No Evidence for Neural Markers of Gaze Direction Adaptation in 2-Year-Olds with High or Low
Likelihood of Autism

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Abstract

Predictive Processing accounts of autism posit that individuals with autism rely less on expectations than those without autism when it comes to interpreting incoming sensory information. Since these expectations are claimed to underlie all information processing, we reason that any differences in how they are formed or adjusted should be persistent across multiple cognitive domains and detectable much earlier than clinicians can currently diagnose autism, around 3 years of age.

This experiment is part of a longitudinal prospective study of young children with increased familial likelihood of autism. Around 20% of these children will receive an autism diagnosis themselves, compared to 1% of the general population. The current EEG study used an adaptation paradigm to investigate whether a reduced effect of expectations is already present in high-risk 2-year-olds, before autism can reliably be diagnosed. While we did not observe the adaptation after-effect we expected, high-likelihood children habituated more than low-likelihood children and the two groups did not differ in their overall responses to the manipulation, contrary to our hypotheses and previous findings.

Key words: Predictive Processing, autism, adaptation, high-likelihood siblings, longitudinal prospective study, EEG

General scientific summary: This paper tested theories of autism which claim that all the various symptoms involved in autism, such as strong special interests, sensory sensitivity and atypical social communication, result from a difference in how autistic individuals use their previous experiences to help them interpret new information. We did not see evidence of young children with high- and low-likelihood of receiving an autism diagnosis using their experience to interpret new information, although we did find some evidence that the high-likelihood group got used to the stimuli more quickly than the low-likelihood group, which is contrary to the predictions of the theories. The results suggest that these theories are difficult to directly test in this population but need to be refined in order to better match our observations.

No Evidence for Neural Markers of Gaze Direction Adaptation in 2-Year-Olds with High and Low Likelihood of Autism

Autism Spectrum Disorder is a developmental disorder characterised by social communication deficits, repetitive behaviours and unusual sensory interests, including hypo- or hyper-sensitivity to sensory stimuli (DSM-V, APA, 2013). Sensory processing difficulties are present for the great majority of children with autism (Baranek, David, Poe, Stone, & Watson, 2006; Tomchek & Dunn, 2007). These symptoms are specific to autism, but previous theories of the underlying causes of autism did not provide a convincing mechanism that should produce this specific cluster of symptoms.

While previous work has produced attempts at an explanatory mechanism of autism – among others, the Theory of Mind deficit hypothesis (Baron-Cohen, Leslie, & Frith, 1985), the Weak Central Coherence theory (Happé & Frith, 2006) and the Enhanced Perceptual Functioning theory (Mottron & Burack, 2001) – these accounts tend to explain one cluster of symptoms and fail to account for the other domains. More recently, proponents of Predictive Processing accounts of autism have made claims of a truly unifying account (Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; van de Cruys, 2014). This framework is based on the Bayesian brain hypothesis and claims that all information processing is based on generative models which consist of a probabilistic combination of prior expectations and incoming sensory input, to compute prediction errors (Clark, 2013).

Predictive Processing accounts of autism posit that autistic individuals rely less on expectations than those without autism when it comes to interpreting incoming sensory information (Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; van de Cruys et al., 2014). They claim that this leads to persistent differences across multiple cognitive domains and cascading consequences leading to larger differences in higher-level cognition and behaviour. Authors of the theoretical accounts claim that the complexity and unpredictability of social interactions leads to these being the most noticeably affected domain (Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; van de Cruys et al., 2014). This difference is proposed to originate from those with autism having an altered mechanism for adjusting expectations (Lawson, Rees & Friston, 2014), weaker expectations overall (Pellicano & Burr, 2012), or from a tendency to over-adjust expectations in response to even slight violations (van de Cruys et al., 2014), however there are very few bespoke empirical studies testing these claims. The first steps in testing these theories are now being made (e.g. Manning, Kilner, Neil, Karaminis & Pellicano, 2017; Manning, Tibber, Charman, Dakin & Pellicano, 2015; Manning, Tibber & Dakin, 2017; van de Cruys, Vanmarcke, van de Put & Wagemans, 2018; van der Hallen, Lemmens, Steyaert, Noens & Wagemans, 2017). So far, this work has shown that autistic individuals do update their expectations similarly to non-autistic individuals in certain tasks, challenging the Predictive Processing framework

(e.g. Manning et al., 2017; van der Hallen et al., 2017), but not in others, with some findings (e.g. Manning et al., 2015; Manning, Tibber & Dakin, 2017; van der Hallen et al., 2017) compatible with accounts claiming that autistic individuals adjust their expectations more readily (van de Cruys et al., 2014). More work to understand the particular ways in which autistic individuals do and do not differ from typically-developing peers on tasks designed specifically to test these theories is crucial for future refinement, or refutation, of the theories.

The difference between information processing by autistic and non-autistic individuals is claimed to be so fundamental that we believe it should also be detectable much earlier than clinicians can currently diagnose autism (around 3 years of age; Charman & Baird, 2002). Therefore, in this study, we attempted to evaluate the Predictive Processing accounts of autism early in development. We used a longitudinal prospective design, in which participants with an older sibling with an autism diagnosis (high-likelihood siblings) and control participants with an older sibling without autism (low-likelihood siblings) are followed throughout their first three years. Around 20% of high-likelihood siblings go on to receive a diagnosis themselves at the age of three, in comparison with 1% of the general population (Ozonoff et al., 2011). A further 30% of high-likelihood siblings who do not receive an autism diagnosis are expected to display the Broader Autism Phenotype: they will experience some symptoms of autism but will not be affected enough to warrant an autism diagnosis (Ozonoff et al., 2014). Because autism cannot generally be diagnosed before age 3, these younger siblings at high likelihood provide us with a way to study the early development of the disorder, as well as an insight into the Broader Autism Phenotype characteristics.

To test whether young children with an increased chance of an autism diagnosis indeed show differences in Predictive Processing, the current study employs an adaptation paradigm (Jenkins et al., 2006; Pellicano, Rhodes, & Calder, 2013). In such paradigms, the participants' perception is biased systematically due to the distribution underlying the stimuli they observe. Participants show reduced responses to certain stimuli based on their experience with this distribution, leading to an adaptation after-effect. The size of this after-effect provides an index of how strongly a participant's expectations are influenced by biasing stimuli, and serves as a proxy for how flexibly participants change their expectations when given new information. As such, this paradigm is a useful test of predictions of the Predictive Processing accounts of autism.

The paradigm has been used extensively to show that in certain circumstances, children with autism experience less of a shift in perception based on their cumulative experience than their typically-developing peers. In the face domain, adaptation after-effects have been shown to be smaller in magnitude for 8- to 16-year-old autistic children than they are for typically-developing children, with experiments targeting face identity (Rhodes, Ewing, Jeffery, Avar, & Taylor, 2014),

facial distortion (Ewing, Pellicano, & Rhodes, 2013), and gaze direction (Pellicano et al., 2013). Autistic children also show smaller after-effects than typically-developing children in a numerosity judgement task (Turi et al., 2015) but not in a causal-motion task (Karaminis et al., 2015), or a task with distorted car and upside-down face stimuli (Ewing, Pellicano, & Rhodes, 2013).

A finding of reduced adaptation is compatible with the Predictive Processing accounts mentioned above. Pellicano and Burr (2012) claim that autistic individuals have weaker priors, so their perception is less biased by previously accumulated experiences, which would lead to smaller adaptation after-effects. Van de Cruys and colleagues (2014) claim that autistic individuals update their expectations in response to every change in the environment, so their perception is heavily biased by their recent experiences but this bias would on average be less strong during the presentation of randomised stimuli. The fact that the findings are in fact mixed, and that for some stimulus types the participants with and without autism seem not to differ in the size of their adaptation after-effects, currently forms a challenge for the theories.

In a clear case of reduced adaptation in autistic individuals, Pellicano and colleagues (2013) used a gaze direction adaptation task in young children and adolescents with and without autism. The children were familiarised with multiple gaze directions in the first, pre-adaptation block, and asked to respond with a button press, categorising the gaze direction as left, right or straight. They were then adapted to one extreme gaze direction in the second, adaptation block. In the final block, post-adaptation, the children again had to categorise the gaze direction of the stimuli. While the typically-developing children were biased away from the adaptor stimuli, by perceiving gaze in the final post-adaptation phase as less like the direction they had been adapted to, children with autism were less biased and perceived the gaze more closely to its true direction.

In order to study whether this after-effect is diminished already in toddlers with increased chance of autism compared to low-likelihood children, we used adaptation to gaze-direction (Jenkins et al., 2006; Pellicano et al., 2013) in an EEG study with no behavioural response required. This allows the paradigm to be used not only with younger children but also with children who could have trouble understanding task instructions or remembering to respond with button presses.

In typical adults, the neural response to a visual stimulus is suppressed when that stimulus is highly expected (Manahova, Mostert, Kok, Schoffelen, & De Lange, 2018). We therefore expected that if adaptation after-effects are induced, the stimuli with the same gaze direction as the adaptor stimuli would evoke a diminished neural response from the young children during post-adaptation than the stimuli with the opposite gaze direction. Our hypothesis was that the high-likelihood children would show less adaptation, that is, less of a difference between their responses to the adapted and unadapted gaze directions, than the low-likelihood children. We focused on the amplitude of the N290

and P400 ERP components, as these are related to face-processing in young children, and they together later form the adult N170 face-specific component (de Haan, 2013). The P400 has also been shown to be modulated by gaze direction, for example in work by Elsabbagh and colleagues (Elsabbagh et al., 2009; Elsabbagh et al., 2012).

We expected to see a reduction in the amplitude of the N290 and P400 components from block 1 (pre-adaptation) to block 3 (post-adaptation). We hypothesised that this reduction in amplitude would be greater for stimuli showing the adapted gaze direction than for the unadapted gaze direction, as adaptation is a specific form of repetition suppression. We further expected this reduction to be greater in the low-likelihood group than in the high-likelihood group, as the cumulative recent sensory experience was expected to influence perception less in the high-likelihood group.

We also tested for a habituation effect. We expected to see habituation, as indexed by smaller ERP responses during block 3 compared to block 1, in all participants, but we expected the high-likelihood group to habituate less than the low-likelihood group based on previous work showing slower habituation to faces in children with autism and high-likelihood siblings (Jones et al., 2016; Webb et al., 2010). This prediction is also in line with Predictive Processing accounts of autism, which say that each new percept is more novel for autistic observers, as it is influenced less by the observer's cumulative previous experience, either because the expectations are less strong or because each new experience is processed with high prediction error.

Method

Participants

In total, sixty-two 2-year-olds took part in the study: 36 high-likelihood siblings and 26 low-likelihood siblings. Of the 62 tested, 56 children, 32 high-likelihood and 24 low-likelihood, contributed data to the analysis. The high-likelihood children all had an older sibling with an autism diagnosis, and the low-likelihood children all had an older typically-developing sibling. Infants were part of the low-likelihood group only if they had no first-degree relatives with autism and no family history of psychiatric or genetic disorders. Parents reported no visual impairments for any of the participants.

The groups did not differ in age ($t(52.04) = -1.31, p = .20$) but the high-likelihood group had lower developmental level as measured by the Mullen Scales of Early Learning composite score ($t(51.75) = -4.64, p = .00002$) and more autism symptoms as measured by their Autism Diagnostic Observation Scale (ADOS-2; Lord et al., 2012; Lord, Luyster, Gotham & Guthrie, 2012) comparison scores ($t(43.74) = 3.12, p = .003$; see Table 1). Due to violation of the assumption of equal variance, degrees of freedom have been adjusted using the Welch approximation.

Table 1

Participant characteristics

	N	Age in days	Mullen	ADOS-2 CS ^a
High-likelihood	32	785.31 (79.90)	87.48 (18.52)	3.16(2.17)
Low-likelihood	24	812.04 (72.30)	106.71 (12.14)	1.82(0.89)
Total	56	796.77 (77.22)	95.87 (18.60)	2.60 (1.86)

^a ADOS Comparison Scores, which allow for comparison of scores from different modules. Conversion tables for module 2 scores can be found in Gotham and colleagues (2009), and for toddler module scores in Esler and colleagues (2015).

This study was part of a large multisite longitudinal prospective study, and was approved by the medical ethics committee (Commissie Mensgebonden Onderzoek Arnhem-Nijmegen, protocol NL42726.091.13). Recruitment was done via the Baby and Child Research Center participant database and through Karakter, a child and youth psychiatry clinic. Participants received a reimbursement of their travel costs and €50 per lab visit as a thank you for taking part.

Materials

Stimuli. Stimuli were a subset of those used by Jenkins and colleagues (2006) and Pellicano and colleagues (2013), with some adjustments to make them more child-friendly; the fixation cross was replaced with a coloured beach ball, and all task instructions were removed (see Figure 1 for schematic). Short 3- to 6-second attention-getter videos could be triggered by the experimenter on demand by a key-press. The first block of the experiment, pre-adaptation, consisted of 36 images: 12 actors with 3 gaze directions each; 0 degrees (straight ahead), 5 degrees left and 5 degrees right. The second block, adaptation, consisted of 12 images, one of each actor, with an extreme gaze direction of 25 degrees. Adaptor images were all looking in the same direction, and each participant was adapted to either left or right gaze, assigned randomly. The third block, post-adaptation, again

consisted of 36 trials, with the same images as shown in pre-adaptation. In this block, however, each image was preceded by a top-up adaptor from the adaptation set.

Figure 1. Schematic showing one example trial for each block. Block 1 consists of 36 trials, block 2 of 12 trials and block 3 of 36 trials.

Images showing gaze directions of 0 and 5 degrees were 16cm by 9.9cm. Adaptor images, showing the 25 degree gaze angle, were 21.4cm by 13.3cm. The two image types were displayed at different sizes to avoid retinotopic adaptation, as in the previous studies (Jenkins et al., 2006; Pellicano et al., 2013). The fixation beach ball had a diameter of 3.6cm.

Apparatus. Electroencephalography (EEG) was recorded from 32 AgCl active electrodes in a child-sized EEG cap (ActiCap, Brain Products, Munich, Germany) using BrainVision Recorder, via a BrainAmp BrainVision Products amplifier. EEG was recorded continuously, with an online reference at FCz, at a sampling frequency of 500Hz and with a band-pass filter (0.1–125 Hz). We also measured eye-movements from all participants for whom we could achieve a successful calibration ($N = 36$; 18 high-likelihood and 18 low-likelihood children) with an Eyelink 1000+ eye-tracker at a sampling frequency of 500Hz. Stimuli were presented with Matlab (versions 2011a and 2013a; MathWorks) together with Psychtoolbox (versions 3.0.9 and 3.1.0; Brainard, 1997; Kleiner et al., 2007) and Eyelink Toolbox (Cornelissen, Peters & Palmer, 2002) on a 24" Benq XL2420T LCD monitor.

Procedure

Participants were fitted with the EEG cap during a play session, which had been prepared with the electrodes already placed in the rings and a small amount of conductive gel applied to each electrode. This reduces the time the child has to wait with the cap on their head before testing can begin. We added more gel to each electrode until impedances were below 20 kOhm or the child no longer tolerated the procedure.

The child and their parent or caregiver were then seated in a shielded testing booth. Parents decided whether the child would be more calm and attentive sitting on their lap or in a highchair. The screen and chair were adjusted so that the child's eyes were approximately 60cm from the screen.

Due to the embedding in the longitudinal multisite study (Loth et al., 2017), some children saw videos before and/or after the current study, but this did not differ between groups. The experiment started with a child-friendly 9-point eye-tracking calibration, after which stimulus presentation commenced. The experiment lasted for approximately 7.5 minutes excluding breaks and attention getters, which were played on demand when the child looked away from the screen. Testing was stopped if the child cried for longer than one minute, could not be reoriented to the screen, or if parents requested to stop.

Data analysis

Video coding for visual attention. Videos of the child were coded offline frame-by-frame using ELAN (version 5.2; Brugman & Russel, 2004). All trials in which the child was not attending the screen for the first 500ms of stimulus presentation were removed from further analysis. In a study of face perception in 7-month-olds, stimulus presentation for 500ms was shown to be long enough to reliably elicit a P400 response (Jessen & Grossman, 2015). Participants visually attended on average 95.10 trials ($SD = 14.31$) out of a possible 120. The groups did not differ in the number of trials visually attended ($t(43.24) = 1.20, p = .24$), with the high-likelihood group on average attending to 97.24 trials ($SD = 13.16$) and the low-likelihood group on average attending to 92.39 trials ($SD = 15.50$).

Eye-tracking. Eye-tracking data recorded during the stimulus presentation were analysed using Matlab to examine how often and for how long the participants fixated the eyes of the stimuli. The default Eyelink 1000+ online filter classified fixations, which were then categorised as within or outside a rectangular area of interest (AOI) around the eyes of the stimuli, 300x150 pixels for the test stimuli and 700x300 pixels for the larger adaptor stimuli. The eye-tracking data quality varied due to participant movement, so we excluded participants with an average fixation duration under 100ms (2 high-likelihood children and 1 low-likelihood child), since this is physiologically implausible. We then analysed the proportion of the number of fixations inside the AOI and the proportion of fixation durations inside the AOI (see Table 2 for descriptive statistics).

The high-likelihood group spent a significantly smaller proportion of the number of fixations inside the AOI ($t(25.87)=-2.56, p = .02$), a significantly smaller proportion of the total duration of all their recorded fixations inside the AOI ($t(25.30)=-2.93, p = 0.007$), and the length of their mean fixation inside the AOI was significantly shorter ($t(23.46) = -2.08, p = 0.048$) than the low-likelihood group. The groups did not, however, differ in the absolute number of fixations inside the AOI ($t(26.99) = -1.09, p = 0.28$).

Table 2

Fixation count, proportion, mean duration, and proportion of duration spent inside the area of interest around the eyes of the stimuli

	N	Mean number fixations in AOI	Proportion fixations in AOI	Proportion of all fixation durations spent in AOI	Mean duration fixations in AOI
High-likelihood	16	111.5 (94.90)	32.68% (22.06)	37.53% (27.04)	348.33 (218.24)
Low-likelihood	17	143.06 (67.65)	49.49% (14.66)	60.89% (17.34)	477.71 (123.89)
Total	33	127.76 (82.26)	41.34% (20.21)	49.56% (25.18)	414.98 (185.24)

EEG data processing. Data were analysed using Matlab and the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Each trial was separately detrended, demeaned and low-pass filtered at 30 Hz, and baseline-corrected to a window of 200ms before stimulus onset. All channels and all trials were then separately visually inspected, and channels and trials with excessive noise or movement artifacts were rejected from further analysis. After poor-quality channels were rejected, the data were re-referenced to the average of the remaining channels. Of a total possible 32 channels, the mean number of channels included in the average was 26.54 (SD = 5.36) for the high-likelihood group and 24.27 (SD = 4.66) for the low-likelihood group. Channels of interest were all ten occipital

and parietal channels in the 10-20 system (P7, P3, Pz, P4, P8, PO9, O1, Oz, O2 and PO10). After poor-quality channels were rejected, the mean number of available channels of interest per child was 8.42 (SD = 2.08) in the high-likelihood group and 8.00 (SD = 1.75) in the low-likelihood group. The groups did not differ in the number of overall channels available ($t(45.96)=1.57, p = .12$) or the number of channels of interest available ($t(45.99)=0.77, p = 0.45$).

We excluded five high-likelihood children and two low-likelihood children from further analysis because they had fewer than three artifact-free, visually attended trials per cell (Kaduk, Elsner & Reid, 2013; Stets & Reid, 2011), and one further high-likelihood child because their average ERP amplitude exceeded $\pm 50\text{mV}$, leading to a total sample size of 48 children; 26 high-likelihood children and 22 low-likelihood children. The average number of trials per cell for the adaptation after-effect analysis was 8.62 (SD =1.48) for the high-likelihood group and 7.95 (SD =1.48) for the low-likelihood group. The two groups did not differ in number of trials included for final analysis ($t(44.64) = 1.55, p = .13$).

Statistical analysis. On visual inspection, we did not observe a consistent canonical N290 (see Figure 4) and therefore did not proceed with these analyses. The remaining tests were performed only on the P400 time window. The P400 component was expected to appear between 320 and 540ms based on findings of Elsabbagh and colleagues with younger participants (Elsabbagh et al., 2009; Elsabbagh et al., 2012), although young children, and autistic children in particular, often show large intra- and inter-individual variability in the latency of ERP components (Milne, 2011). We therefore used Fieldtrip to conduct mass univariate analyses consisting of a t-test performed on each sample in the time window, using False Discovery Rate correction for multiple comparisons. This approach allows increased sensitivity when testing for effects with uncertain timing or topography while controlling for false positives in a conservative manner (Groppe, Urbach, & Kutas, 2011). However, False Discovery Rate correction assumes independence of samples, which cannot be assumed for consecutive time-points in electrophysiological data. In contrast, non-parametric cluster-based permutation testing takes into account the inherent temporal structure of such data, and is thus a more appropriate method for multiple comparison correction in the current analyses (Maris & Oostenveld, 2007). We therefore present results from both FDR and non-parametric cluster-based permutation testing for our between-participants comparisons.

In order to quantify the amount of evidence for the null hypothesis and the alternative hypothesis, we also conducted Bayesian t-tests using JASP (version 0.9.0.1, JASP team, 2018). For these tests we extracted a peak value per participant, rather than performing the mass univariate analysis with tests for each time sample. This is not directly comparable to the frequentist tests performed in Fieldtrip, since JASP is not designed for mass univariate analyses, but taking the peak

values per participant during the time window of interest is relatively common in ERP analyses and this gives an indication of the direction of an effect.

Bayesian tests have the advantage of providing more detailed information than frequentist tests about the ratio of evidence for the alternative versus the null hypothesis, and importantly can distinguish between the lack of an observed effect due to strong evidence for the null hypothesis and the lack of an observed effect due to too little information (Wagenmakers et al., 2018). The resultant test statistic is a Bayes Factor (BF), a ratio of the amount of evidence for the alternative hypothesis to the amount of evidence for the null hypothesis, where values around 1 indicate equivalent levels of evidence for both the null and alternative hypotheses. Values of less than 0.3 or more than 3 are considered moderate evidence for the null and alternative hypotheses respectively; values of less than 0.1 or more than 10 are considered strong evidence for the null and alternative hypotheses respectively. For the current analyses we used the default Cauchy prior width of 0.75 since we did not have strong expectations about the size of the difference.

Results

Habituation Effect

We first examined the habituation effect indicated by the ERP responses to faces, that is, the reduction in amplitude of the ERPs after repeated exposure. When comparing the grand average ERP response during block 1 to the grand average during block 3, two separate two-tailed one-sample *t*-tests revealed that both groups individually showed a reduced response during block 3. For the high-likelihood group, the critical *t* value was ± 2.01 , and *t* values (*df* = 50) exceeded this for time points 320ms – 936ms, all *ps* below .006 (see Figure 2C). For the low-likelihood group, the critical *t* value was ± 2.02 , and *t* values (*df* = 42) exceeded this for time points 438 – 440ms and 618ms – 864ms, all *ps* below .003 (see Figure 2D).

Figure 2. Habituation effects in the high- and low-likelihood groups.

Top row: ERP responses to all faces in block 1 (pre-adaptation, in blue) and block 3 (post-adaptation, in green), averaged over channels of interest. A: High-likelihood group. B: Low-likelihood group. Bottom row: Difference between the mean ERP to all faces in block 1 (pre-adaptation) and the mean ERP to all faces in block 3 (post-adaptation), averaged over channels of interest. Bold portions indicate where the habituation effect is significantly different from zero. C: High-likelihood group. D: Low-likelihood group.

The conservative two-tailed independent samples t -test with False Discovery Rate correction showed all t values below 3.14 ($df = 46$). Uncorrected p values were all greater than 0.003, but False Discovery Rate corrections yielded no values below 0.05. However, cluster-based permutation tests, which take into account the inherent structure of the data, yielded two positive clusters, one of which showed that the groups did significantly differ from each other in the extent of their habituation (338 – 498ms, cluster = 208.21, SD = 0.0041, $p = .02$; see Figure 3). A Bayesian t -test calculated in JASP on the maximum difference between block 1 and block 3 per participant revealed that there is moderate evidence that the two groups do not differ in the extent of their habituation (BF = 0.29) when each participant contributes their individual point of maximal difference, independent of the time-course of the effect. The lack of difference between groups in the Bayesian analysis should not be considered contradictory, as this analysis answers a different question; namely, do the groups differ in their habituation when values are taken from the time-point representing each individual child's maximum

difference. We designed the analysis this way in order to avoid the problem of uncertainty in the timing of the habituation effect. Taken together, the results suggest that the timing of the habituation effect is heterogeneous, and that both groups habituated to the stimuli, but that the high-likelihood group habituated more than the low-likelihood group in the P400 time window specifically.

Figure 3. Differences in habituation between high- and low-likelihood groups. Mean ERP to all faces in block 1 (pre-adaptation) minus mean ERP to all faces in block 3 (post-adaptation), averaged over channels of interest. Bold portions indicate where the groups differ significantly according to cluster-based permutation testing. High-likelihood group shown in blue, low-likelihood group shown in red.

Adaptation After-Effect

To isolate the adaptation after-effect, we took the difference per participant between their ERP responses to the direction they were adapted to in block 1 and block 3, the difference between their ERP responses to the direction they were not adapted to in block 1 and block 3, and then took the difference of the resulting difference waves, and compared these differences in the two groups. This is functionally equivalent to a three-way interaction of Group X Block X Condition, and ensures that any change in observed response is due only to the experience with the adaptor gaze direction in block 2, correcting for habituation over the course of the experiment.

A two-tailed one-sample t -test taking all participants together showed that when comparing difference waves continuously across the time window of interest, the combined group did not differ from zero. The critical t value was ± 1.99 . The absolute values of the t values ($df = 94$) were all below

0.90. Cluster-based permutation testing confirmed this finding, with 5 positive clusters but none of them significant, all p s > 0.06. Bayesian t-tests also showed that there was moderate evidence for the null hypothesis using the point of maximum difference between the conditions and blocks per participant during the time window (BF = 0.33).

A two-tailed, independent samples t-test showed that the high- and low-likelihood groups did not differ significantly from each other on the size of the adaptation after-effect. The critical t value was ± 2.03 , and the absolute values of t in the time window specified ranged from 0.70 to 2.34 ($df = 46$). Uncorrected p values were all above 0.02, but False Discovery Rate corrections yielded no p values below 0.05. A Bayesian t-test showed that there is moderate evidence that the two groups do not differ from each other in their response to the adaptation manipulation (BF = 0.29).

Figure 4. Adaptation after-effects. ERP responses pre- and post-adaptation, i.e. in block 1 (blue) and block 3 (green), averaged over channels of interest. The time window of interest for the P400 is indicated by the red rectangle. The shaded areas represent one standard error of the mean. A: High-likelihood group in adapted direction. B: High-likelihood group in unadapted direction. C: Low-likelihood group in adapted direction. D: Low-likelihood group in unadapted direction.

Discussion

We tested whether young children with older autistic siblings differed from those with older non-autistic siblings in the extent to which their perception was influenced by their previous experience, using an adaptation paradigm during passive viewing while we recorded EEG. We observed signs of habituation in both groups, and found some evidence that the high-likelihood group

habituated more than the low-likelihood group did. However, neither of the groups showed adaptation after-effects, which we had expected to see in the difference of the difference, representing the interaction between block and condition.

We also failed to observe an N290 modulation in the early portion of the experiment, which is surprising since this component is reliably evoked during face perception. There are few EEG studies available with children of this age, so it is difficult to establish a time window of interest for the component for 2-year-olds. Even so, we expected to see a negative deflection before the positive P400, and it is unclear why this was not always the case.

Predictive Processing accounts of autism claim to explain all aspects of the condition as consequences of an altered balance between expectations and prediction errors, and as a result predict that those with autism perceive the world differently to those without autism. The two instantiations of Predictive Processing accounts of autism mentioned above – reduced influence of prior experience (Pellicano & Burr, 2012) and over-adjusting expectations based on small expectation violations (van de Cruys et al., 2014) – both predict reduced adaptation in individuals with autism. In a previous study, Pellicano and colleagues (2013) did show using the current paradigm that autistic children aged 8 to 16 years recalibrate their perceptual expectations less than their peers without autism, and experience less of an adaptation after-effect. Other studies have shown the same phenomenon with variations on stimuli (Ewing et al., 2013; Rhodes et al., 2014; Turi et al., 2016), although there are studies that show no difference between after-effect magnitude in neurotypical and autistic children (Ewing et al., 2013; Karaminis et al., 2015). Although the studies showing reduced adaptation in autistic children do tend to be those using social stimuli, there is no clear dividing line between the stimuli that seemingly induce reduced adaptation and those that induce typical adaptation in autistic children. It should also be noted that some adaptation studies with adult participants report equivalent adaptation after-effects for autistic and non-autistic groups (e.g. Cook, Brewer, Shah & Bird, 2014; Palmer, Lawson, Shankar, Clifford & Rees, 2018; Pell et al., 2016) While others show reduced adaptation in autistic adults (e.g. Corbett, Venuti & Melcher, 2016; Lawson, Aylward, Roiser & Rees, 2018; Walsh, Vida, Morrissey & Rutherford, 2015). It is possible that some autistic adults have learnt idiosyncratic compensatory strategies, leading to more mixed findings in individuals with more diverse life experiences and personal coping mechanisms.

Predictive Processing accounts of autism suggest that autistic individuals either weigh their previous experience less during information processing, or that they weigh any difference to expectations (their prediction errors) highly even when this is not warranted. Since, in the Predictive Processing view, this type of computation is inherent to all information processing, such a difference from neurotypical weightings should cascade into all domains and be present from the age at which

an individual can sense and perceive. If this were true, this would mean that such a difference in perception could possibly be used as an early marker of autism. Experimental studies testing this claim could have large implications for the theories, which are currently being widely discussed in theoretical papers but just beginning to be tested empirically.

Most of the evidence cited as consistent with the theories comes from existing studies with adult participants. To rule out any processing differences due to compensatory behaviours or lived experience as an autistic person, strong evidence in favour of these accounts should be derived from studies with children as young as possible. Longitudinal prospective studies are a well-suited forum for this investigation as they provide the best opportunities to test children with autism before they are old enough to be diagnosed.

Habituation

The fact that our high-likelihood group appears to habituate to a greater extent than the low-likelihood group was unexpected, not only from within a Predictive Processing framework but also in the context of other work on habituation in autism. Young children at high-likelihood and those with autism have been shown to exhibit reduced habituation when hearing repeated tones (Guiraud et al., 2011), or seeing images of neutral faces with direct gaze (Jones et al., 2016; Webb et al., 2010), while those same infants did not show reduced habituation to images of houses (Webb et al., 2010) or images of toys (Jones et al., 2016). Previous fMRI studies examining amygdala activation have shown reduced habituation in autistic adults to images of emotional faces (Kleinhans et al., 2016; Tam et al., 2017), however one ERP study comparing face-specific components similar to those in the current study showed that autistic and non-autistic adults did not differ in the extent of their habituation (Webb et al. 2010b). Taken together, the literature suggests that autistic and high-likelihood groups generally habituate slower than non-autistic and low-likelihood groups, however nuances in methodology and stimuli may require close attention to draw conclusions about the underlying mechanisms.

Upon inspection of the time-course of the currently observed habituation effect in the two groups separately, we see that the low-likelihood group show less extensive habituation, while the high-likelihood group already show habituation from the beginning of the P400 time window onwards. Cluster-based permutation testing of the group comparison revealed that the groups do differ from each other more than could be expected by chance during this time window. The lack of difference between the groups when correcting for multiple comparisons with False Discovery Rate can be put down to the conservative nature of this correction, and the unfounded assumption of independence of samples in data of this nature (Maris & Oostenveld, 2007). We therefore consider this likely to be a false negative.

The high-likelihood group habituating more than the low-likelihood group during the time window associated with gaze processing is challenging for the theories to accommodate, since any Predictive Processing account of autism would predict the opposite result. Regardless of whether children with high-likelihood of autism have reduced influence of their previous experience on perception (Pellicano & Burr, 2012), or over-adjust their expectations based on each new piece of evidence (van de Cruys et al., 2014), they should perceive each image as more novel and thus habituate less than their low-likelihood peers. It seems, however, that the high-likelihood children perceived the individual images, which differed in both identity and gaze direction, as less distinct from one another than the low-likelihood children did. The high-likelihood children may put less weight on identity or gaze direction as a relevant cue, rendering the images more similar to one another, but this result is not easily integrated into a Predictive Processing framework. Since these findings are not in line with a large body of previous work, we interpret these results cautiously and emphasise that replication is necessary. Specifically, it would be important to explore habituation to stimuli which, like ours, differ only in a socially salient cue like gaze direction. Should the current findings of increased habituation in high-likelihood or autistic participants be confirmed in future studies, they would contribute to a building body of work showing that the Predictive Processing framework for understanding autism requires further refinement.

Adaptation After-Effect

The fact that we do not observe evidence of an adaptation after-effect in the ERP responses makes further interpretation difficult. It is possible that our failure to find adaptation after-effects is due to low power, as both groups are small given the low number of trials available. Since young children do not tolerate EEG for much longer than ten minutes, we reduced the length of the stimulus presentation as much as possible while retaining a maximum of 12 trials per cell. The children did attend to most trials, contributing an average of around 8 trials per cell, but these numbers are much lower than could be expected from adult experiments. Our sample size is sufficient to detect an effect of a size comparable to previously observed group X condition interactions in infant face and gaze processing ERP studies (Dawson et al., 2002; Jones et al., 2016; Key & Stone, 2012; Key et al., 2015), as well as a previously observed main effect of adaptation in an adult ERP study (Schweinberger, Kloth & Jenkins, 2007). This points to neural markers of adaptation after-effects being subtle in the current study, although the Bayes Factors indicate that there is moderate evidence that the effect is simply not present. Since our Bayesian analysis was based on maximum values, multivariate analyses and statistics that account for the variability between and within individuals may reveal more than we see with the current method of taking maximum values from a complex and complicated data set.

It is possible that adaptation after-effects are not measurable in the current paradigm because the participants did not perceive the subtle difference between the 0° and 5° gaze directions, especially since they moved much more than adult participants would and spent less time spontaneously fixating the eyes of the stimuli than an adult instructed to respond to gaze direction would. We attempted to mitigate this by presenting the colourful fixation ball and all attention getters in the centre of the screen, directly between where the eyes of the stimuli appeared during critical trials, but the rates of fixations in the area of interest around the eyes were still relatively low. It is also possible that 2-year-olds still need to further refine their gaze perception tuning functions, meaning that their gaze direction discrimination is not yet as precise as that of adults. Since adaptation is inherent to all perception, it should be measurable in younger children and infants, and further progress in paradigms to capture this perceptual effect will be crucial to understand the development of information weighting and expectation-adjustment in this population.

Conclusion

The current habituation findings are not well-explained by Predictive Processing theories, although the lack of evidence of any adaptation after-effects in the group as a whole do not allow for our main intended comparison. We are continuing to follow our longitudinal sample of high-likelihood and low-likelihood siblings, with tasks designed to test different aspects of the Predictive Processing theories. Such an approach, using multiple complementary tasks, is key to providing convergent evidence to ascertain the extent to which Predictive Processing accounts of autism are supported by behavioural and neuroimaging results.

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