the LIFG (broadly corresponding to Broca’s area) compared to the TD group. Because this area has been associated with semantic integration processes, the authors interpreted this finding as indicative of difficulties with integrating the individual words into a coherent conceptual structure and processing the meaning of complex sentences. In sum, these findings from fMRI studies corroborate those from EEG studies in suggesting that individuals with ASD have difficulties with semantic processing at both the single-word and the sentence level.

Lexico-Semantic versus Visuo-Semantic Processing

Although some of the literature suggests that individuals with ASD experience deficits in semantic processing of language, other studies suggest that semantic processing of nonverbal stimuli is not impaired in individuals with ASD (Kamio and Toichi 2000; McCleery et al. 2010; Sahyoun et al. 2009, 2010). For example, Kamio and Toichi (2000) compared picture-word and word-word priming in children with ASD to that in TD children. Both groups showed priming effects in both conditions, but the children with ASD performed better on the picture-word task whereas TD children performed similarly on the two, suggesting an advantage for visuo-semantic processing in ASD. McCleery et al. (2010), in addition to the picture-spoken word condition described above (in which children with ASD showed a reduced N400 effect), also presented matching or mismatching pairs of pictures and environmental sounds [e.g. a picture of a car followed by the sound of a car engine starting (match condition) or a ball bouncing (mismatch condition)] to children with ASD and TD controls. In contrast to their linguistic condition they reported no group differences in N400 effect magnitude in this environmental sound condition, suggesting that semantic processing in children with ASD is intact for non-linguistic stimuli but is impaired for linguistic stimuli.

In a slightly different paradigm, Sahyoun et al. (2009) compared linguistic and visuospatial processing during a pictorial reasoning task that required either lexico-semantic processing (semantic reasoning from linguistic pictures), visuospatial processing (visuospatial transformations of geometric patterns or shapes), or a combination of both (visuospatial reasoning using pictures with verbal labels). This study included a higher-functioning group of individuals with autism (HFA, characterized by delayed and/or atypical language development), a group of individuals with Asperger's syndrome (characterized by no history of early language delay), and age- and IQ-matched controls. Sahyoun et al. (2009) found that the control group and the Asperger's group were fastest in the combined condition, indicating they benefitted from the availability of both linguistically- and visuospatially-mediated routes. In contrast, the HFA group was faster in the visuospatial and combined conditions compared to the lexico-semantic condition, which the authors interpreted as suggesting that the HFA individuals favored visual processing over lexico-semantic mediation. In an fMRI study using the same paradigm, Sahyoun et al. (2010) found that both the lexico-semantic and combination conditions led to activation of frontal and temporal language regions for TD children but activation of occipito-temporal and ventral temporal areas for HFA children. The authors interpreted this finding as reflecting a greater reliance on visual mediation during lexico-semantic processing and an impaired frontal language system in individuals with ASD. These studies thus further suggest intact visual processing but atypical lexico-semantic processing in individuals with ASD.

If non-linguistic semantic processing is relatively unimpaired in ASD, as research suggests (Kamio and Toichi 2000; McCleery et al. 2010; Sahyoun et al. 2009, 2010), this would imply that the general semantic system is intact but a language-specific deficit exists in semantic processing. However, no studies have tested this hypothesis by directly comparing linguistic and non-linguistic semantic processing in individuals with ASD. The previous studies reporting intact non-linguistic semantic processing (Kamio and Toichi 2000; McCleery et al. 2010) have both used cross-modal priming in one of their conditions, which may have obscured effects. Specifically, the “visuo-semantic”¹ condition in Kamio & Toichi (2000) included both linguistic stimuli (written words) and non-linguistic stimuli (pictures); yet if individuals with ASD truly have difficulties with semantic processing of language, the presence of

linguistic stimuli in these cross-modal pairs may have mitigated priming effects for these participants. Similarly, the “linguistic” condition in McCleery et al. (2010) included both linguistic stimuli (spoken words) and non-linguistic stimuli (pictures); yet if individuals with ASD have intact non-linguistic semantic processing, this cross-modal pairing could have enhanced priming effects for the ASD population in this study. A true test of whether a language-specific deficit exists for semantic processing in individuals with ASD would directly compare within-modality pairs of linguistic and non-linguistic stimuli.

The existence of such a disparity is important to establish because it would shed light on the nature of semantic processing in individuals with ASD. The absence of a language-specific deficit would suggest that semantic processing more generally is impaired in ASD, regardless of stimulus modality. On the other hand, the presence of a language-specific deficit would suggest that semantic processing is generally intact, but that impairments stem from the additional need for linguistic processing. From a theoretical point of view, the distinction between lexico-semantic and visuo-semantic processing could be related to ease of access: because pictures are a more direct representation of their associated concepts, access to semantic information is relatively easy, whereas a written word is an arbitrary and abstract label that needs to be translated to its associated concept. The less direct access for words could explain why individuals with ASD have a harder time with semantic processing of linguistic material. The distinction could also be related more concretely to the underlying neurobiology of autism and of the functional representation of semantic processing in the brain. In general, areas of the temporal and parietal cortices are thought to be involved in semantic processing of objects (Bookheimer 2002; Martin and Chao 2001; Vandenberghe et al. 1996). Semantic processing of language specifically is thought to additionally recruit areas of the language network in the frontal cortex, as well as temporo-parietal brain areas (Cabeza and Nyberg 2000; Price 2010; Vandenberghe et al. 1996). Semantic processing of language (or lexico-semantic processing) therefore requires long-range communication across distributed semantic and linguistic networks in frontal and temporo-parietal areas. In contrast, semantic processing of pictures may be more centralized in temporo-parietal regions, requiring shorter-range communication. Previous literature has reported underconnectivity of long-range connections in the brains of individuals with ASD (Anderson et al. 2011; Barttfeld et al. 2011; Catrino et al. 2013; Cherkassky et al. 2006; Coben et al. 2008; Jones et al. 2010; Just et al. 2004; Kana et al. 2006; Murias et al. 2007). This underconnectivity has also been noted between frontal and parietal brain regions in the left hemisphere—a connection which is critical for language (Just

¹ Note that in principle, ‘visuo-semantic’ processing could refer to any link between visual stimuli and concepts, including printed words. However, for the purposes of the current study, we use the term “visuo-semantic processing” to refer to semantic processing of picture stimuli specifically.

et al. 2004; Kana et al. 2006). Therefore the distinction between linguistic and non-linguistic semantic processing in individuals with ASD could be related to the underlying neurobiology of neural communication: long-range frontoparietal networks involved in linguistic semantic processing may be underconnected in individuals with ASD, resulting in language difficulties (Sahyoun et al. 2010). In contrast, shorter-range, local connections between temporal and parietal brain regions may be less affected by neural underconnectivity in ASD, resulting in intact non-linguistic semantic processing (Sahyoun et al. 2010).

Regardless of the underlying mechanism, the presence of a distinction between linguistic and non-linguistic semantic processing has not been satisfactorily established. To the best of our knowledge, the current study is the first to evaluate whether a language-specific deficit exists for semantic processing in individuals with ASD by directly comparing linguistic and non-linguistic semantic processing using pairs of written words (linguistic stimuli) and pairs of pictures (non-linguistic stimuli). We use a semantic priming ERP paradigm in which participants viewed the prime and target stimuli and made a judgment as to whether the two stimuli were semantically related. Because we wish to tap explicit semantic processing with this paradigm, we use a long stimulus onset asynchrony (SOA) between prime and target (1300 ms).

Due to its precise temporal resolution, EEG is well-suited to characterize subtle differences in semantic processing that may not be observable at the behavioral level. Based on its well-established involvement in semantic processing, we use the N400 ERP component as a marker of semantic processing in each modality. Previous literature has reported that an N400 effect is elicited for pictures as well as for words (Kutas and Federmeier 2011), although differences exist between the two modalities in both topographic distribution (being typically more frontal for pictures and more parietal for language; Ganis et al. 1996; Hamm et al. 2002; McPherson and Holcomb 1999), and latency (being slightly earlier for pictures than for words; Hamm et al. 2002; McPherson and Holcomb 1999; West and Holcomb 2002). Importantly, differences in the presence and magnitude of the N400 effect for each modality between individuals with and without ASD could indicate differences in semantic processing.

To the best of our knowledge, the present study is also the first to examine whether deficits in semantic processing at the single-word level exist in adults with ASD. The majority of previous studies examining semantic processing in ASD have tested children (Dunn et al. 1999; Dunn and Bates 2005; Kamio and Toichi 2000; McCleery et al. 2010). However, it is possible that adults with ASD develop compensatory strategies to account for their difficulties with semantic processing of language, meaning that deficits

may not be as apparent in this population. Only two studies have examined semantic processing in adults with ASD (Braeutigam et al. 2008; Pijnacker et al. 2010); however, both of these studies used more complex sentence stimuli, as opposed to lexical-level items that are used in the current study. It is important to examine whether a language-specific deficit in semantic processing also exists at the lexical level for adults with ASD, since impairments at the lexical level could be compounded at later processing stages.

In sum, the current study seeks to determine whether semantic processing deficits in individuals with ASD are restricted to the linguistic domain by directly comparing within-modality semantic priming of linguistic stimuli (pairs of written words) and non-linguistic stimuli (pairs of pictures) in a group of adults with ASD and a group of age- and sex-matched TD adults. We use the N400 ERP effect as a measure of semantic processing: if individuals with ASD have a language-specific impairment in semantic processing, we would expect a reduced or absent N400 effect in response to linguistic stimuli in the ASD group compared to the TD group, reflecting impaired lexico-semantic processing. We expect no group differences in the magnitude of the N400 effect in response to non-linguistic stimuli, reflecting intact visuo-semantic processing.

Methods

Participants

The TD group consisted of 20 adults with typical development, ages 19–69 ($M=34.3$, $SD=15.8$); 17 males, 3 females; 17 Caucasian, 1 Asian, 2 African American. The ASD group consisted of 20 adults with autism, ages 18–68 ($M=33.3$, $SD=15.0$); 17 males, 3 females; 18 Caucasian, 1 Hispanic, 1 mixed race. The clinical diagnosis of autism or ASD (along the guidelines of the DSM-IV or DSM-5, depending on how recent the diagnosis/evaluation) was established through record review and confirmed through the administration of the Autism Diagnostic Observation Schedule [First Edition (ADOS-1) or Second Edition (ADOS-2)], depending on the current version of the assessment at the time of testing (Lord et al. 2000, 2012).²

² The mean length of time between ADOS testing and participation in this study was approximately 8 months (range 0–41). One participant had approximately 41 months (3 years 5 months) between initial ADOS administration and EEG testing. This participant was unavailable for further testing; however, because the ADOS has been shown to have good test–retest reliability at the item, domain, and classification levels (Lord et al. 2000, 2012), it is unlikely that his classification will have changed significantly in this time. In addition, analyses of the data without this participant did not change the overall patterns of effects. The maximum length of time between ADOS administration and EEG testing for all other participants was 18 months or fewer.

Table 1 Participant characteristics for the TD and ASD groups. Means and ranges^a are reported for each measure. The ‘group difference’ column shows the results of independent-samples *t* tests

	TD group (n=20)	ASD group (n=20)	Group difference
Age	34 (19–69)	33 (18–68)	<i>t</i> (37.9)=0.22, <i>p</i> =0.83
PPVT	119 (100–136)	103 (71–137)	<i>t</i> (28.2)=3.25, <i>p</i> <0.01**
K-BIT			
Verbal	115 (92–139)	100 (71–154)	<i>t</i> (31.1)=2.58, <i>p</i> <0.05*
Nonverbal	112 (96–132)	99 (44–132)	<i>t</i> (30.6)=2.48, <i>p</i> <0.05*
Autism quotient	16 (6–28)	29 (17–41)	<i>t</i> (35.8)=6.23, <i>p</i> <0.0001***

^aAll participants had verbal abilities (PPVT and verbal K-BIT scores) within the “normal” range (>70). Two participants had nonverbal K-BIT scores outside of this range (44 and 68, respectively). The overall results were similar both when running the analyses without these participants and when including nonverbal K-BIT as a covariate in the analyses (see Footnote 4); therefore we include their data

Although intellectual and verbal ability are sometimes used to determine functioning level, we defined all participants in the ASD group to be “high-functioning.” Criteria for identifying these participants as high-functioning were based on the severity of core features of autism as stated in DSM-5; the level of environmental support and supervision needed; and the total score from the Autism Diagnostic Observation Schedule (ADOS). All participants met the criteria for Level 1 severity according to the DSM-5 (APA 2013) and all were given a diagnosis of autism or ASD on the ADOS.

Demographic information for each group can be found in Table 1. The ASD and TD groups did not differ on age (*p*=0.83); however, the ASD group had significantly lower receptive vocabulary knowledge (as measured by the PPVT); verbal IQ (as measured by the K-BIT), and nonverbal IQ (as measured by the K-BIT; all *p*’s<0.05) than the TD group.

All participants had normal or corrected-to-normal vision. Participants were recruited through newspaper advertisements, public announcements, and fliers at The Johns Hopkins University and Hospital. Subjects were recruited with the assistance of the Interactive Autism Network (IAN) Research Database at the Kennedy Krieger Institute, Baltimore. All procedures were approved by the Johns Hopkins University Institutional Review Board. Written informed consent was obtained from all individual participants before experimental testing. All participants were monetarily compensated for their participation.

Task Stimuli

Four hundred pairs of concrete nouns were created. Half of the pairs (*n*=200) were semantically related as assessed by latent semantic analysis (LSA; mean LSA value=0.58). The other half were semantically unrelated (mean LSA value=0.03). Half of the related and half of the unrelated stimuli were chosen to be represented as pictures; for each word, a high-quality digital image was

selected from online sources to represent the word. Pre-testing with a group of three normal adults ensured that the pictures accurately represented the concepts. The picture stimuli were matched across related and unrelated conditions for luminance. The other half of the stimulus pairs were represented as words. Altogether, 100 of each stimulus type (picture related, picture unrelated, word related, word unrelated) were created. Stimuli did not repeat between modalities or relatedness conditions.

Stimuli in each pair and condition type were matched for frequency using SUBTLEX (Brysbaert and New 2009; see Table 2). Stimuli were also matched in each pair and condition type for number of letters (for words) or number of syllables (for pictures). Stimulus pairs were chosen such that the two words did not overlap in initial letters (for word stimuli) or phonemes (for picture stimuli).

Procedure

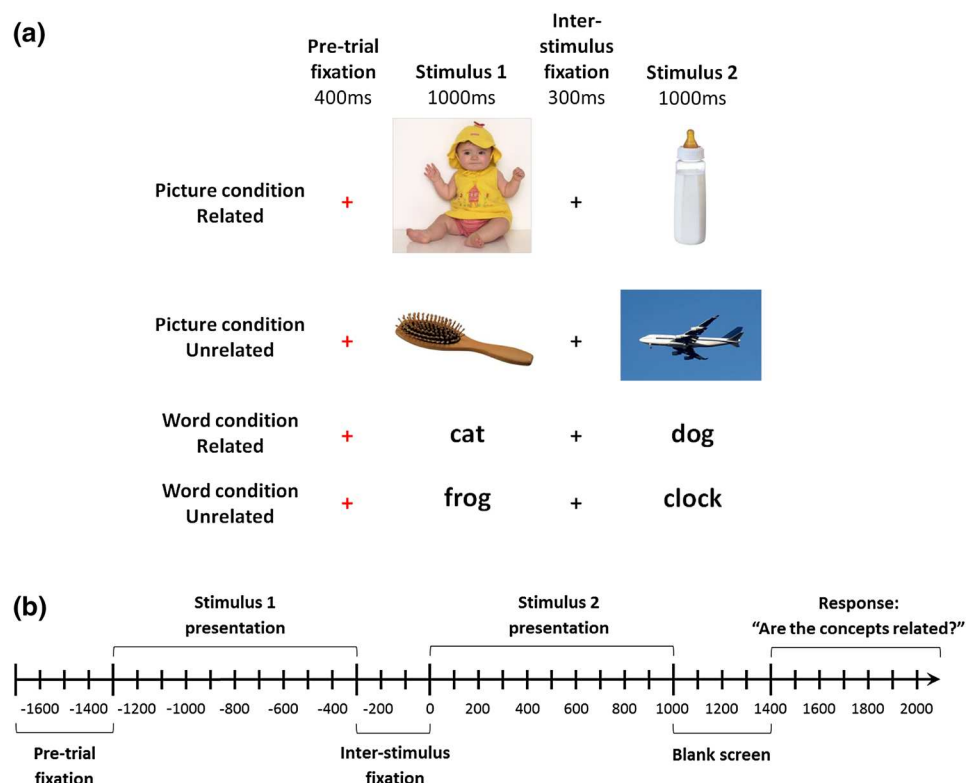
The experimental session lasted approximately 1.5 h including consenting, paperwork, EEG net application, and testing.

Table 2 Descriptive data on the word and picture stimuli used in the semantic priming experiment

	Word stimuli		Picture stimuli	
	Related	Unrelated	Related	Unrelated
LSA value	0.61	0.02	0.55	0.03
Stimulus 1 frequency	2.77	2.21	2.61	2.19
Stimulus 2 frequency	2.76	2.17	2.67	2.21
Stimulus 1 length ^a	5.92	6.49	1.92	2.02
Stimulus 2 length ^a	5.77	6.46	1.78	1.92

^aLength is reported as number of letters for word stimuli and number of syllables for picture stimuli

Fig. 1 **a** Example stimuli of the semantic priming task. Participants viewed pairs of related or unrelated words and pictures and judged whether they were related. **b** Timeline of stimuli presentation. (Note that here and in the ERP plots below, timing information is provided relative to the onset of the second stimulus)



Stimuli were presented using E-Prime version 2.0.8.74. The semantic priming task consisted of four blocks of picture pairs and four blocks of word pairs (50 pairs per block: 25 related, 25 unrelated) for a total of 100 trials in each of the four stimuli types. Participants performed all four blocks of one modality followed by all four blocks of the other, in a counterbalanced fashion (i.e. picture and word blocks were not interleaved, so half of the participants saw picture blocks first, and the other half saw word blocks first).

On each trial, a red fixation cross was presented for 400 ms, followed by the first word or picture for 1000 ms; an inter-stimulus blank screen for 300 ms; and the second word or picture for 1000 ms. Following the offset of the second stimulus a blank screen was presented for 400 ms, followed by a black fixation cross presented at an inter-trial interval ranging from 1000 to 1400 ms (mean 1200 ms). Participants were asked to wait until this black cross appeared, and then to judge using a button press whether the stimuli were semantically related or not (see Fig. 1). Stimuli were presented on a Dell 17" LCD monitor with a resolution of 1280×1024. Participants sat approximately 24" away from the computer screen. Picture size ranged from 3 to 5.5" in height and 3 to 5" in width, yielding a visual angle between 7° and 13°. Word stimuli were presented in size 28 Courier New font and ranged from 0.67 to 2.5" in width and 0.38" in height, yielding a visual angle between 1° and 6°.

During the semantic priming task, EEG data were acquired using EGI's Geodesic EEG System (GES) 300 and a 256-channel Geodesics Sensor net. Data were digitized at 250 Hz using EGI's NetStation software version 4.3 and were referenced to the Cz electrode. Impedances were kept under 50 kΩ wherever possible.³

Data Preprocessing

Data were preprocessed using EEGLab version 13.3.2 and Matlab 2014a. The data were filtered using a 0.1–50 Hz bandpass filter and rereferenced using an average reference transform. Bad channels were replaced using spherical interpolation. Following filtering and bad channel replacement, the continuous data were segmented into epochs time-locked to the onset of the second stimulus. Segments

³ Because we used a dense electrode array, it was often impractical to get all electrodes under this impedance threshold, especially with electrodes near the ears or at the back of the neck. For example, depending on the shape of a participant's head some electrodes near the ears might not make good contact with the scalp. However, we ensured that roughly 90 to 95% of channels, and all electrodes in the center of the scalp, were under the 50 kΩ threshold before initiating the experimental session or proceeding with testing after checking impedances. Impedances were always checked after initial net application. The electrode sponges were rewet and impedances were rechecked approximately every 10–15 min throughout the EEG session.

extended from 1400 ms before to 1000 ms after the second stimulus (in order to capture the response to the first stimulus, presented at -1300 ms). Eye movement artifacts were identified and removed from the data using independent component analysis (ICA). Prior to ICA decomposition, the mean of each trial was removed (Groppe et al. 2009) and the data were reduced to 32 dimensions. After ICA decomposition, eye movements, blinks, muscle artifacts, and other noise components were visually identified and manually removed from the data.

Statistical Analyses

To evaluate behavioral performance, we performed repeated-measures ANOVAs on the average accuracy and average reaction time (RT) with levels of *condition* (related/unrelated) and *modality* (word/picture) as within-subjects factors and *group* (TD/ASD) as a between-subjects factor. To account for group differences in language abilities, PPVT was included as a covariate in all ANOVAs.⁴ Note that participants were asked to withhold their response until a fixation cross was shown in order to minimize response preparation or motion artifacts in the N400 window (see Procedure), which may have affected RTs. Only correct trials were included in the RT analysis.

ERP amplitude was evaluated at nine regions across the scalp taken from the 10–20 distribution. Clusters were centered around F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4 (see Fig. 2). Only correct trials were included in the ERP analyses. Due to the inclusion of multiple stimulus modalities and participant groups, there is a possibility that the N400 might occur at slightly different latencies (e.g. Hamm et al. 2002; McPherson and Holcomb 1999; West and Holcomb 2002). To avoid restricting our analyses to one time window and missing these potential latency differences, we first performed exploratory ERP analyses to determine the time window(s) of interest for each comparison. Exploratory ERP analyses within groups compared conditions at each electrode using mass univariate comparisons in which paired-samples *t*-tests were computed between conditions at each of the nine electrode clusters and at every other timepoint (i.e. every 8 ms, or a frequency of 125 Hz) from 100 to 1000 ms after presentation of the second stimulus. Correction for multiple comparisons was performed over all timepoints and electrode clusters of interest at a false discovery rate (FDR) threshold of $p < 0.05$ (see Groppe

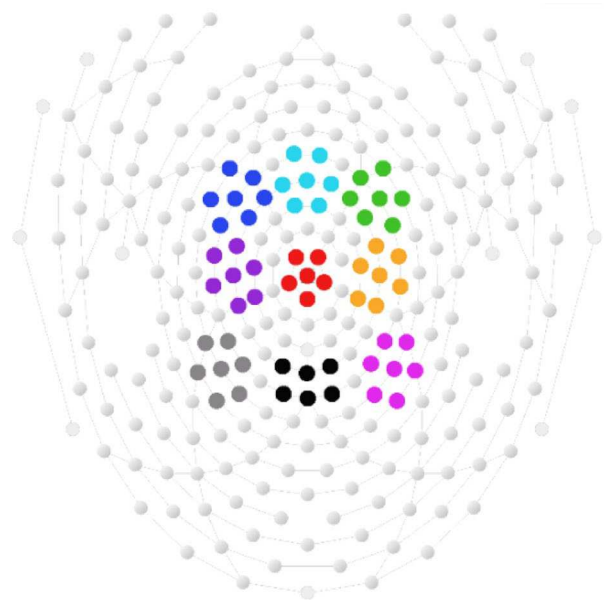


Fig. 2 Illustration of the nine electrode clusters used for EEG analysis

et al. 2011 for details). This mass univariate technique has been proposed by Groppe et al. (2011) for exploratory analyses, and has been adopted and promoted by a number of EEG researchers (e.g. Keil et al. 2014; Lau et al. 2013); it is also implemented in the Mass Univariate Toolbox in ERPLab toolbox for preprocessing of EEG data (Lopez-Calderon and Luck 2014).

Exploratory analyses were used to determine windows of interest for further statistical testing of group differences, which were performed using repeated-measures ANOVAs for each modality separately, with *condition* (related/unrelated), *site* (frontal/central/parietal), and *laterality* (left/midline/right) as within-subjects factors and *group* (TD/ASD) as a between-subjects factor. To account for group differences in language abilities, PPVT was included as a covariate in all ANOVAs (see Footnote 4).

Results

Behavioral Data

Accuracy rates and mean reaction times (RTs) for each group, modality, and condition are presented in Table 3.

The ANOVA for accuracy rates showed a significant interaction of modality and condition [$F(1,38)=4.67$, $p < 0.05$]. In the picture modality, there was a main effect of condition [$F(1,39)=10.86$, $p < 0.01$] such that, across both groups, accuracy rates were higher for unrelated

⁴ We also ran all analyses with nonverbal K-BIT as a covariate instead of PPVT and the results were highly similar. Because this study investigates language processing, in part, we report the results with PPVT as a covariate in order to equate the groups on language ability. This allows us to investigate group differences arising from the ASD classification that go beyond language abilities.

Table 3 Accuracy rate and reaction time for each group, modality, and condition

Group	Picture modality		Word modality	
	Related	Unrelated	Related	Unrelated
Accuracy rate (%)				
TD	76%	80%	85%	87%
ASD	68%	71%	80%	79%
Reaction Time (ms)				
TD	365	383	327	367
ASD	346	366	334	353

conditions ($M=75\%$, $SE=0.04\%$) than for related conditions ($M=72\%$, $SE=0.04\%$). However, there were no main effects of group and no interactions of any other factors with group in the picture modality. In the word modality, there was no significant main effect of condition [$F(1,39) < 1$].

The ANOVA for RTs showed a main effect of modality [$F(1,38)=4.29$, $p<0.05$] such that RTs were faster over both groups and conditions for word stimuli ($M=345$ ms, $SE=13$ ms) than for picture stimuli ($M=365$ ms, $SE=12$ ms). There was also a main effect

of condition [$F(1,38)=10.68$, $p<0.01$] such that RTs were faster over both groups and modalities for related conditions ($M=343$ ms, $SE=12$ ms) than unrelated conditions ($M=367$ ms, $SE=12$ ms). However, there was no main effect of group and no interaction with group (all p 's > 0.24).

ERP Data

Picture Modality

ERPs for picture conditions for the TD and ASD groups are presented in Figs. 3 and 4. Difference waveforms and topographic plots are presented in Fig. 5.

Exploratory analyses were first performed for each modality and group using running t -tests with an FDR correction of $p<0.05$ (Groppe et al. 2011). The results of these tests are shown as colored bars underneath the waveforms in Figs. 3 and 4. Both the TD and ASD groups showed a significant N400 effect, such that unrelated conditions were more negative than related conditions, in response to picture pairs. In the TD group, the N400 occurred from approximately 200–800 ms over frontal and central sites and approximately 400–900 ms over parietal

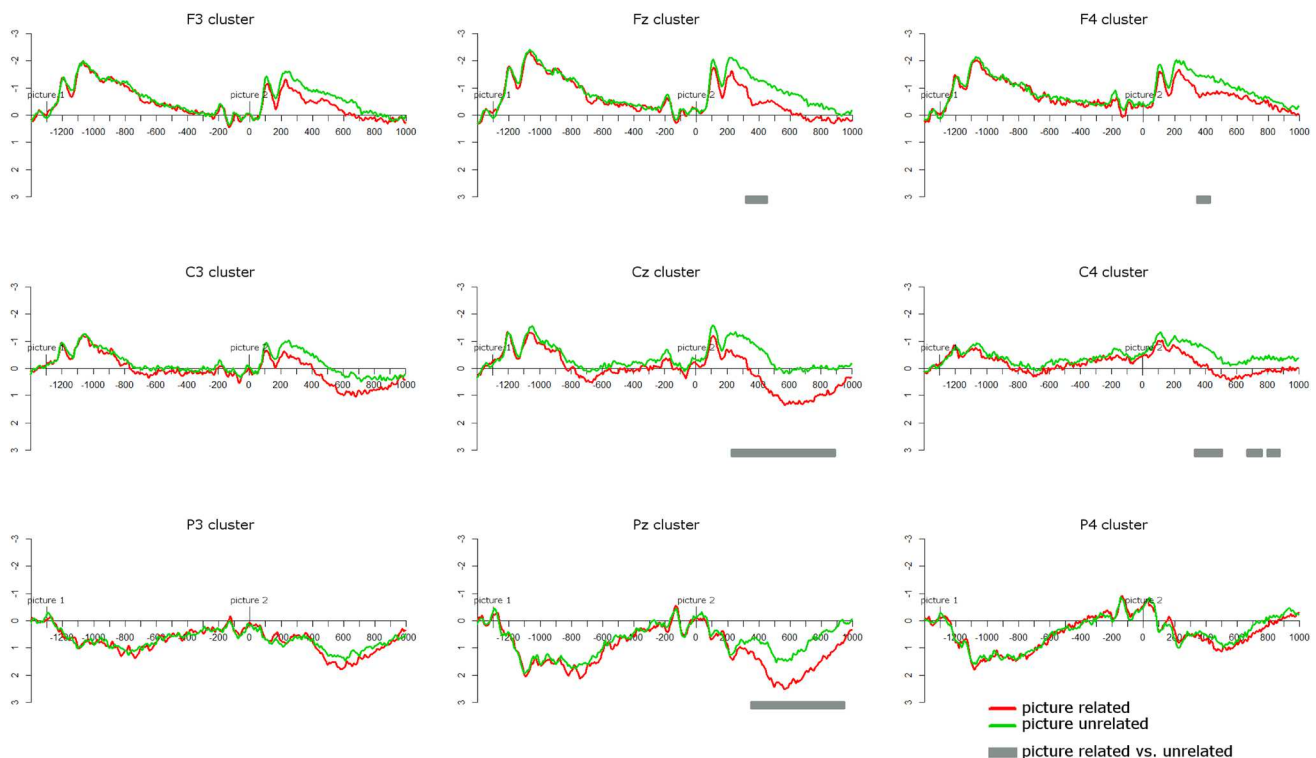


Fig. 3 ERPs for picture conditions in the TD group. Colored bars underneath the waveforms indicate the results of running t -tests at an FDR correction of $p<0.05$. (Color figure online)

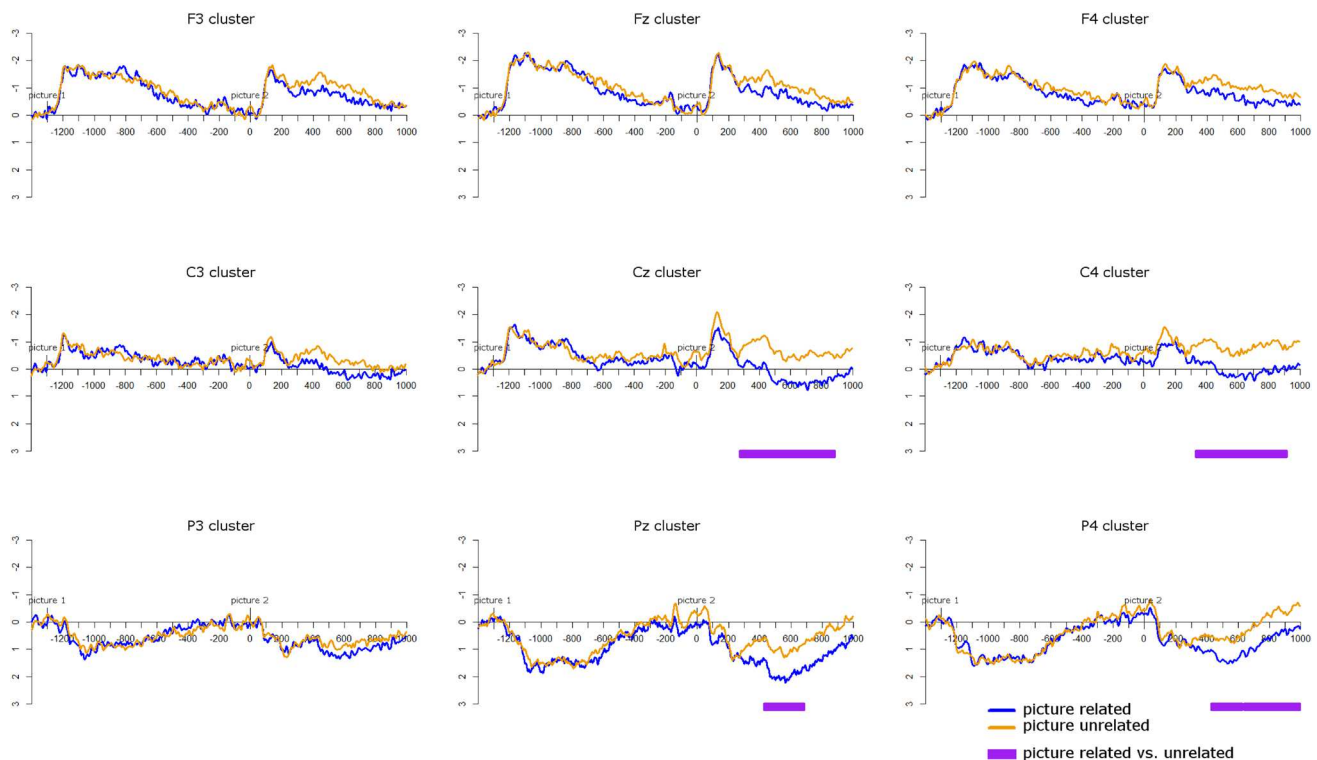


Fig. 4 ERPs for picture conditions in the ASD group. Colored bars underneath the waveforms indicate the results of running *t*-tests at an FDR correction of $p < 0.05$. (Color figure online)

sites. In the ASD group, the N400 occurred from approximately 300–900 ms over frontal and central sites and from approximately 300–800 ms over parietal sites.

These exploratory analyses revealed a significant N400 effect to pictures in both groups from approximately 200–800 ms, although the timing of effects differed by site. To investigate group differences in both early and late effects, we ran repeated-measures ANOVAs in three different time windows: 200–400 ms, 400–600 ms, and 600–800 ms. PPVT score was included as a covariate in all ANOVAs. The full results for each time window and modality are shown in Table 4.

In the picture modality, there were no main effects of or interactions with group in either the 200–400 ms or 400–600 ms time windows. In the 600–800 ms time window, there was a significant interaction of group, condition, and laterality [$F(2,76) = 5.15$, $p < 0.01$] which arose from an interaction of group and condition at right-hemisphere sites [$F(1,38) = 6.68$, $p < 0.05$]. There were main effects of condition, such that unrelated conditions were more negative than related conditions, for both groups but the effect was larger for the ASD group [$F(1,19) = 52.89$, $p < 0.0001$, $\eta^2 = 0.19$] than for the TD group [$F(1,19) = 7.22$, $p < 0.05$, $\eta^2 = 0.05$]. This suggests a more right-lateralized N400

effect to pictures from 600 to 800 ms for the ASD group compared to the TD group.

Word Modality

ERPs for word conditions for the TD and ASD groups are presented in Figs. 6 and 7. Difference waveforms and topographic plots are presented in Fig. 8.

Exploratory analyses were first performed for each modality and group using running *t*-tests with an FDR correction of $p < 0.05$ (Groppe et al. 2011). The results of these tests are shown as colored bars underneath the waveforms in Figs. 6 and 7. The TD group showed an N400 effect from approximately 250–500 ms over frontal sites and from approximately 400–800 ms over central and parietal sites. Surprisingly, the ASD group also showed an N400 effect in the word modality. This effect occurred from approximately 400–600 ms over central sites and from approximately 400–800 ms over parietal sites.

These exploratory analyses suggested differences in the topography and timing of the N400 effect between groups. To investigate these group differences, we ran repeated-measures ANOVAs in three different time windows: 200–400 ms, 400–600 ms, and 600–800 ms. PPVT was included as a covariate in all ANOVAs. The full results

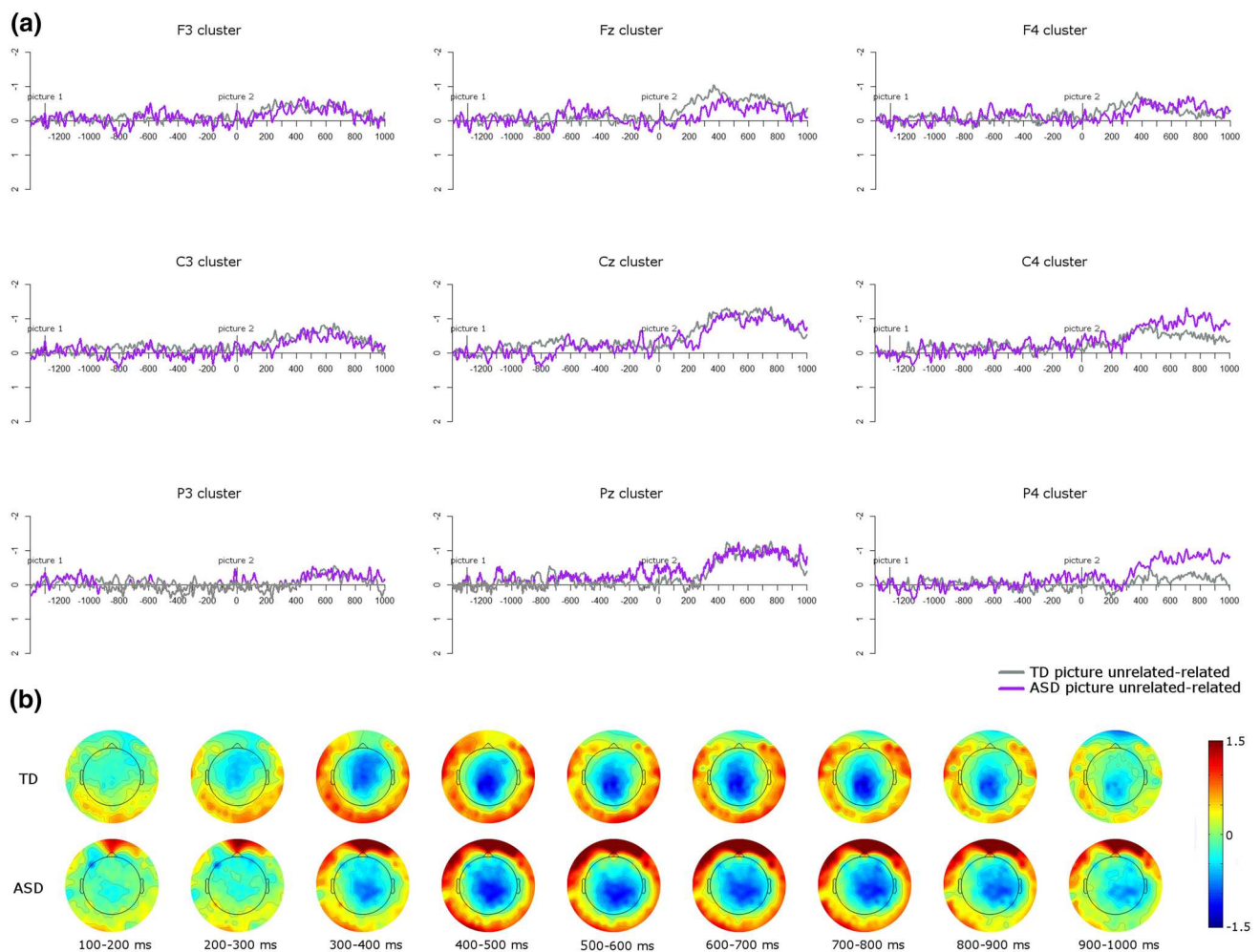


Fig. 5 Group comparisons in the picture modality. **a** ERP difference waves (unrelated minus related) for each group in the picture modality. **b** Topographic plots of unrelated minus related conditions in the picture modality in 100 ms windows from 100 to 1000 ms for each group

for each time window and modality are shown in Table 4. Below we summarize only the interactions with group, as this was the main interest of the current study.

To summarize the results in the 200–400 ms window, the TD group showed a fronto-central N400 effect over midline and right-lateralized scalp whereas the ASD group did not show this early fronto-central effect. In this window the ANOVA showed a three-way interaction of group, condition, and site [$F(2,76)=5.58$, $p<0.01$]. This arose from a significant interaction of group and condition at frontal sites [$F(1,38)=6.10$, $p<0.05$] and a trend toward a significant interaction at central sites [$F(1,38)=3.27$, $p=0.08$]. At both frontal and central sites, there was a significant effect of condition (unrelated more negative than related) for the TD group (all p 's <0.01) but not for the ASD group (all p 's >0.50). In the 200–400 ms time window there was also a three-way interaction of group, condition, and laterality [$F(2,76)=5.15$, $p<0.01$]. This arose from an

interaction of group and condition in the left hemisphere [$F(1,38)=10.56$, $p<0.01$] such that there was a significant main effect of condition (unrelated more negative than related) for the TD group [$F(1,19)=6.88$, $p<0.05$] but this was only a statistical trend for the ASD group [$F(1,19)=4.10$, $p=0.06$].

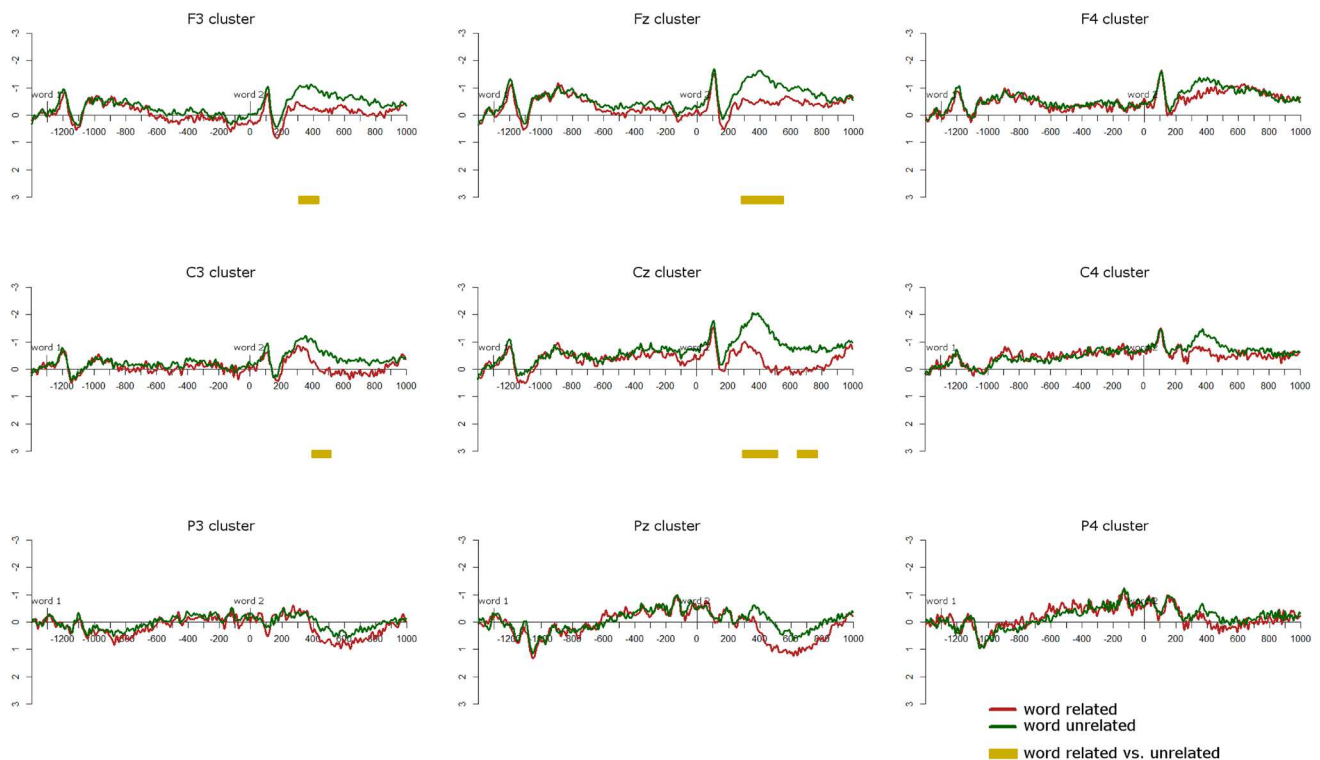
To summarize the results in the 400–600 ms window, the ASD group showed a more central and right-lateralized N400 effect whereas the effect was more distributed across the scalp for the TD group. In this window the ANOVA showed a three-way interaction of group, condition, and laterality [$F(2,76)=9.43$, $p<0.001$]. This arose from an interaction of group and condition in the left hemisphere [$F(1,38)=7.56$, $p<0.01$], such that there was a main effect of condition (unrelated more negative than related) in the TD group [$F(1,19)=13.43$, $p<0.01$] but not the ASD group [$F(1,19)<1$].

To summarize the results in the 600–800 ms window, the ASD group showed a more central and right-lateralized

Table 4 *F*-values for the repeated-measures ANOVAs, with a between-subjects factors of group (TD/ASD), within-subjects factors of condition (related/unrelated), site (frontal/central/parietal), and laterality (left/right/midline), and PPVT as a covariate, in each modal-

ity and analysis window. Statistically significant main effects of group and interactions with group are highlighted in bold. Asterisks indicate statistically significant results (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

Main effect or interaction	Picture modality			Word modality		
	200–400 ms	400–600 ms	600–800 ms	200–400 ms	400–600 ms	600–800 ms
PPVT	0.05	0.14	0.34	3.71	2.40	1.38
Condition	29.06***	66.12***	69.14***	7.78**	23.30***	14.65***
Site	37.00***	38.63***	24.81***	4.32*	14.16***	15.71***
Laterality	0.72	1.89	5.67**	0.23	0.81	3.54*
Group	0.35	1.11	2.32	1.51	0.55	0.68
Group × condition	1.02	0.09	0.28	3.32	0.67	0.12
Group × site	0.01	0.18	0.27	0.19	0.19	0.03
Group × laterality	0.01	0.67	1.02	1.87	2.14	1.10
Condition × site	5.34**	3.33	3.60*	2.45	3.95*	5.84*
Condition × laterality	4.12**	8.72***	13.46***	7.78***	13.53***	5.07**
Site × laterality	6.14***	5.08***	6.59***	9.01***	6.61***	7.99***
Condition × site × laterality	1.59	5.17***	5.05***	1.97	3.12 *	3.56***
Group × condition × site	1.58	0.30	0.18	5.58*	1.58	2.41
Group × condition × laterality	0.43	1.49	5.15**	5.15*	9.43***	6.07**
Group × site × laterality	0.68	0.47	0.21	0.66	0.39	0.36
Group × condition × site × laterality	0.67	1.51	0.48	1.33	0.95	0.83

**Fig. 6** ERPs for word conditions in the TD group. *Colored bars* underneath the waveforms indicate the results of running *t*-tests at an FDR correction of $p < 0.05$. (Color figure online)

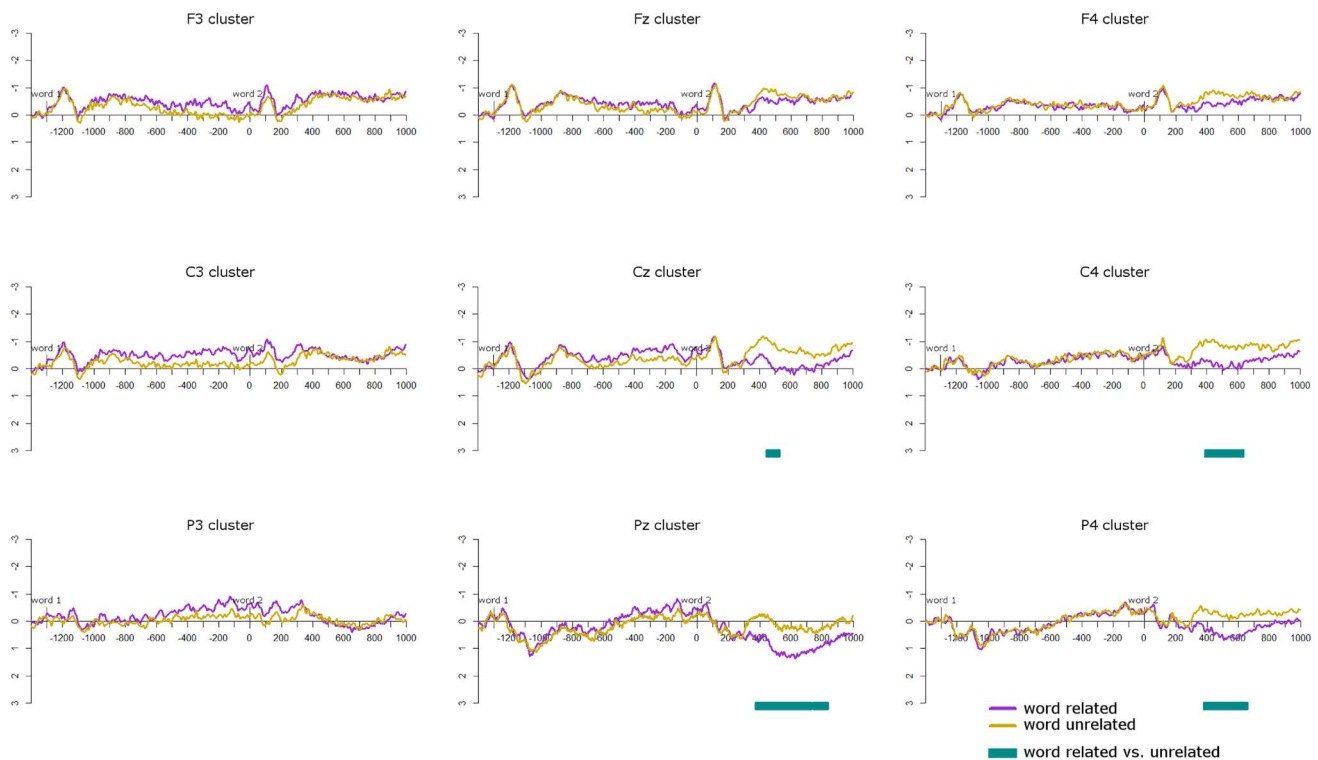


Fig. 7 ERPs for word conditions in the ASD group. *Colored bars* underneath the waveforms indicate the results of running *t*-tests at an FDR correction of $p < 0.05$. (Color figure online)

N400 effect whereas the effect was more distributed across the scalp for the TD group. In this window the ANOVA showed a three-way interaction of group, condition, and laterality [$F(2,76)=6.07$, $p < 0.01$]. This arose from an interaction of group and condition in the left hemisphere [$F(1,38)=4.14$, $p < 0.05$] such that the TD group showed a significant effect of condition (unrelated more negative than related; [$F(1,19)=7.01$, $p < 0.05$]) but the ASD group did not [$F(1,19) < 1$].

Discussion

The current study aimed to better characterize the purported language-specific deficit in semantic processing in individuals with ASD by directly contrasting lexico-semantic and visuo-semantic processing. We expected that semantically unrelated stimuli would be more difficult to integrate, leading to a larger N400 response compared to related stimuli (the N400 effect). We predicted a reduced or absent N400 effect in response to linguistic stimuli (pairs of semantically related or unrelated words) for the ASD group compared to the TD group but no group differences in response to non-linguistic stimuli (pairs of semantically related or unrelated pictures).

Visuo-Semantic Processing

Previous literature reports that an N400 effect is elicited for pictures as well as for words (Kutas and Federmeier 2011). However, the N400 effect for pictures typically has a more frontal distribution than the more parietal N400 elicited by language (Ganis et al. 1996; Hamm et al. 2002; McPherson and Holcomb 1999). This effect also generally begins slightly earlier than for words, leading some researchers to suggest that this frontal negativity is a separate component from the N400 termed the ‘N300’ (Hamm et al. 2002; McPherson and Holcomb 1999; West and Holcomb 2002).

In the current data, both groups showed a significant N400 effect in response to picture pairs, with unrelated conditions showing more negative waveforms than related conditions. In the TD group, the N400 occurred from approximately 200–800 ms over frontal and central sites and approximately 400–800 ms over parietal sites. In the ASD group, the N400 occurred from approximately 300–900 ms over frontal and central sites, and approximately 400–800 ms over parietal sites. The early onset of the congruity effect in both groups at frontal sites may reflect the earlier N300 effect reported in previous literature.

The only group difference that emerged in the picture modality occurred in the 600–800 ms time window,

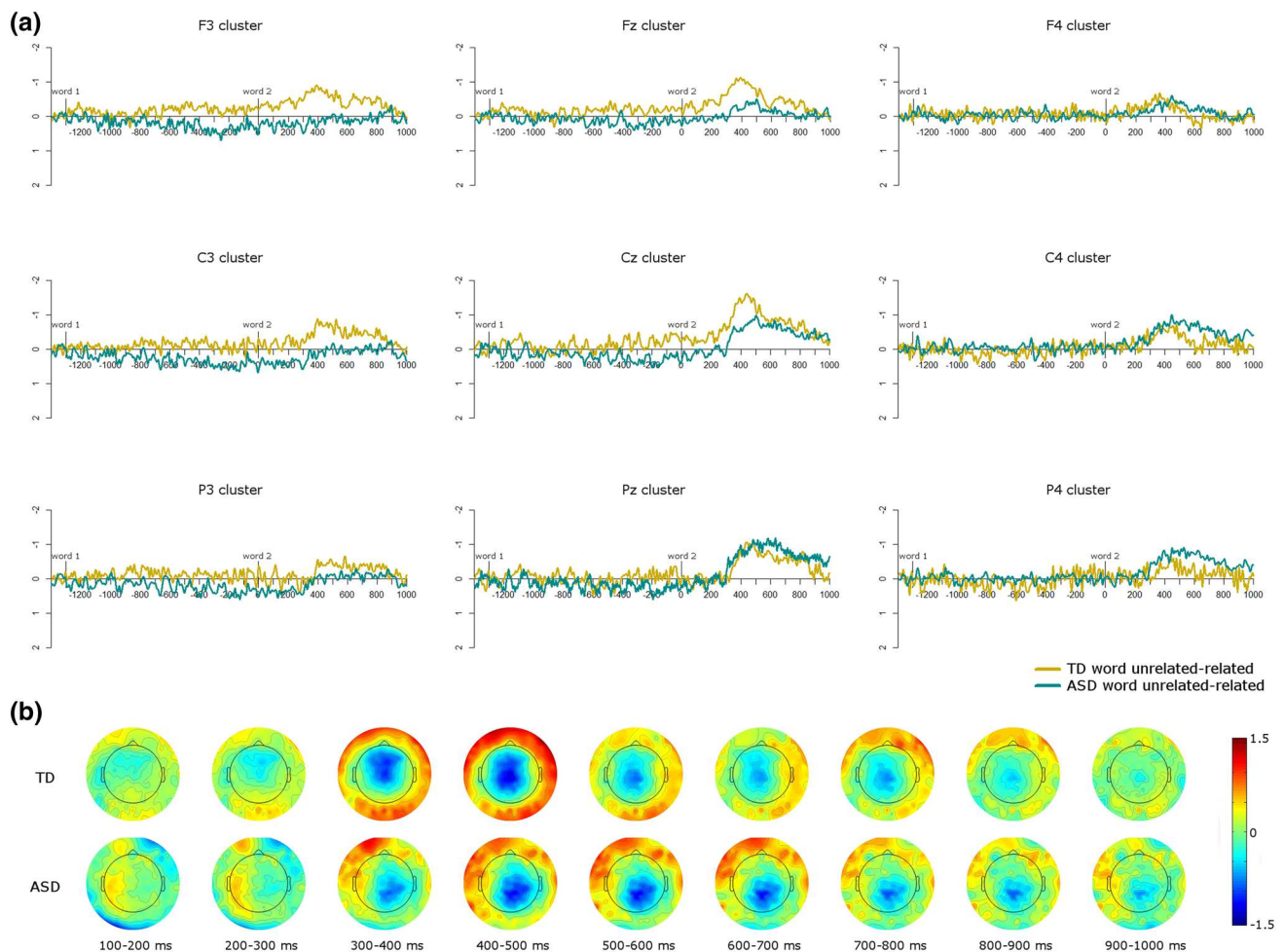


Fig. 8 Group comparisons in the word modality. **a** ERP difference waves (unrelated minus related) for each group in the word modality. **b** Topographic plots of unrelated minus related conditions in the word modality in 100 ms windows from 100 to 1000 ms for each group

such that the N400 effect over right-hemisphere sites was stronger for the ASD group than for the TD group. There is evidence in the literature that pictures elicit greater right-hemisphere activation than words (Chee et al. 2000; Vandenberghe et al. 1996). Previous studies have also reported atypical visual processing in individuals with ASD (Samson et al. 2012) as well as atypical recruitment of the visual system and areas involved in imagery during language processing (Kana et al. 2006). Our observation of larger N400 effects in the right hemisphere for picture stimuli may reflect such atypical visual processing, although the fact that this group difference only emerged at late time windows (600–800 ms) points to differences in post-semantic processing of picture stimuli. As no prior studies have compared semantic processing of pictures in ASD and TD groups using ERPs, this finding should be investigated in more detail in future studies. Importantly, the lack of group differences in N400 effect magnitude in earlier time windows (200–600 ms) and the enhanced N400

effect magnitude for the ASD group from 600 to 800 ms suggests that visuo-semantic processing is intact in individuals with ASD. This is further borne out by the behavioral results, which revealed no effects of or interactions with group in the picture modality, indicating that both groups were able to successfully perform the semantic priming task with picture stimuli. Thus overall, our findings in the picture modality support our predictions that non-linguistic semantic processing would not be impaired in individuals with ASD.

Lexico-Semantic Processing

In the linguistic modality, exploratory analyses for the TD group showed a condition-related negativity (with unrelated conditions more negative than related conditions) from approximately 400–800 ms over central and parietal sites, which we interpret as an N400 effect. The timing and

topography of this effect are in line with previous reports of the N400 (Kutas and Federmeier 2011).

The N300 Component

In addition to this typical centro-parietal N400 effect, the TD group also showed an earlier frontal negativity occurring from approximately 250–500 ms in response to linguistic stimuli. Given the topography and earlier onset of this component, this could be an N300 effect. Although the N300 has been most commonly associated with semantic processing of picture stimuli (Hamm et al. 2002; McPherson and Holcomb 1999; West and Holcomb 2002), there have also been reports of an early N300-type component occurring in response to linguistic stimuli (Franklin et al. 2007; Frishkoff 2007; Frishkoff et al. 2004, 2010; Nobre and McCarthy 1994). For example, Nobre & McCarthy (1994) reported that an N330 effect over left frontotemporal scalp was enhanced by semantic priming, whereas the N400 effect was attenuated by semantic priming, suggesting that they are two separate components. They proposed that the N330 may reflect the temporal summation of spreading activation from the prime. In a semantic priming study, Franklin et al. (2007) compared electrophysiological effects of short (350 ms) and long (500 ms) SOAs, and also of forward primes (where there is an association from prime to target but not the other way around, e.g. fruit-FLY), backward primes (where there is an association from target to prime but not the other way around, e.g. fly-FRUIT), and symmetrical primes (where the association between prime to target is equally strong in both directions, e.g. picture-FRAME). Franklin et al. (2007) reported an N300 only for symmetric priming pairs in the long SOA. Because the N300 was sensitive only to symmetric primes, the authors suggested that it reflects expectancy processes and is sensitive to category membership, as has also been proposed by Hamm et al. (2002). Furthermore, because the N300 only occurred in the long SOA condition, the authors suggested that it may reflect a more controlled form of priming. In a later study using source localization and fMRI, this language-induced N300 was also localized to the dorsal posterior cingulate (O'Hare et al. 2008), suggesting that the N300 is indeed a separable component from the N400.

Overall, our observation of an N300 effect in response to lexico-semantic priming in the TD group in the current study is in keeping with prior literature reporting that an N300 can be elicited by language stimuli and is sensitive to semantic priming. Although we did not manipulate the specific type of priming in the current study, and therefore cannot speak to whether our N300 was only sensitive to symmetric primes as was found in Franklin et al. (2007), the fact that the current study also used a long SOA

(1300 ms) is in keeping with the observations of Franklin et al. (2007), who observed this component only in their long-SOA condition.

In addition to a centro-parietal N400 effect that was sensitive to the semantic relatedness of words, the TD group also showed an earlier anterior N300 effect. Importantly, the ASD group did not show this same early anterior negativity in response to words, as can be seen in Figs. 7 and 8, and as indicated by the significant interaction of group, condition, and site in the 200–400 ms ANOVA analysis window. This may reflect the presence of an N300 effect for the TD individuals but not the individuals with ASD. Furthermore, as the N300 was proposed in Franklin et al. (2007) to reflect expectancy processes in semantic priming, this may suggest differences in processing strategies during lexico-semantic priming between the groups such that TD individuals use a more expectancy-based strategy for semantic processing.

The N400RP Component

In contrast to our predictions, the ASD group *did* show an N400 effect in response to linguistic stimuli in the 400–600 ms and 600–800 ms analysis windows. Furthermore, the magnitude of this effect was largely similar to that of the TD group, as can be seen in the difference waves illustrated in Fig. 8. This finding is in contrast to previous studies reporting reduced or absent N400 effects in response to linguistic stimuli in individuals with ASD (Dunn et al. 1999; McCleery et al. 2010; Pijnacker et al. 2010). There are a number of possible reasons for this unexpected finding, which we will discuss in the next section. Overall, in the current study we cannot conclude that individuals with ASD show a deficit in lexico-semantic processing, as their semantic processing of linguistic stimuli seems largely intact.

However, there were interesting group differences in the topography of the N400 effect in response to linguistic stimuli that point to differences in underlying lexico-semantic processing strategies. Specifically, the N400 effect between 400 and 800 ms was bilaterally distributed in the TD group, but more centrally-distributed and right-lateralized in the ASD group. Inspection of Fig. 8 also indicates that this N400 effect was largest over central and parietal sites in the ASD group, whereas the effect was largest over central and frontal sites for the TD group (although this interaction by site was not statistically significant in the overall ANOVA). This right-lateralized effect seen in the ASD group is similar to a semantic priming ERP component referred to by Franklin et al. (2007) as an “N400RP” (for a “right-lateralized parietal N400 effect”; see also Dien et al. 2006). In their manipulation of symmetric, forwards, and backwards priming, Franklin et al. (2007) observed an

N400RP only for backwards priming and long SOAs. They proposed that this component reflected a more strategic process of post-lexical semantic integration for backwards priming and long SOAs. Specifically, they propose that the N400RP may reflect semantic matching when the usual expectancy approach to semantic processing has failed. In the current study, the observation of a more right-lateralized parietal N400 in the ASD group but not the TD group may reflect the presence of an N400RP for individuals with ASD but not for TD individuals. A more pronounced and sustained N400RP in individuals with ASD may indicate a more extensive semantic matching strategy due to inefficient expectancy processes.

This proposal also supports a previous finding by Pijnacker et al. (2010), who investigated semantic processing in a sentence comprehension paradigm with semantic violations (e.g. “Finally the hikers reached the top of the *mountain/tulip*”). Pijnacker et al. (2010) reported that the N400 effect was absent in an HFA group compared to an Asperger’s group and a TD group. They did, however, find a late positive component (LPC) in all three groups. The LPC is sometimes reported to occur after the N400 effect and has been proposed to reflect a more elaborate monitoring process that triggers reanalysis of semantic information when the initial integration fails (van de Meerendonk et al. 2010). Pijnacker et al. (2010) concluded that semantic integration was less automatic in their HFAs, as reflected by the absence of an N400 effect, and, therefore, required later re-evaluation processes, as reflected by the LPC. In this current study, the more pronounced and more sustained N400RP, which has been proposed to reflect a post-integration semantic matching strategy, in the ASD group may reflect these differences in lexico-semantic processing strategies. Therefore while TD individuals appear to utilize a more expectancy-based strategy (as evidenced by the N300 effect), individuals with ASD appear to employ a more controlled post-lexical integration strategy (as evidenced by the N400RP effect).

Why Does the ASD Group Show an N400 Effect in Response to Linguistic Stimuli?

The observation of an N400 effect in the linguistic condition for the ASD group is surprising and contradicts both our predictions and previous literature. Although the absence of an N300 effect and the presence of an N400RP in the ASD group may suggest differences in lexico-semantic processing strategies in individuals with ASD, we cannot conclude that this group shows a deficit in semantic processing of linguistic stimuli. This is also borne out in the behavioral results: behaviorally, there was no evidence of difficulties with semantic processing within the ASD group. The lack of significant effects of or interactions with

group in the linguistic modality for either accuracy or reaction times indicates that both groups were able to successfully perform the semantic priming task at a similar level of performance. This is in line with other studies reporting no group differences in behavioral performance but atypical N400 effects in individuals with ASD (Braeutigam et al. 2008; Dunn et al. 1999; Dunn and Bates 2005; Strandburg et al. 1993), and highlights the fact that ERPs can be a valuable way of probing more subtle differences in cognitive processes between groups that may not be observable at the behavioral level.

There are several explanations for the unexpected finding of an N400 effect in the linguistic conditions for individuals with ASD. The nature of the task may have generated explicit processing strategies that mitigated group differences. Previous research has suggested that the specific instructions given to participants with ASD may influence their performance on language processing tasks (Koolen et al. 2014). Specifically, instructing participants to attend or respond to the semantic relations between stimuli may trigger explicit semantic processing strategies in ASD participants, attenuating group differences. In the current study, participants performed an explicit semantic processing task in which they judged whether the two words or two pictures were semantically related. Participants were explicitly required to process the semantic relationship between stimuli, which may have introduced a more targeted processing strategy in the ASD group, leading to a significant N400 effect that did not differ in magnitude from that of the TD group.

One theory of autism (Frith 1989), the theory of weak central coherence, proposes that difficulties with semantic integration in individuals with ASD arise from a reduced tendency to process information in its larger context. However, this tendency for fragmentary processing of information does not mean this predisposition cannot be overcome. It is possible that as individuals with ASD mature and become more aware of their difficulties with semantic processing they develop explicit compensatory strategies to aid their understanding of language. Such explicit strategies may be especially apparent during explicit semantic processing tasks, leading individuals with ASD to perform comparably with TD individuals.

However, a reduced tendency to process the semantic relations in language by individuals with ASD may become more apparent during an implicit semantic processing task in which participants are not directly instructed to attend to the semantic relations between stimuli. Certain paradigms such as a passive semantic priming task (e.g. similar to the current study but with passive viewing rather than explicit judgements) or a lexical decision task (in which participants make a judgement as to whether the target is a legal word or not) may

tap more automatic and implicit semantic processing. If individuals with ASD have a reduced tendency to automatically and implicitly process the semantic properties of language, such paradigms may elicit larger group differences.

Previous studies report reduced or absent N400 effects in ASD for both implicit tasks (McCleery et al. 2010; Pijnacker et al. 2010) and explicit semantic tasks (Dunn et al. 1999). For instance, McCleery et al. (2010), in the paradigm described in the Introduction, reported an absent N400 effect for participants with ASD using an implicit semantic priming task. Using an explicit task in which participants responded when they saw an animal word, Dunn et al. (1999) also reported an absent N400 effect in the ASD group compared to the TD group. Nevertheless, further research should be done comparing the effects of task instruction on semantic priming performance. Extending the current study to a more implicit semantic task to determine if similar effects are present will be an interesting direction for future research.

Another possibility for finding an intact N400 response in the current ASD sample is that these participants were all adults (ages 18–68). Having struggled with semantic processing for much of their life, adults with ASD may have developed explicit compensatory strategies to overcome their semantic processing deficits. In contrast, children with ASD may be less aware of their difficulties, or may not have had as much time to develop compensatory strategies, which may lead to larger group differences in N400 responses. The two previous studies investigating semantic processing of single words (Dunn et al. 1999; McCleery et al. 2010) both tested children with ASD, which may explain why they observed absent N400 effects in the ASD group. Extending the current semantic priming paradigm to children to determine if patterns are comparable to those of adults may be an interesting direction for future research.

It is also worth noting that the finding of atypical semantic processing in the current results does not speak to the specific level of semantic processing that is abnormal in individuals with ASD. Other theories of autism (Brock et al. 2002; Frith 1989) and other investigators (e.g. McCleery et al. 2010; Pijnacker et al. 2010) have invoked specific differences in semantic integration as underlying the language difficulties observed in individuals with ASD. Due to the nature of the semantic priming paradigm, we were unable to tease apart specific sublevels of semantic processing; for instance, we cannot rule out the possibility that differences in semantic *access*, rather than *integration*, were responsible for the observed group differences. Determining the specific level at which atypical semantic occurs will be an important area for future research.

Conclusions

As predicted, the current study demonstrated intact semantic processing of picture stimuli between individuals with ASD and TD individuals, suggesting that individuals with ASD do not have difficulties with non-linguistic semantic processing. In contrast to previous findings, the ASD group showed an N400 effect in response to linguistic stimuli of similar magnitude to that of the TD group. While we cannot conclude that individuals with ASD have a deficit in lexico-semantic processing, the current data suggest more subtle differences in processing strategies between the groups: TD individuals utilize a more expectancy-based strategy while individuals with ASD employ a more controlled post-lexical integration strategy. These strategic differences could be related to the explicit nature of the semantic priming task or to the adult populations we tested. Determining the nature of semantic processing deficits in autism has important implications for future interventions and treatment strategies. The current results point to intriguing differences in lexico-semantic processing between groups and pave the way for future research investigating the nature of semantic processing in ASD.

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Author Contributions EC conceived of the study, participated in its design and coordination, collected data, performed the statistical analysis, interpreted the data, and drafted the manuscript. MC participated in the design and coordination of the study, collected data, and helped draft the manuscript. BG participated in the coordination of the study and helped draft the manuscript. KL participated in the design of the study and helped draft the manuscript. All authors read and approved the final manuscript.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical Approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards.

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