**Action predictability is reflected in beta power attenuation and predictive eye movements
in adolescents with and without autism**

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Abstract

Most theoretical accounts of autism posit difficulties in predicting others' actions, and this difficulty has been proposed to be at the root of autistic individuals' social communication differences. Empirical results are mixed, however, with autistic individuals showing reduced action prediction in some studies but not in others. It has recently been proposed that this effect might be observed primarily when observed actions are less predictable, but this idea has yet to be tested. To assess the influence of predictability on neural and behavioural action prediction, the current study employed an action observation paradigm with multi-step actions that become gradually more predictable. Autistic and non-autistic adolescents showed similar patterns of motor system activation during observation, as seen in attenuated mu and beta power compared to baseline, with beta power further modulated by predictability in both groups. Bayesian statistics confirmed that action predictability influenced beta power similarly in both groups. The groups also made similar behavioural predictions, as seen in three eye-movement measures. We found no evidence that autistic adolescents responded differently than non-autistic adolescents to the predictability of an observed action. These findings show that autistic adolescents do spontaneously predict others' actions, both neurally and behaviourally, which calls into question the role of action prediction as a key mechanism underlying autism.

Keywords: Autism, action prediction, beta power, mu power, anticipatory eye movements

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Autism is a developmental condition characterised by differences in social communication, sensory sensitivities and restricted repetitive behaviours (Diagnostic and Statistical Manual of Mental Disorders, 5th edition; American Psychiatric Association, 2013). The former is characterised by reductions in joint attention, sharing pleasure, and engaging in co-operative play and reciprocal conversations. Various theoretical accounts of autism have attempted to identify cognitive and neural mechanisms underlying these social differences (for example, Theory of Mind Deficit Hypothesis, Baron-Cohen, Leslie, & Frith, 1985; Mirror Neuron Dysfunction Theory, Perkins, Stokes, McGillivray & Bittar, 2010; Social Motivation Theory, Chevallier, Kohls, Troiani, Brodtkin & Schultz, 2012). While these theories differ in their focus, they all posit that autistic individuals have difficulty understanding other people's intentions. The understanding of a partner's intentions is crucial for social interaction (Bekkering et al., 2009; Meyer, Bekkering, Paulus, & Hunnius, 2010; Sebanz, Bekkering & Knoblich, 2006), and relies on the ability to predict others' actions. Importantly, while theoretical accounts of autism differ in their specific rationales, they all posit that autistic individuals show diminished intention understanding as measured by action prediction. Despite strong theoretical support for this idea, the empirical findings are very heterogeneous.

There is some behavioural evidence that autistic individuals do predict others' actions similarly to non-autistic children. For example, when presented with videos of balls moving towards containers, autistic adults looked less at action targets than non-autistic adults, but when they did attend, they made predictive eye movements as quickly as the non-autistic group (Marsh, Pearson, Ropar & Hamilton, 2014). Five-year-old children with autism have also been shown to make predictive eye movements as quickly as 5-year-olds without autism while watching an actor place objects in a bucket, but not while watching the same objects move into the bucket without an actor present. Furthermore, in an active imitation task, autistic children did not differ from verbal-mental-age-matched non-autistic children in goal imitation or using imitation to complete a task in the optimal way (Hamilton, Brindley & Frith, 2007).

However, there is also behavioural evidence showing that autistic individuals do have difficulty predicting the actions of others. Children with autism have more difficulty arranging pictures of everyday actions in chronological order than non-autistic children with and without intellectual disabilities (Zalla et al., 2006) and make more errors when asked to choose pictures representing the outcome of everyday actions than non-autistic children and children with intellectual disabilities (Zalla et al., 2010). Schuwerk and colleagues (2016) further showed that autistic children made fewer

predictive eye movements than non-autistic children when observing an actor repeatedly performing an action.

There has also been a large body of work on the neural signature of action prediction in autism. The prediction of others' actions is implemented through motor system activation (Kilner et al., 2004; 2007; Monroy, Meyer, Schröder, Gerson & Hunnius, 2019; Schubotz, 2007), and the Mirror Neuron Dysfunction theory posits a reduction in this activation in autism (Williams, Whiten, Suddendorf & Perrett, 2001; Perkins, Stokes, McGillivray & Bittar, 2010). Motor system activation can be measured with EEG over the sensorimotor cortex, and is typically seen as a decrease in power in mu and beta frequency bands. Some empirical studies have indeed shown less mu suppression in autistic participants than in non-autistic participants during action observation (Bernier, Dawson, Webb & Murias, 2007; Enticott et al., 2012; Oberman et al., 2005; Oberman et al., 2013). For example, in one study, a group of autistic adults and age-matched non-autistic adults both showed mu suppression while observing their own simple hand movements, but only the non-autistic group also showed mu suppression while observing another person's simple hand movements (Oberman et al., 2005). However, again, the findings are mixed, with some studies showing no difference between groups in such paradigms (Oberman et al., 2008; Avikainen, Kulomäki & Hari, 1999; Fan, Decety, Yang, Liu, & Cheng, 2010; see Southgate & Hamilton, 2008 for a broader critique).

Based on these conflicting results, some have proposed that autistic individuals predict simple actions similarly to non-autistic individuals, but that in circumstances in which the progression of the action is less predictable, for example when there are more potential outcomes, autistic individuals predict less than non-autistic individuals (Schuwerk, Sodian & Paulus, 2016; Braukmann et al., 2018). The conflicting findings above may therefore be a consequence of the field mostly focussing on simple hand movements (Avikainen et al., 1999; Enticott et al., 2012; Fan et al., 2010; Oberman et al., 2005) or single-step actions such as actors placing items in a bucket (Falck-Ytter, 2009) or in their mouth (Cattaneo et al., 2007). This line of reasoning is consistent with findings from other domains which suggest that autistic individuals differ more from non-autistic individuals when the environment is more uncertain (Karaminis et al., 2016; Lawson, Mathys & Rees, 2017; van de Cruys, van der Hallen & Wagemans, 2017). For instance, in an associative learning task, autistic adults differed from IQ-matched non-autistic adults most in their responses to unexpected events, which modelling showed was due to an overestimation of environmental volatility (Lawson, Mathys & Rees, 2017). In order to best understand the circumstances in which action understanding in autistic individuals differs from that in non-autistic individuals, the next step is to focus on how observers build these predictions over the course of actions that have more unpredictable progressions. We therefore examined action prediction as indexed by neural and behavioural responses during actions that become gradually more predictable.

Actions with multiple steps become gradually more predictable over time, as observers accumulate evidence with which to infer the actor's goal. Action predictability has been shown to modulate motor system activation, and has been observed specifically in the beta frequency band. During participants' own movements, for example, Tzagarakis and colleagues (2010) found that MEG-recorded beta power decreased more from baseline during actions with less response uncertainty. Tan and colleagues (2016) showed that beta power over sensorimotor cortex immediately following a movement was reduced when uncertainty derived from a Bayesian model was high, and the authors claim that beta power is related to uncertainty in the internal model (although see Palmer, Zapparoli & Kilner, 2016 for comment on the direction of the effect). Similar effects have also been shown during action observation. For example, van Pelt and colleagues (2016) showed that MEG-recorded beta power increased parametrically with the predictability of an observed action's kinematics and outcome. Additionally, Braukmann and colleagues (2017) found that during a multi-step action, EEG-recorded mu power over the vertex was lower during action observation than baseline, but that only beta power over the vertex decreased incrementally as the unfolding action became more predictable to the observer. Concurrent eye-tracking supported this interpretation of beta as an index of predictability, with more frequent, longer and earlier predictive fixations to later action steps, showing that participants integrated the accumulating evidence to form stronger predictions as the actions unfolded.

Beta power and predictive eye movements therefore seem to also be useful measures of the predictability of an action, we therefore examine the beta band in addition to the mu band in the current study. If the mixed findings regarding mu suppression in autistic individuals during action observation are indeed due to differences in the predictability of actions used as stimuli, then we would expect to see differential modulation of mu power by action predictability in autistic and non-autistic individuals. If, however, the beta frequency is in fact the better index of action predictability, the inconsistencies in the mu-power literature remain unexplained. It is an open question whether action predictability does explain the difference between autistic and non-autistic observers.

Since action predictability facilitates processing, and theoretical accounts claim that autistic individuals have difficulties understanding actions and may predict others' actions less, or in a different manner, we assessed whether autistic observers show weaker or slower predictions than non-autistic observers to less predictable actions. In order to quantify this, we measured observers' mu and beta power and predictive eye movements during observation of multi-step actions that become incrementally more predictable. We expected that mu power would be reduced during action observation compared to baseline, but that it would be unaffected by predictability during the unfolding of the multi-step actions in non-autistic participants (Braukmann et al., 2017). If action

predictability is indeed the source of the mixed findings described above, then we should also see group differences in μ modulated by predictability.

In contrast, we expected that beta power would be modulated by predictability in non-autistic participants (Braukmann et al., 2017). We therefore expected that this would be the critical comparison between autistic and non-autistic individuals,

Current study

The true nature of action prediction in autism is unclear, due to the large number of contradictory findings. Recent work has suggested that autistic individuals may primarily differ from non-autistic individuals when the observed actions are unpredictable, but this idea has yet to be empirically tested. We therefore conducted an action observation study using the same design as Braukmann and colleagues (2017) with autistic and non-autistic adolescent participants. As a preliminary check of the basic mirror neuron dysfunction theory, we assessed whether autistic participants show less μ attenuation during action observation than non-autistic participants (as seen, for example, by Bernier, Dawson, Webb & Murias, 2007; Enticott et al., 2012; Oberman et al., 2005; Oberman et al., 2013). We then assessed our main research question: whether autistic observers' μ and beta power parametrically decreased during observation of multi-step actions, as the action goal became more predictable, and whether their predictive eye movements increased over the same time period. If autistic participants have difficulty with all action prediction, we would expect that compared to non-autistic peers, autistic participants would show less μ and beta attenuation and less behavioural prediction as measured by anticipatory fixations. If, however, autistic participants only make fewer predictions when actions are more uncertain, we would expect that they would show reduced beta attenuation and behavioural predictions only to initial action steps. As the actions progress, participants can accumulate evidence from the preceding steps, so we would expect that autistic and non-autistic participants would differ less in their predictions at later steps.

Method

Participants

In total, 58 participants visited the lab: 27 participants with an autism diagnosis and 31 participants without. Two non-autistic participants began to feel unwell before data acquisition began, leaving 56 participants in the current dataset (27 autistic; 29 non-autistic). All 56 participants contributed EEG data, and 53 contributed both EEG and eye-tracking data (26 autistic). All participants were between the ages of 12 and 18, and participants in the autistic group had a diagnosis of Autism Spectrum Disorder according to the DSM-5 (APA, 2013), or with Asperger's Syndrome, Autistic Disorder or Pervasive Developmental Disorder Not Otherwise Specified according to the DSM-IV (APA, 2000).

Interested participants were only invited to take part if they or their parents or caregivers reported no history of epilepsy, no current serious psychiatric illness, and no uncorrected vision problems.

The mean age of the autistic participants was 15.03 years, and the mean age of the non-autistic participants was 15.58 years. The groups did not differ significantly in age or in IQ, as measured by the short-form WISC-III (Wechsler, 1991) for participants aged 15 and under, and the WAIS-IV (Wechsler, 2008) for participants aged 16 and over. The range of IQ scores was slightly wider in the autistic group (78 – 131) than the non-autistic group (85 – 137). The autistic group did show higher levels of alexithymia as measured by the Bermond-Vorst Alexithymia Questionnaire (BVAQ, Vorst & Bermond, 2001) and more autism symptoms as measured by the Social Communication Questionnaire (SCQ, Berument et al., 1999; Rutter et al., 2003; see Table 1). Two participants in the non-autistic group reported after data collection that they did suspect they may be autistic, but their SCQ scores indicated that autism is very unlikely and they were kept in the non-autistic group. Due to violation of the assumption of equal variance, degrees of freedom have been adjusted using the Welch approximation. Parents or caregivers of 24 of the autistic participants also completed the Autism Diagnostic Interview-Revised (ADI-R; Lord, Rutter & Couteur, 1994) to confirm their children's diagnoses.

Table 1

Participant characteristics: Mean (standard deviation)

Group	N	Sex (M:F)	Age	IQ	SCQ	BVAQ
Autistic	27	20:7	15.03 (852 days)	109 (14.6)	16.5 (7.38)	114 (16.5)
Non-autistic	31	11:20	15.58 (660 days)	109 (11.2)	4.0 (3.61)	104 (16.0)
Statistic			$t(47.01) = -0.93$, $p = .35$	$t(46.71) = -0.39$, $p = .70$	$t(32.83) = 7.57$, $p < .0001$	$t(27.38) = 33.07$, $p < .0001$

This study was approved by the medical ethics committee (Commissie Mensgebonden Onderzoek Arnhem-Nijmegen, protocol NL49584.091.14). Recruitment was done via local schools, online flyers, and Karakter, a child and adolescent psychiatry clinic. Participants received a reimbursement of their travel costs and €20 in gift vouchers as a thank you for taking part.

Materials

Stimuli. The current study used an adapted version of the task used by Braukmann and colleagues (2017). The stimuli consisted of 27 unique videos of a woman with her face hidden behind a wide-brimmed hat performing various everyday actions, for example putting money in a purse and then the purse into a handbag (see Figure 1A). Each action was divided into three steps, and each step had a target, in this case the first target was the money, the second was the purse and the third was

the handbag. The three targets provide information about the gist of the scene, but the action course is uncertain until the actor begins to move. The action course then becomes incrementally more predictable as the targets are used and there are fewer remaining possible sub-steps. Rectangular Areas of Interest around each target were defined according to Braukmann and colleagues (2017).

In addition to the stimuli used by Braukmann and colleagues (2017), we also added a condition in which the action targets were occluded (see Figure 1B). During any action observation, there is a build-up of motor activity over the course of a trial merely due to observing an actor move for longer. In the current study, actions become more predictable over time, and this is confounded with time spent observing someone move. We therefore introduced occluded trials in which activation can only be due to global movement of the actor, but not to predicting the specific action targets, to dissociate these two sources of activation. The occluded condition consisted of the original stimulus videos with the addition of occluders consisting of grey boxes covering the objects, such that the model's actions were broadly visible but there was no direct visual access to the objects and thus the targets of the action were unknown to the observer. The video clips varied in length slightly, but lasted around 10 seconds.

Figure 1: Stills taken from an example trial, unoccluded (A) and occluded (B).

Apparatus. Electroencephalography (EEG) was recorded from 32 Ag/AgCl active electrodes in an EEG cap (ActiCap, Brain Products, Munich, Germany) using BrainVision Recorder, via a BrainAmp amplifier (BrainVision Products, Munich, Germany). EEG was recorded continuously, with an online reference at the left mastoid, at a sampling frequency of 1000Hz and with a band-pass filter (0.1–125 Hz). EOG was measured from four passive electrodes; one placed at each outer canthus and one above the left eye and one below the left eye, with a reference on the chin. Eye-movements were

recorded from all participants for whom we could achieve a successful calibration with an SMI RED500 remote eye-tracker and iView software (SensoMotoric Instruments GmbH, Teltow, Germany) at a sampling frequency of 500Hz. Stimuli were presented with Presentation software (versions 20.2 and 20.3, Neurobehavioral Systems, Albany, CA, USA) on a 27" BenQ XL2420Z monitor.

Procedure

Participants were informed about the procedure and asked if they had any questions before the experiment began. Parents generally stayed in the room during preparation. When participants were ready to begin, they were fitted with the EOG electrodes and the EEG cap with electrodes already placed in the rings. Impedances of the active electrodes were improved by adding gel until they were below 25 kOhm or the participant no longer tolerated the procedure. Impedances of the passive EOG electrodes were kept below 100kOhm.

Participants were seated 60-70 cm from the screen, and a 9-point eye-tracking calibration and 4-point validation was carried out directly before the stimulus presentation started, and immediately repeated if the pupils were lost or validation was deemed unsatisfactory. Participants were asked to sit still during stimulus presentation, and were told to watch the videos passively, with no behavioural task. They saw each of the 27 videos repeated 4 times; twice with occluders and twice without, to give a total of 108 trials. The trials were split into 4 blocks of around 10 minutes each and participants took short breaks between blocks.

Data analysis

EEG data processing. EEG data were analysed using Matlab (R2014b, The Mathworks Inc., Natick, MA, 2000) and the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) according to the analysis protocol of Braukmann and colleagues (2017). Each trial was segmented into one 1000ms baseline period during the fixation cross, and three 1200ms segments corresponding to the three action steps. Action step segments were defined as the 1200ms preceding the hand of the actor entering the Area of Interest surrounding the target for that step, and these segments were separately detrended, demeaned and band-pass filtered between 1 and 45Hz, and baseline-corrected to a window of 1000ms during the fixation cross.

All channels and all trial segments were then separately visually inspected, and channels and segments with excessive noise or high-frequency activity associated with movement artifacts were inferred to represent non-neural sources and were rejected from further analysis. Independent Component Analysis was then used in conjunction with the EOG signal to identify components with spatial distribution and physical characteristics of eye movements and heart rate artifacts. These components were rejected manually, and the data were reconstructed. The data from previously rejected channels were then interpolated from the nearest neighbours and data were re-referenced to the average of all channels. A second round of visual artifact rejection then took place to remove

any remaining artifacts. One autistic participant was excluded from further analysis at this point due to excessively noisy data, leading to a final sample of 55 participants (26 autistic). All data were then Fast Fourier Transformed using a multi-taper frequency transformation, and each action step segment was baseline-corrected by taking the log of the power during the action step divided by the power during the nearest preceding baseline segment.

EEG statistical analysis. In order to maximise comparability with the original study (Braukmann et al., 2017), to quantify the effect of action step and occlusion on motor system activation, average values of mu (8-12 Hz) and beta (15-25 Hz) power recorded at Cz during each action step were extracted for each participant. We then ran one-tailed one-way t-tests on each frequency band to determine whether power during action observation was on average lower than power during baseline, to test for overall attenuation during action observation. Then, to investigate the role of action step, we ran repeated measures ANOVAs for each frequency band, each with Action Step and Occlusion as within-subjects factors and Group as a between-subjects factor. We then used Bayesian statistics to quantify the amount of evidence in favour of or against each effect. We expected to see reduced beta and mu power during action observation compared to baseline in the non-autistic participants. We also expected to see parametric attenuation of beta power by action step, but no effect of action step in the mu frequency band, consistent with findings from Braukmann and colleagues (2017). In the beta band, we expected that Action Step and Group would interact, with autistic participants showing less of a decrease in power from baseline at the beginning of the action compared to non-autistic participants, with the groups converging at the final action step when there was less uncertainty about the upcoming event. Furthermore, we expected an interaction between Action Step and Occlusion in the beta frequency band, such that the occluded stimuli would elicit less of a parametric modulation of beta power since occluded stimuli should not have become incrementally more predictable as the multi-step action progressed.

In order to investigate whether participants with more autism symptoms showed less action prediction, we also calculated a correlation between SCQ score and beta attenuation over action steps. This analysis was exploratory and not pre-specified.

Eye-tracking data processing. The eye-tracking data were also analysed according to the previous study (Braukmann et al., 2017). Data were classified into fixations with a minimum duration of 50ms and a peak velocity of 40°/s in BeGaze 3.0 software (SensoMotoric Instruments GmbH, Teltow, Germany). Two autistic participants were excluded from further analysis due to technical problems during recording resulting in fewer than 5 recorded fixations, leading to a final sample of 51 participants (24 autistic).

Fixations within areas of interest surrounding the objects in the stimulus videos were then extracted and processed further in Matlab (R2014b, The Mathworks Inc., Natick, MA, 2000). Two

time windows of interest were determined for each action step: a predictive time window and a reactive time window. Predictive time windows began when the actor began to move their hand towards the target for that action step, and ended when the hand entered the target area of interest. This marked the beginning of the reactive time window. The end of the reactive time window was set such that the predictive and reactive time windows for each step had equal duration.

Eye-tracking statistical analysis. In order to quantify behavioural predictions during the experiment, we calculated three dependent eye-tracking measures: Predictive Looking Time, Predictive Gaze Onset and Predictive Count Ratio (cf. Braukmann et al., 2017). Predictive Looking Time is the duration of all fixations to an object during the predictive time window, as a percentage of the length of the predictive time window. Predictive Gaze Onset is the time between the onset of the first fixation to the object and the arrival of the actor's hand in the area of interest. Predictive Count Ratio is the number of trials in which a fixation was made to an object during the predictive time window divided by the number of trials in which there was no predictive fixation but a fixation was made to the object during the reactive time window. Action steps in which no fixations were made to the target object were excluded from this measure. For each of these three dependent measures we again computed a repeated measures ANOVA with Action Step and Condition as within-subjects factors and Group as a between-subjects factor. We then used Bayesian statistics to quantify the amount of evidence in favour of or against each effect. We expected to see an increase in all three measures over action steps, and if the autistic participants made fewer predictions or formed predictions more slowly, we would expect to see an Action Step by Group interaction.

Results

EEG

Mu power. Visual inspection revealed that changes in mu power from baseline were focused near the vertex, notably mostly centred above C3 and C4 electrodes, consistent with the fact that the observed actions involved mostly the hands and arms (see Supplementary Figure 1). A one-tailed one-sample t-test confirmed that average mu power per participant measured at Cz was lower than baseline during action observation ($t(54) = -6.60, p < .0001$, Cohen's $d = -0.89$), indicating activation of the motor system. The ANOVA comparing mu power over action step, occlusion and group showed no main effect of action step ($F(2, 106) = 1.75, p = .18, \eta^2 = 0.003$), no main effect of occlusion ($F(1, 53) = 0.003, p = .96, \eta^2 = 0$), no main effect of group ($F(1, 53) = 1.89, p = .18, \eta^2 = 0.028$), and no interactions (see Figure 2). Effect sizes were calculated with the sjstats R package (Lüdtke, 2021). Levene's test showed that the data satisfied the assumption of homogeneity of variance ($F(11, 318) = 1.44, p = .15$), and visual inspection confirmed the normality of distribution of the residuals.

Figure 2: Mu power as a function of action step. Error bars indicate 95% confidence intervals. Mu power was not modulated by group, action step or occlusion.

The Bayesian ANOVA for mu power showed that there was moderate evidence for a null effect of action step ($BF = 0.199$, $\log(BF) = -1.62$) and occlusion ($BF = 0.12$, $\log(BF) = -2.12$) and approximately as much evidence for the null and alternative hypotheses regarding group ($BF = 0.781$, $\log(BF) = -0.25$). We therefore conclude that action step and occlusion of the target objects do not modulate mu power, but we cannot draw any firm conclusions about the effect of autism diagnosis on mu power during action observation. It seems likely that if there is a true group difference in overall mu power for these stimuli, the effect is small and the current experiment was not designed to detect it.

Beta power. Visual inspection revealed that changes in beta power from baseline were diffuse, presumably reflecting the domain general nature of the predictions (see Supplementary Figure 2). A one-tailed one-sample t-test confirmed that mean beta power per participant measured at Cz was lower than baseline during action observation ($t(54) = -8.53$, $p < .0001$, Cohen's $d = -1.15$), indicating motor system activation. The ANOVA comparing beta power over action step, occlusion and group showed a main effect of action step ($F(2, 106) = 25.15$, $p < .0001$, $\eta^2 = 0.053$), a main effect of occlusion ($F(1, 53) = 5.68$, $p = .02$, $\eta^2 = 0.004$), and no main effect of group ($F(1, 53) = 0.27$, $p = .61$, $\eta^2 = 0.003$; see Figure 3). The main effect of occlusion was driven by lower beta power during occluded trials ($M = -0.15$, $SD = 0.15$) than during unoccluded trials ($M = -0.14$, $SD = 0.15$). To further assess the main effect of action step, planned comparisons between steps were conducted with paired-samples t-tests. These showed that beta power during step 1 ($M = -0.10$, $SD = 0.13$) was significantly higher than beta power during step 2 ($M = -0.15$, $SD = 0.15$; $p = .007$) and step 3 ($M = -0.18$, $SD = 0.15$; $p = .00032$), but beta

power during step 2 was not significantly different from power during step 3 ($p = .12$). There were no significant interactions, but the interaction between action step and occlusion was close to the significance threshold ($F(2, 106) = 3.03, p = .053, \eta^2 = 0.005$). Effect sizes were calculated with the sjstats R package (Lüdtke, 2021). Levene's test showed that the data satisfied the assumption of homogeneity of variance ($F(11, 318) = 1.20, p = .29$), and visual inspection confirmed the normality of distribution of the residuals.

Figure 3: Beta power as a function of action step. Error bars indicate 95% confidence intervals. Beta power was lower for occluded compared to unoccluded trials and beta power was modulated by action step across trial types. There were no significant group effects.

The Bayesian ANOVA for beta power showed very strong evidence for a main effect of step ($BF = 895200000, \log(BF) = 20.61$), with post-hoc tests showing that there is very strong evidence for a difference between Step 1 and Step 2 ($BF = 6143, \log(BF) = 8.72$), between Step 1 and Step 3 ($BF = 3488000, \log(BF) = 15.07$) and moderate evidence for a difference between Step 2 and Step 3 ($BF = 3.533, \log(BF) = 1.26$). Further, the test showed approximately as much evidence for and against a null effect of occlusion ($BF = 0.635, \log(BF) = -0.45$), and moderate evidence for a null effect of group ($BF = 0.39, \log(BF) = -0.93$). The crucial interaction between Action Step and Group showed moderate evidence for a null effect ($BF = 0.27, \log(BF) = 0.94$).

Since there was a large range of SCQ scores (range: 0 – 25, with scores of over 11 suggesting autism), indicating that participants had fairly diverse levels of social communication skills, and given the heterogeneity of autism (Masi et al., 2017), we further investigated whether this continuous

measure of autism characteristics predicted decrease in beta power over action steps. To this end, we ran a linear regression per participant with Action Step predicting beta power, and extracted the β coefficient that characterised the slope of beta power over action steps. Due to the non-normality of the SCQ score distribution even after transformation, we decided to perform a Spearman's rank correlation between β coefficients and the raw SCQ scores. There was no monotonic relationship between β coefficients and SCQ score ($\rho = 0.19$, $p = 0.19$, $N = 55$), giving no indication that autism characteristics predict the change in beta power over action steps (see Figure 4).

Figure 4: Individual differences in the slope of the individual regression line of beta power change over action steps and their relation to participants' SCQ scores.

Regarding the occlusion manipulation, designed to serve as a control condition in which participants made no predictions, the results were somewhat surprising; We saw no evidence of an effect of occlusion on the mu power band, and some suggestion of more predictions during occluded trials in the beta power band. The occluded trials were intended to elicit no predictions, but the results as well as informal participant reports showed that this was not the case. During data collection, participants reported trying to guess which objects were being hidden on the occluded trials, and, if anything, beta power indicated more active prediction formation in the presence of fewer environmental cues. The effect of occlusion was not the focus of this study, but this result urges caution in selecting control stimuli for action prediction paradigms.

Eye-tracking

The planned repeated measures ANOVAS were not feasible due to missing values for multiple participants. This is unsurprising as the measures could only be computed if there was a reliable signal from the eye-tracker and participants made predictive eye movements, neither of which can be taken for granted in the current study. In order to allow for missing data, we proceeded with a multi-level modelling approach with the pre-specified fixed effects of Action Step, Occlusion and Group, and an additional random intercept of Participant. Models with random intercepts by Participant as well as a random slope of Action Step by Participant returned as singular, so the slope term was dropped. Contrasts were set as sum-to-zero coding, so all effects are in reference to the grand mean. t values of more than $|1.96|$ were considered as significantly different from zero. Variance explained by the models (R^2) was calculated using the method explained by Snijders and Bosker (2012), in the `mitml` package (Grund, Robitzsch & Leudtke, 2019). Bayes Factors for model comparison are calculated as $Bayes\ Factor \approx e^{(Difference\ in\ Bayesian\ Information\ Criteria / 2)}$ (Masson, 2011).

Predictive Looking Time. Predictive looking time was defined as the total duration of fixations during the predictive time window as a percentage of the length of the predictive time window. This gives a measure of how long participants looked at objects during the actor's reach towards the objects, standardised for the duration of the reach. This predictive looking time was longer for non-autistic participants than autistic participants, indicating that autistic participants were less anticipatory than non-autistic participants, and longer for later action steps, indicating that as the action progressed it became more predictable. This change in predictive looking time over action steps was less steep for occluded compared to non-occluded trials. Overall, the participants were more anticipatory in later action steps than earlier steps, but this relationship was weakened by the occlusion of the targets. The model showed that Predictive Looking Time was modulated by Action Step (Step 1: $\beta = -0.05$, $SE = 0.005$, $t = -9.67$; Step 2: $\beta = 0.002$, $SE = 0.005$, $t = 0.42$), Occlusion (Occluded trials: $\beta = -0.02$, $SE = 0.003$, $t = -5.84$) and Group (Autistic group: $\beta = -0.02$, $SE = 0.008$, $t = -2.12$), qualified by an interaction between Step and Occlusion (Step 1, Occluded trials: $\beta = 0.01$, $SE = 0.005$, $t = 2.07$; Step 2, Occluded trials: $\beta = -0.004$, $SE = 0.005$, $t = -0.80$; see Figure 5A and supplementary table 1 for regression output). This model explained approximately 26% of the variance. Removing the Group and Group by Action Step interaction terms produced a model which better explained the data, with a BIC approximately 57 less than the full model (BIC full model: -509.03, BIC reduced model -565.73), and this reduced model explained around 27% of the variance. The Bayes Factor for the difference in models is 2384474784798, $\log(BF) = 28.5$, indicating very strong evidence for the absence of a group effect and group by action step interaction.

Predictive Gaze Onset. Predictive gaze onset was defined as the time between the first predictive fixation and the arrival of the actor's hand at the target area of interest. Notably, this first fixation could occur before the start of the predictive time window, in order to capture larger-scale predictions. This measure was longer for later action steps than earlier action steps, and longer during unoccluded trials than during occluded trials, indicating that the actions became more predictable as they progressed, and that unoccluded trials were more predictable than occluded trials. Predictive gaze onset was not significantly different between autistic and non-autistic participants, indicating that both autistic and non-autistic participants made behavioural predictions. The model showed that Predictive Gaze Onset was modulated by Step (Step 1: $\beta = -221.35$, $SE = 16.46$, $t = -13.45$; Step 2: $\beta = 42.910$, $SE = 16.457$, $t = 2.607$) and Occlusion, but the groups did not differ significantly (Autistic group: $\beta = -9.73$, $SE = 17.85$, $t = -0.55$). The main effects were qualified by an interaction between Step and Occlusion (Step 1, Occluded trials: $\beta = 39.34$, $SE = 16.42$, $t = 2.40$; Step 2, Occluded trials: $\beta = -31.43$, $SE = 16.42$, $t = -1.91$; see Figure 5B and supplementary table 2 for regression output). This model explained approximately 40% of the variance. Removing the Group and Group by Action Step interaction terms produced a model which was a worse fit for the data, with a BIC approximately 15 higher than the full model (BIC full model: 3916.92, BIC reduced model 3931.67), with the reduced model explaining around 39% of the variance. The Bayes Factor for the difference in models is 0.0005, $\log(BF) = -7.5$, indicating very strong evidence for model including a group effect and group by action step interaction.

Predictive Count Ratio. Predictive count ratio was defined as the ratio of trials in which participants made predictive fixations to trials in which they made only reactive fixations. Predictive count ratio was larger to later action steps than earlier steps, and larger to unoccluded trials, indicating that participants were more anticipatory in later action steps than earlier steps, and to unoccluded compared to occluded trials. The model showed an effect of Step (Step 1: $\beta = -0.19$, $SE = 0.02$, $t = -11.08$; Step 2: $\beta = 0.02$, $SE = 0.02$, $t = 0.95$) and Occlusion (Occluded trials: $\beta = -0.06$, $SE = 0.01$, $t = -5.106$) but no effect of Group (Autistic group: $\beta = -0.02$, $SE = 0.02$, $t = -1.14$). There were no significant interactions (see Figure 5C and supplementary table 3 for regression output). This model explained approximately 33% of the variance. Removing the Group and Group by Action Step interaction terms produced a model which better explained the data, with a BIC approximately 43 less than the full model (BIC full model: 94.58, BIC reduced model 51.32), and the reduced model explained around 33% of the variance. The Bayes Factor for the difference in models is 2174359554, $\log(BF) = 21.5$, indicating very strong evidence for the absence of a group effect and group by action step interaction.

The models explain the eye-tracking data very well, with high R^2 values. Taken together, the three measures show converging evidence of an effect of action step, such that participants predicted later action steps more than earlier steps, and converging evidence that participants predicted unoccluded trials more than occluded trials. Removing the terms representing group and the

interaction between group and action step improved model performance for two of the three measures. This is consistent with the parameter estimates, with autistic participants only significantly different from non-autistic participants on the Predictive Looking Time measure. Autistic participants therefore do predict upcoming action steps spontaneously during action observation, but they fixate the targets of those upcoming actions for less time than non-autistic participants. This shorter fixation length may have implications for depth of processing, especially for the first action step, in which the autistic participants on average fixated the targets for around half the length of the non-autistic participants' average.

Figure 5: Eye-tracking measures as a function of action step. A: Predictive Looking Time. B: Predictive Gaze Onset. C: Predictive Count Ratio.

Discussion

Previous work on action prediction in autism has yielded mixed findings, and it has been suggested that one factor influencing this inconsistency is the level of uncertainty in the observed actions (Schuwerk, Sodian & Paulus, 2016; Braukmann et al., 2018). The current experiment therefore aimed to quantify the predictions made by adolescents with and without autism during observation of multi-step action sequences that gradually become less uncertain. Autistic and non-autistic adolescents showed activation of their motor systems as indexed by both mu and beta power, during action observation compared to baseline, and a stepwise modulation of beta power by action step showing that more predictable actions lead to more beta suppression. Bayesian statistics further provided moderate evidence for the lack of an interaction between group and action step. Both groups also showed behavioural predictions as measured by three eye-movement measures. We found no evidence that the groups differed in neural or behavioural predictions, and conclude that autistic individuals spontaneously predict observed actions, contrary to many theories of autism.

We specifically aimed to build on the work of Braukmann and colleagues (2017), who showed that motor system activation increased in response to increasingly predictable action steps when measured in the beta frequency band but not in the mu frequency band. We successfully replicated these findings: Both mu and beta power were attenuated during action observation compared to baseline, and the beta rhythm showed modulation by action step, while the mu rhythm did not. These findings together confirm that mu and beta power are both signatures of the motor system response but that they reflect different processes: mu power indexes general activation of the motor system while beta power specifically responds to action predictability. This is consistent with previous findings relating beta power to uncertainty (Palmer et al., 2016; Tan et al., 2016; Tzagakiris et al., 2010), action familiarity (Gerson, Meyer, Hunnius & Bekkering, 2017), and action errors (Meyer, Braukmann, Stapel, Bekkering & Hunnius, 2016). In addition, participants made more predictive fixations and spent more time predictively fixating later action steps, and the onset of their fixations to the later action steps were more anticipatory than those to the earlier action steps. This confirms that participants were able to use the accumulating evidence over the course of the action to better predict the later action steps.

Crucially, we also examined whether these findings were different in autistic and non-autistic observers. We saw no group differences in power in either the mu or beta frequency band. Furthermore, we observed no group differences in the Predictive Onset or the Predictive Count Ratio measures extracted from the eye-tracking data. The only group difference we did observe was a main effect in the Looking Time measure. Autistic participants spent less time looking at the upcoming action goal than non-autistic participants, but this was not modulated by action step and not reflected in their prediction onset or ratio of predictive to reactive fixations. We therefore conclude that while autistic

participants may show slightly lower levels of behavioural predictions, they are capable of making them and do so spontaneously during action observation.

The lack of an effect of group in the EEG data was contrary to the idea that autistic participants may activate their own motor systems less than non-autistic participants during action observation only under conditions of uncertainty (Schuwerk, Sodian & Paulus, 2016; Braukmann et al., 2018). However, this theoretical proposal was developed in order to address an inconsistency in the literature, that is, that some results show reduced motor system activation in autistic participants while others do not. Unfortunately, the literature consists of studies with very small samples; both those showing this group difference (e.g. 17 participants with autism and 16 without; Bernier, Dawson, Webb & Murias, 2007; 7 with autism and 8 without; Cattaneo et al., 2007; 34 with autism and 36 without; Enticott et al., 2012; 10 with autism and 10 without; Oberman et al., 2005) and those that do not detect a group difference (e.g. 13 with autism and 13 without; Oberman et al., 2008; 5 with autism and 8 without; Avikainen, Kulomäki & Hari, 1999; 20 with autism and 20 without; Fan, Decety, Yang, Liu, & Cheng, 2010) have very low power. As such, previously reported effects are not likely to be reliable (Ioannidis, 2005; Button et al., 2013). This highlights the importance of conducting well-powered studies for the progression of the field, since theoretical work building on an underpowered literature base may be misdirected.

To attempt to more precisely quantify the amount of evidence for the null and alternative hypotheses, in addition to the frequentist analysis techniques comparable to those in previous studies we also conducted Bayesian statistics. We saw moderate evidence for the absence of a group effect on beta power; it seems that autistic participants predicted the multi-step actions to the same extent as non-autistic participants. Mu power was not modulated by action step, suggesting that beta and mu power fulfil different functions in action understanding (Gerson, Meyer, Hunnius & Bekkering, 2017; Meyer, Braukmann, Stapel, Bekkering & Hunnius, 2016), and that this distinction is also present in autistic individuals. We also did not detect group differences in two out of three eye-tracking measures. We interpret these findings as converging evidence that autistic adolescents do predict others' actions spontaneously during action observation, and that any difficulties in social interactions are not caused by a fundamental difference in the neural or behavioural prediction processes.

The Bayesian analyses were largely in agreement with the frequentist analyses, with the added benefit of indicating that some non-significant frequentist terms may be worth further exploration because the evidence was equivocal regarding presence or absence of an effect. Specifically, the lack of a group difference in mu power in the frequentist ANOVA is qualified by a Bayes factor close to 1, so future studies targeting mu power differences in autistic and non-autistic participants may need to increase sample size or optimise stimuli to elicit more mu activity.

Statistical justifications are of course not necessarily an indication that our interpretation is valid outside the current sample, and our findings should be further explored with regard to generalisability. Our participants were of average to high intelligence and volunteered to participate in an EEG study which lasted 3 hours, was unfamiliar to the participants, and involved close contact with an experimenter during preparation. It is likely, therefore, that these autistic adolescents are not representative of the wider autistic population. This is a common situation in autism research and despite calls to include a more diverse range of participants (Russel et al., 2019), it remains a challenge for the field. This does not mean, however, that the current data should not be accommodated by autism theories. Autism is heterogeneous, and theoretical accounts claiming to explain core mechanisms underlying the condition should apply to all autistic individuals. Furthermore, while not necessarily representing the larger autistic community, our autistic participants did clearly differ from our non-autistic participants in their social communication style as measured by the SCQ (Berument et al., 1999; Rutter et al., 2003) and their alexithymia traits as measured by the BVAQ (Vorst & Bermond, 2001). These differences demonstrate that the autistic group did in fact experience traits that various accounts purport stem from action understanding differences.

The fact that the autistic participants did predict multi-step actions to the same extent as non-autistic participants forms a challenge for the claim that action understanding is a key element in the mechanisms underlying autism. While initial claims of a lack of mirroring were simplistic, adding nuance, for example by specifying additional parameters such as uncertainty, has thus far not led to an increased understanding of the mechanisms underlying autism. The sheer number of theories attempting to explain autism, and the growing body of conflicting empirical support, seems to point to a fundamental flaw in this approach (Astle & Fletcher-Watson, 2020). More recently, theorists have proposed moving away from the search for symptom-centred mechanisms and instead looking for fundamental differences in neural coding (e.g., Lawson, Rees, & Friston, 2014; Pellicano & Burr, 2012; van de Cruys, 2014), or even abandoning the idea that developmental disorders like autism have a single core mechanism (Astle & Fletcher-Watson, 2020; Happé, Ronald & Plomin, 2006). Regardless of philosophy, it is clear that autism is more complex than current theories have allowed for. If researchers continue to pursue an account of the mechanisms underlying autism, they will need to account for the diversity of autistic experience and its variation between contexts.

Conclusion

The current study provides evidence that adolescents with and without autism predict observed actions in a broadly similar manner. Both groups showed reduced beta power as actions became more predictable and both groups made behavioural predictions by fixating upcoming action targets before the actor's hand reached them. This is contrary to some theories and empirical findings regarding action observation and prediction in autism. Of course, additional well-powered studies will

be needed to confirm, but should the findings be supported, theoretical accounts of autism will need to be adjusted to accommodate them.

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Supplementary Figures

Unoccluded: Action compared to Baseline,8-12Hz

Occluded: Action compared to Baseline,8-12Hz

Unoccluded: Action compared to Baseline,8-12Hz

Unoccluded: Action compared to Baseline,8-12Hz

Autistic Group

Non-autistic Group

Supplementary Figure 1B: Scalp distribution of mu response to action observation compared to baseline

Supplementary Figure 1B: Scalp distribution of mu response to action steps

Autistic Group

Non-autistic Group

Supplementary Figure 2A: Scalp distribution of beta response to action observation compared to baseline

Supplementary Figure 2B: Scalp distribution of beta response to action steps

Supplementary Table 1: Summary of Multi-level Model for Predictive Looking Time

Fixed Effects	Estimate	Standard Error	t Value
Occlusion	-0.023	0.004	-5.836
Group	-0.018	0.009	-2.115
STEP 1	-0.053	0.005	-9.673
STEP 2	0.002	0.005	0.417
Occlusion * Group	0.0008	0.004	0.215
Occlusion * STEP 1	0.011	0.005	2.069
Occlusion * STEP 2	-0.004	0.005	-0.800
Group * STEP 1	-0.0009	0.005	-0.164
Group * STEP 2	0.001	0.005	0.194
Occlusion * Group *	0.004	0.005	0.733
STEP 1			
Occlusion * Group *	0.0009	0.005	0.165
STEP 2			
Random Effects	Variance	Standard Deviation	
Participant	0.003	0.05	
Residual	0.004	0.07	

Supplementary Table 2: Summary of Multi-level Model for Predictive Gaze Onset

Fixed Effects	Estimate	Standard Error	t Value
Occlusion	-64.302	11.796	-5.451
Group	-9.731	17.848	-0.545
STEP 1	-221.347	16.457	-13.450
STEP 2	42.910	16.457	2.607
Occlusion * Group	-11.556	11.796	-0.980
Occlusion * STEP 1	39.344	16.422	2.396
Occlusion * STEP 2	-31.428	16.422	-1.914
Group * STEP 1	-17.856	16.457	-1.085
Group * STEP 2	-24.475	16.457	-1.487
Occlusion * Group *	19.891	16.422	1.211
STEP 1			
Occlusion * Group *	1.824	16.422	0.111
STEP 2			
Random Effects	Variance	Standard Deviation	
Participant	9061	95.19	
Residual	39806	199.51	

Supplementary Table 3: Summary of Multi-level Model for Predictive Count Ratio

Fixed Effects	Estimate	Standard Error	t Value
Occlusion	-0.062	0.012	-5.106
Group	-0.021	0.018	-1.144
STEP 1	-0.1878	0.017	-11.082
STEP 2	0.016	0.017	0.946
Occlusion * Group	0.017	0.012	1.416
Occlusion * STEP 1	0.023	0.017	1.356
Occlusion * STEP 2	-0.028	0.017	-1.646
Group * STEP 1	-0.030	0.017	-1.798
Group * STEP 2	0.0005	0.017	0.029
Occlusion * Group *	-0.004	0.017	-0.237
STEP 1			
Occlusion * Group *	-0.014	0.017	-0.839
STEP 2			
Random Effects	Variance	Standard Deviation	
Participant	0.001	0.01	
Residual	0.04	0.21	