

# Predictive Sensorimotor Control in Autism

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## Abstract

Autism Spectrum Disorder has been characterised by atypicalities in how predictions and sensory information are processed in the brain. To shed light on this relationship in the context of sensorimotor control we assessed prediction-related measures of cognition, perception, gaze and motor functioning in a large general population ( $n = 92$ ; experiment one) and in clinically-diagnosed autistic people ( $n = 29$ ; experiment two). In both these experiments perception and action were strongly driven by prior expectations of object weight, with large items typically predicted to weigh more than equally-weighted smaller ones. Interestingly, these predictive action models were employed comparably at a sensorimotor level in both autistic and neurotypical individuals with varying levels of autistic-like traits. Specifically, initial fingertip force profiles and resulting action kinematics were both scaled according to participants' pre-lift heaviness estimates, and generic visual sampling behaviours were notably consistent across groups. These results suggest that the weighting of prior information is not chronically underweighted in autism, as proposed by simple Bayesian accounts of the disorder. Instead, our results cautiously implicate context-sensitive processing mechanisms, such as precision modulation and hierarchical volatility inference. Together, these findings present novel implications for both future scientific investigations and the applied autism community.

**Key Words:** Prediction, sensory, object lifting, perception, action.

## Introduction

Autism Spectrum Disorder (ASD) is a neurodevelopmental condition which is diagnosed in 1-2% of individuals on the basis of persistent difficulties within two distinct domains: i) social communication and interaction; and ii) restricted and repetitive patterns of behaviours, activities or interests (World Health Organisation, 2012; American Psychiatric Association, 2013). In addition to these diagnostic criteria, sensorimotor impairments are considered as ‘cardinal’ features of ASD that remain throughout the lifespan (Fournier *et al.*, 2010; Gowen & Hamilton, 2013). Frequently reported sensorimotor issues in ASD include: clumsiness, postural instability, sensory disturbances and/or impaired visuomotor coordination (Fournier *et al.*, 2010). These functional difficulties have been shown to co-vary with the disorder’s clinical symptomology (Sutera *et al.*, 2007) and socio-behavioural traits (MacDonald *et al.*, 2013), suggesting that they may be underpinned by common neurobiological mechanisms. However, little is known about the aetiology of these movement-related atypicalities and their consequences for quality of life. Therefore, investigations into the mechanisms that contribute to impaired sensorimotor control in ASD could offer valuable implications for both the scientific and applied autism community (Gidley-Larson *et al.*, 2008; Foster *et al.*, 2019).

It is established that sensorimotor functions depend on various, interlocking sensory inputs and neurobiological pathways, which are coordinated by generative models about the world (see Friston, 2010). In order to optimally control and learn motor skills, *predictions* are computed from prior expectations and incoming sensory data, before being transmitted hierarchically across the cerebral cortex (Shipp *et al.*, 2013). However, it is proposed that autistic people display chronic attenuations in this use of prior information (Pellicano & Burr, 2012; Sinha *et al.*, 2014; Van de Cruys *et al.*, 2014), a processing atypicality which can explain various characteristics of the disorder, including sensorimotor impairments (e.g., see Van de Cruys *et al.*, 2014). These ‘simple’ Bayesian hypotheses draw on empirical evidence from perception, action, and neurological research. For example, autistic individuals have been shown to display reduced anticipatory postural adjustments (Schmitz *et al.*, 2003), atypical error-based gaze adaptation (Mosconi *et al.*, 2013), and impaired motor learning capabilities (e.g., Gidley Larson & Mostofsky, 2006). Furthermore, anatomical and functional abnormalities are commonly displayed by autistic people in neural regions said to drive predictive control, such as the cerebellum (e.g., Fatemi *et al.*, 2002; Allen & Courchesne, 2003), anterior cingulate (Dichter *et al.*, 2009) and basal ganglia (Hollander *et al.*, 2005).

However, research has shown that various prediction-dependent processes are not chronically impaired in autistic individuals (e.g., Gidley-Larson *et al.*, 2008; Tewolde *et al.*, 2018), and findings are often task- or context-sensitive (e.g., Palmer *et al.*, 2017). For example, recent studies examining the fingertip forces used during object interaction (Buckingham *et al.*, 2016; Arthur *et al.*, 2019) have explored how sensorimotor prediction correlates with autistic-like traits in large neurotypical populations (e.g., behavioural characteristics relating to communication, social skills, imagination, attention to detail and attention switching; Baron-Cohen *et al.*, 2001), where such traits are continuous and normally-distributed (Ruzich *et al.*, 2015). These studies examined the degree to which participants predictively lift ‘heavy-looking’ objects (e.g., large objects) with greater fingertip force rates than ‘lighter-looking’ ones (e.g., small objects; Buckingham *et al.*, 2016) - a type of ‘sensorimotor prediction’ generated in the dorsal premotor cortex (Chouinard *et al.*, 2005). Here, although participants with higher autistic-like traits showed reduced sensorimotor prediction when interacting with different-sized objects (Buckingham *et al.*, 2016), such effects did not replicate when objects differed in material properties (Arthur *et al.*, 2019). This suggests that predictive processing atypicalities in autism may be driven by task- or context-specific mechanisms.

These task-specific findings are noteworthy, as sensorimotor control is underpinned by context-sensitive adjustments in predictive processing (Friston, 2005; Wolpert & Landy, 2012; Adams *et al.*, 2013). For instance, expectation-driven signals are typically down-regulated when uncertainty about one’s prior beliefs is high to ensure that unbiased sensory cues can be processed (Yu & Dayan, 2003; Kwon & Knill, 2013). Notably, such context-sensitive neurobiological responses appear to be diminished in autistic individuals (Ewbank *et al.*, 2014; Lawson *et al.*, 2017), prompting suggestions that autism may be characterised by inflexibilities in how predictive processing is adjusted according to environmental statistics (Lawson *et al.*, 2017; Palmer *et al.*, 2017). These arguments are supported by recent findings in the rubber-hand illusion (Palmer *et al.*, 2015) and object lifting (Arthur *et al.*, 2019), where participants with higher autistic-like traits display a lower degree of uncertainty-driven adjustments in gaze and motor control. However, it remains unclear whether sensorimotor difficulties in ASD are underpinned by chronic attenuations in the use of prior information (e.g., as proposed in ‘simple’ Bayesian theories), or context-sensitive mechanisms relating to how this prior information is integrated with environmental statistics (Palmer *et al.*, 2017).

The current study examined how predictive sensorimotor control differs in autistic people across two object lifting experiments. First, we examined actions in a large neurotypical

sample, exploring the correlations between autistic-like traits and various measures related to sensorimotor prediction (*Experiment one*). By adopting this initial trait-based approach, we were able to identify novel markers of sensorimotor prediction which are related to autism-like traits, whilst avoiding the potential confounds with differences in cognitive ability and co-occurring disorders (Landry & Chouinard, 2016). We followed this initial experiment with a second study, analysing how these prediction-related sensorimotor variables differ between neurotypical individuals and participants with a clinical diagnosis of ASD (*Experiment two*).

In both experiments, participants lifted objects which differed in physical size and mass (Figure 1), before reporting how heavy they felt on a numerical scale. To examine predictive processing at a *perceptual* level, we averaged these numerical heaviness ratings across each lift for each object. Here, prior expectancies bias perception in a non-veridical ‘anti-Bayesian’ manner (Brayanov & Smith, 2010), with small objects typically perceived to feel heavier than equally-weighted larger ones (Charpentier, 1891). To examine predictive processing at a *sensorimotor* level, we calculated peak grip (pGFR) and load (pLFR) force rate differences between the initial lifts of the large and smaller objects, alongside resulting action kinematics (as in Arthur *et al.*, 2019). Here, tendencies to underestimate and overestimate lifting force can be derived from unexpectedly-heavy and unexpectedly-light object lifts. Such profiles are subject to distinct, situation-specific computations, and thus permit scrutiny into the use of predictions at both chronic (i.e., *context-independent*) and precise (i.e., *context-sensitive*) hierarchical levels. Specifically, underestimation and overestimation motor responses have divergent consequences on action and are accompanied by distinct error computations (Jenmalm *et al.*, 2006). These potential ‘cost functions’ are said to be computed by the brain during sensorimotor control (see Wolpert & Landy, 2012), and can lead to non-linear action responses (e.g., Stevenson *et al.*, 2009). For example, when lifting a mug of tea, prior uncertainty about the weight of the mug may have little effect on pGFR *overestimation* tendencies, as the consequence of prediction error is relatively minor (i.e., unnecessary energy expenditure, increased effort). Conversely though, as *underestimation* can lead to detrimental error effects (i.e., slips or drops), it would be expected that high grip force ‘safety margins’ are employed under uncertain conditions (Hadjiosif & Smith, 2015). Therefore, individuals may utilise the same overall prediction (e.g., that larger mugs will weigh more than smaller ones) in a distinct, context-sensitive manner.

To further supplement this multi-modal analysis, we also monitored participants’ gaze patterns, with ‘Bayesian Brain’ hypotheses having direct implications for visual sampling

behaviours (see Palmer *et al.*, 2017), and shorter, more frequent goal-directed fixations signalling inefficiencies and/or impairments in predictive sensorimotor control (e.g., Murray & Janelle, 2003; Wilson *et al.*, 2013). Together, this multi-modal approach enabled us to directly test whether autism-related atypicalities reflect chronic, domain-general attenuations in predictive control, or context-sensitive patterns linked to specific sensorimotor pathways. Our working hypothesis, on the basis of previous findings (Buckingham *et al.*, 2016), was that autistic participants, and neurotypical participants with higher levels of autistic-like traits, would show chronic attenuations in sensorimotor prediction across all sensorimotor levels.

## Materials and Methods

### Participants

The experiments received approval from the School of Sport and Health Sciences Ethics Committee (University of Exeter) and informed consent was obtained from all participants in accordance with British Psychological Society guidelines. All participants were naïve to the study objectives and had normal or corrected-to-normal vision.

In *Experiment One*, we tested a large general population ( $n = 89$ : 46 male, 43 female;  $23.10 \pm 3.37$  years; 90% right-handed), who did *not* report any cognitive disabilities or neurological disorders. Participants were excluded if they reported any conditions known to affect sensorimotor control, including ASD, meaning that one individual with developmental co-ordination disorder (DCD) and two with musculoskeletal injuries were excluded. As such, the study was robust to clinically-related confounds (Landry & Chouinard, 2016).

In *Experiment Two*, we recruited 33 participants with a clinical diagnosis of ASD, recognised according to *DSM-V* or *ICD-10* criteria (American Psychiatric Association, 2013; World Health Organisation, 2012). Data from four participants was removed from the study, after reporting co-occurring conditions known to affect sensorimotor control (DCD:  $n = 3$ ; musculoskeletal injury  $n = 1$ ). Remaining participants ( $n = 29$ : 19 male, 10 female;  $21.28 \pm 3.63$  years; 25 right-handed) demonstrated a broad range of autistic-like traits, as confirmed from Social Communication Questionnaire responses (SCQ; Berument *et al.*, 1999; Total; Total Scores:  $18.46 \pm 5.91$ , Current scores:  $8.65 \pm 3.49$ ) which correspond with previously reported clinical values (e.g., Schuwerk *et al.*, 2016). Although all SRS-S scores exceeded the

clinical ‘cut-off’ of 11, three participants scored below the recently-recommended SCQ threshold of 12 (Schanding *et al.*, 2012). However, since the presence of a formal ASD diagnosis was the criterion variable for group assignment, and none of our reported effects were altered by excluding these low-SCQ cases, we included all participants in our primary analysis (as in Schuwerk *et al.*, 2016). Any trait-based effects were then examined using correlation analysis. To permit between-group comparisons, an individually-matched group of neurotypical participants (NT Group: 19 male, 10 female,  $21.31 \pm 3.30$  years; 25 right-handed), selected based on age, gender and dominant hand, were also tested. These individuals did not report any conditions known to affect sensorimotor control, including ASD, and did not participate in Experiment one.

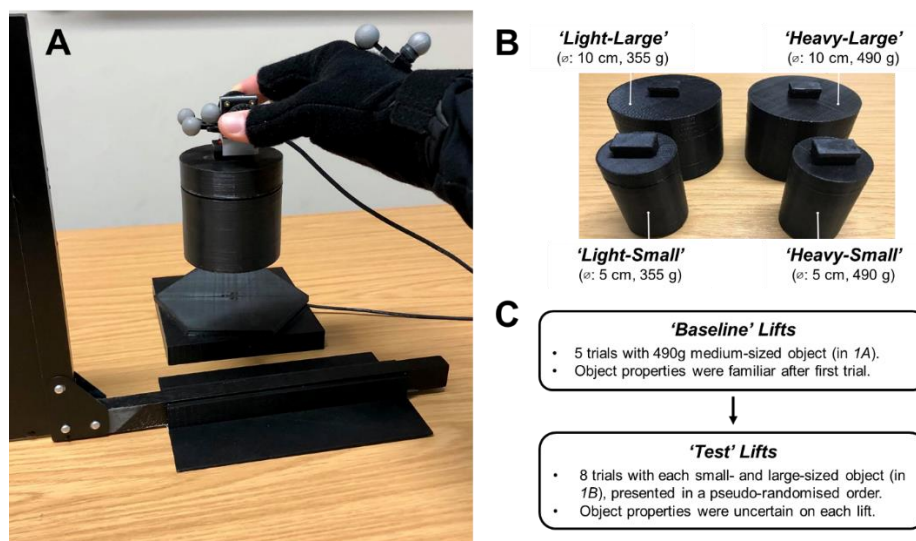
### **Apparatus and Stimuli**

Participants lifted homogenous 7.5-cm tall black plastic cylinders using an aluminium and plastic lifting handle, which was fitted with an ATI Nano-17 Force transducer. Objects differed in physical diameter (small: 5 cm, large: 10 cm) and mass (light: 355 g, heavy: 490 g), presenting a total of four ‘test’ items (Figure 1B). An additional medium-sized ‘control’ object (diameter: 7.5 cm; mass: 490 g) also provided baseline comparisons for grip and load force outcomes, all of which were recorded at 500 Hz. During lifting, participants wore a Pupil Labs mobile eye gaze registration system (Pupil Labs, Sanderstrasse, Berlin, Germany; Kassner *et al.*, 2014), which calculated gaze positions at 90 Hz. The eye-tracking system was calibrated using the manufacturer’s built-in screen marker routine prior to data collection, and following any displacement of the gaze registration cameras and/or loss of data quality during testing. A manual clapper board concealed objects and restricted visual feedback prior to the onset of each trial (see Arthur *et al.*, 2019 for further details). To enable kinematic analysis in experiment *one*, the position of rigid bodies comprised of three reflective markers, attached to the lifting handle and to a worn glove, were tracked by an 8-camera optical motion capture camera system at 120 Hz (OptiTrack, NaturalPoint, Corvallis, Oregon). Conversely, in experiment *two*, these markers were replaced by coloured tape, which could be identified from the ‘world’ eye-tracking camera footage to segment the onset and offset of each trial. Such procedures were undertaken using a custom algorithm in MATLAB, with trial onset representing the first frame in which the lifting handle tape became visible.

To index autistic-like traits in *experiment one*, participants completed the 50-item adult Autistic Quotient (AQ; Baron-Cohen *et al.*, 2001). The AQ assesses five sub-traits associated with ASD, namely: attention to detail, attention switching, imagination, communication and

social skills. Participants self-reported whether they “definitely agree”, “slightly agree”, “slightly disagree” or “definitely disagree” with fifty itemised statements that assess each of these subscales. This method provides an overall score out of 50, whereby higher numbers reflect greater autistic-like traits.

Conversely, in *experiment two*, participants completed the shortened version of the Social Responsiveness Scale (SRS-S), a 16-item questionnaire, designed for clinical populations (Sturm *et al.*, 2017), which measures: use of language, social information processing, capacity for reciprocal responses, and stereotypic/repetitive behaviours. Items are rated from 0 (never true) to 3 (almost always true) so as to yield a total SRS-S score. To supplement this self-report data, and enable between-study comparisons, the Social Communication Questionnaire (SCQ; Berument *et al.*, 1999) was completed by parents or guardians for the ASD group. The SCQ is a widely-used and validated clinical assessment tool, which indexes current (items 1-19) and lifetime (items: 20-40) aptitudes in social responsiveness, verbal communication, and restricted repetitive stereotyped behaviours.



**Figure 1.** The experimental set-up for object lifting trials (a), the four ‘test’ objects lifted by participants (b), and a schematic overview of the testing session (c). Objects were concealed by a manual clapper-board prior to each trial. Following an auditory tone (trial onset), participants reached and lifted objects with their thumb and forefinger to a comfortable height above the table. Objects were held steady until hearing a second auditory tone (trial offset), before being placed back on the platform. These procedures were repeated for ‘baseline’ and subsequent ‘test’ trials, where various prediction-related sensorimotor measures were obtained. See *Supplementary Video 1* for illustration of this protocol (available at: <https://osf.io/p52h8/>).



## Procedures

All measures of autistic-like traits were completed before the lifting protocol. Thereafter, participants repeated a previously-described set of standardised lifting procedures, both for ‘baseline’ and ‘test’ trials (Figure 1; see Arthur *et al.*, 2019 for more detail). Specifically, during both conditions, participants lifted objects from a seated position with the thumb and forefinger of their dominant hand, and held them steady at a comfortable height above the table surface. The onset and offset of each trial were signalled by two computer-generated auditory tones, each separated by four seconds. Participants were instructed to lift objects in a ‘smooth, controlled and confident manner’, and to ‘gently place the object back on its starting platform’. Each session started with 5 ‘baseline’ trials, and was followed by 32 ‘test’ trials (Figure 1C), where each object was lifted 8 times in one of three pseudo-randomised orders. These pre-determined trial sequences presented objects in an uncorrelated, entropic order, but guaranteed that each ‘heavy’ item was lifted at least once before any ‘light’ trials. Such precautions would minimise order effects (e.g., Maiello *et al.*, 2018), while ensuring initial ‘test’ lifts were unexpectedly-heavy or light, relative to baseline trials. After each lift, participants verbally reported a numerical judgement about how heavy the object felt, with larger numbers instructed to represent heavier weights. Importantly, no constraints were placed on these values to minimise ratio scaling biases (as in Buckingham *et al.*, 2016). Prior to the lifting protocol in experiment two, participants also verbally rated how heavy they *predicted* each object would be, based on their visual appearance (as in Buckingham & Goodale, 2013).

## Data Analysis

**Perceived Heaviness Scores:** Heaviness ratings were normalised to a z-score distribution to permit inter-individual analyses. To quantify the magnitude of the Size-Weight Illusion (SWI), where small objects are erroneously perceived to weigh more than equally-weighted larger ones (Charpentier, 1891), average values for the larger objects were subtracted from those of the smaller ones (as in Buckingham *et al.*, 2016). Conversely, to quantify detection of *real*-weight changes, averages for the heavy objects were subtracted from lighter objects.

**Force Data:** Extracted force data were smoothed using a 14-Hz Butterworth filter, with forces perpendicular to the surface of the handle defined as grip force and resultant vectors of the tangential forces interpreted as load force. To determine peak force rates, data were differentiated with a 5-point central difference equation. From here, broad size-related prediction errors were assessed for grip (pGFRdiff) and load (pLFRdiff) force rate outcomes,

through subtracting values from the first ‘test’ lift of the smaller objects from those of the larger objects (as in Buckingham *et al.*, 2016). To isolate more context-specific mechanisms, we also assessed sensorimotor prediction for small and heavy objects separately. Here, tendencies to underestimate and overestimate an object’s weight are accompanied by contrasting error signals and movement consequences, meaning that the use of prior expectations will be distinctly influenced by context-sensitive processing mechanisms (e.g., expected uncertainty, volatility representations). Accordingly, to index underestimation of force, pGFR from the first test trial of the small-heavy object was subtracted from that of the final baseline lift. Conversely, to index overestimation, pGFR exhibited during this final baseline trial was subtracted from the first large-heavy test trial. This analysis was conducted on pGFR, and not pLFR, following inspection of trial-by-trial lifting profiles (Figure 2), which suggested that prediction-related differences were more context-sensitive for this measure. For all these outcomes, higher index values would indicate a greater degree of sensorimotor prediction (as in Buckingham *et al.*, 2016).

**Gaze Data:** Visual fixations were extracted from the gaze data using Pupil Player software (Kassner *et al.*, 2014). Fixations were defined as gaze that remained on a location, within 1° of visual angle, for a minimum of 120 ms, with the total number and average duration of fixations recorded for baseline trials and for the first lift of each object. To monitor context-sensitive adjustments in visual sampling (Experiment two), the total number of fixations across a trial were divided by their average duration. This provided a search rate score (as in Arthur *et al.*, 2019), whereby higher values would highlight the occurrence of shorter, more frequent fixations (i.e., patterns associated with inefficient sensorimotor coordination). As most visual fixations are directed towards the object in our task (see *Supplementary Video 2*), higher values would likely signal greater sampling of uncertain goal-relevant sensory cues. Such visual sampling behaviours are highly sensitive to contextual statistics (e.g., environmental uncertainty; Tong *et al.*, 2017; Hayhoe & Matthis, 2018) and appear atypical in autistic children (Sasson *et al.*, 2008; Sasson *et al.*, 2011). This search rate analysis was *not* conducted in experiment one, as a frequent loss of gaze tracking during ‘test’ trials would have led to exclusion of 14 additional participants. Nevertheless, correlations between AQ scores and search rate have been previously documented in object lifting (Arthur *et al.*, 2019), and should be explored in future sensorimotor research (see *main discussion*).

***Kinematic Data (Experiment one only):*** Raw positional data for each infrared marker were smoothed using a dual-pass, zero-phase lag 10-Hz Butterworth filter, with hand and object velocity then calculated from the average position of each rigid body. These signals were then combined into resultant 3-dimensional vectors and differentiated with a five-point central difference equation to yield velocity values. From here, Reach and Lift movement phases were segmented for each trial. Specifically, the reach phase began when hand velocity first exceeded 50 mm/s for three consecutive frames and concluded upon the onset of grip force. The Lift phase was determined from the timepoint where both hand and object velocity first exceeded 50 mm/s until the point where the object reached its maximum vertical position. The maximum velocity of the hand during reach (MRV) and lift (MLV) phases was then recorded, as were the timepoints where these events occurred (as a % of total movement time). Kinematic outcomes were not examined in experiment two. Instead, only force-based motor outcomes were analysed to facilitate a more-refined, iterative investigative approach (*see results below*).

***Statistical Analysis:*** Statistical analyses were performed using JASP (version 0.12.2), with significance accepted at  $p < 0.05$  and data presented  $\pm$  SD. Outliers were removed from their respected analysis, with univariate outliers identified as values  $> 3.29$  SD above or below the mean ( $p < .001$ ) and multivariate outliers ascertained by extreme Mahalanobis distances ( $p < .001$ ). In both experiments, Pearson's Correlation analysis explored relationships between sensorimotor outcomes and autistic-like trait scores (Experiment one: AQ scores; Experiment two: SCQ and SRS-scores), while independent  $t$ -tests were used to compare between groups. ANOVA's assessed the effects of size and mass on perceived heaviness scores and fingertip lifting forces (pGFR and pLFR), with main effects of Group additionally examined in Experiment two. Here, any significant effects were examined with planned  $t$ -tests, and effect sizes were calculated using partial-eta squared ( $\eta p^2$ ). Any non-spherical data were adjusted using the Greenhouse-Geisser correction, and Holm-Bonferroni corrections (Holm, 1979) were used to correct for multiple comparisons. Bayes Factors quantifying the strength of evidence for the alternative and null hypotheses were also obtained, using a symmetric Cauchy prior.

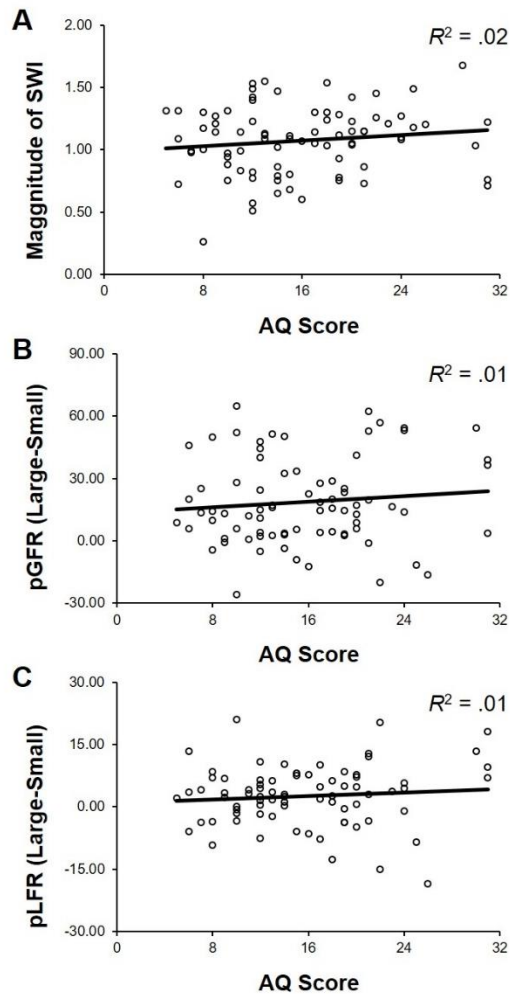
***Data Availability:*** Data from both experiments can be found at <https://osf.io/p52h8/>.

## Results

### Experiment One: Associations between sensorimotor prediction and non-clinical autistic-like traits.

The aim of Experiment one was to investigate the associations between sensorimotor prediction and autistic-like traits, using an exploratory non-clinical approach that would be minimally affected by co-occurring disorders and cognitive ability (Simonoff *et al.*, 2008). To ensure that analyses were not influenced by “clinically significant” participant characteristics, participants were excluded if they exhibited total scores  $\geq 32$  ( $n = 4$ ; as recommended by Baron-Cohen *et al.*, 2001). Remaining participants ( $n = 82$ ) exhibited AQ scores ranging from 5-31 (Mean:  $15.87 \pm 6.39$ ), values which are consistent with large, representative neurotypical populations (Baron-Cohen *et al.*, 2001). There were no statistical violations relating to normality, homoscedasticity, or linearity. However, one participant’s heaviness ratings (remaining  $n = 81$ ), and five participants’ force data (remaining  $n = 77$ ), were excluded following detection of univariate outliers in the associated outcome measures ( $p < .001$ ). Additionally, eight participants were removed from kinematic analysis (remaining  $n = 74$ ) and twenty-two from gaze analysis (remaining  $n = 60$ ) due to poor data quality and/or outliers.

First, to assess the influence of predictive processing at a perceptual level, a repeated measures ANOVA was conducted with average heaviness scores for each ‘test’ object (small-light, small-heavy, large-light, large-heavy) entered as dependent variables. ANOVA revealed significant effects of size and mass on perceived heaviness (Size:  $F(1, 81) = 1150.86$ ,  $p < .001$ ,  $\eta p^2 = .93$ ,  $BF_{10} = 3.22 * 10^{33}$ ; Mass:  $F(1, 81) = 1395.16$ ,  $p < .001$ ,  $\eta p^2 = .95$ ,  $BF_{10} = 2.13 * 10^{48}$ ). Average scores for smaller ‘test’ objects were greater than those for larger ones ( $p < .001$ ,  $BF_{10} = 1.44 * 10^{45}$ ) and scores for heavier objects were greater than those for the lighter ones ( $p < .001$ ,  $BF_{10} = 9.34 * 10^{48}$ ). Together, effects show that both illusory *and* physical differences in mass were detected. However, Correlation analysis showed that there were no significant associations between AQ scores and heaviness ratings (SWI:  $r = .13$ ,  $p = .25$ ,  $BF_{10} = 0.27$ ; Real-Weight:  $r = -.17$ ,  $p = .14$ ,  $BF_{10} = 0.40$ ; Figure 2A).



**Figure 2.** Scatter plots highlighting associations between autistic-like traits (AQ scores) and the magnitude of the perceptual Size-Weight Illusion (SWI; **A**), prediction-related differences in peak Grip Force Rate (pGFR; **B**) and peak Load Force Rate (pLFR; **C**) in Experiment one. No significant relationships emerged (all  $p > 0.05$ ).

To then assess the prediction-related effects of size and weight on lifting forces, one-way ANOVAs compared pGFR and pLFR from the initial lifts of ‘test’ objects. ANOVA revealed no significant effects for object mass on pLFR ( $F(1,77) = 1.03$ ,  $p = .31$ ;  $\eta p^2 = 0.01$ ,  $BF_{10} = 0.18$ ) and marginal effects on pGFR ( $F(1,77) = 4.03$ ,  $p = .05$ ,  $\eta p^2 = 0.05$ ,  $BF_{10} = 1.01$ ). However, as expected, strong effects for size emerged (pGFR:  $F(1,77) = 62.03$ ,  $p < .001$ ,  $\eta p^2 = .45$ ,  $BF_{10} = 1.10 * 10^9$ ; pLFR:  $F(1,77) = 9.24$ ,  $p = .003$ ,  $\eta p^2 = .11$ ,  $BF_{10} = 12.96$ ), with force rates lower when lifting the smaller compared to larger objects (pGFR:  $p < .001$ ,  $BF_{10} = 4.06 * 10^8$ ; pLFR:  $p = .003$ ,  $BF_{10} = 8.53$ ). This indicates that the object lifting paradigm elicited size-related expectation biases on initial ‘test’ lifts. Interestingly though, the magnitude of these predictive biases was not significantly related to AQ values ( $p$ 's  $> .37$ ; Figure 2B-C), with

Bayes factors reflecting strong evidence for null trait-based effects (pGFRdiff:  $r = .10$ ,  $p = .37$ ,  $BF_{10} = 0.21$ ; pLFRdiff:  $r = .09$ ,  $p = .43$ ,  $BF_{10} = 0.19$ ). Furthermore, no significant correlations emerged between AQ scores and lifting kinematics (Table 1;  $p$ 's  $> .24$ , all  $BF_{10}$  values  $< 0.30$ ).

**Table 1.** Bivariate Correlations between Autistic Quotient Scores and Sensorimotor Outcomes in Experiment One.

	<i>Mean (SD)</i>	<i>R</i>
<b><i>Force Measures</i></b>		
pGFRdiff (N/s)	18.70 (20.95)	0.10
pLFRdiff (N/s)	2.61 (7.26)	0.09
pGFR Underestimation (N/s)	21.49 (28.62)	-0.25*
pGFR Overestimation (N/s)	6.25 (32.30)	0.20
<b><i>Gaze Measures</i></b>		
Fixation Number	3.93 (0.55)	0.03
Fixation Duration (ms)	427.03 (115.47)	0.14
<b><i>Kinematic Measures</i></b>		
MRV (mm/s)	917.34 (157.83)	-0.11
MLV (mm/s)	341.70 (82.47)	0.14
Time to MRV (%)	37.56 (6.39)	0.03
Time to MLV (%)	35.30 (7.04)	-0.05

*pGFRdiff: differences in peak Grip Force Rate between initial lifts of the large and small 'test' objects; pLFRdiff: differences in peak Load Force Rate between initial lifts of the large and small 'test' objects; MRV: maximum reach velocity; MLV: maximum lift velocity; \* denotes significant relationship with AQ scores.*

Gaze patterns were markedly consistent both within- and across-subjects (see *Supplementary Video II* at <https://osf.io/p52h8/> for illustration). Specifically, participants tended to fixate upon the stationary 'test' object throughout the reach and grasp phases, before employing pursuit and saccadic eye movements to track its in-flight lift trajectory. Upon reaching a stable 'hold' position, subsequent object-directed fixations were then maintained until the offset of the trial, when an anticipatory saccade would draw gaze back towards the starting platform (i.e., final object location). Such gaze patterns are consistent with previous studies (e.g., Johansson *et al.*, 2001), and are said to be 'supervised' by predictive action models

(Land, 2009). Interestingly, our data provided strong evidence that AQ scores were unrelated to these fixation behaviours (Fixation number:  $r = .03$ ,  $p = .85$ ,  $BF_{10} = 0.16$ ; Duration:  $r = .14$ ,  $p = .28$ ,  $BF_{10} = 0.28$ ; Table 1). This reinforces null associations between autistic-like traits and prediction-controlled behaviour in this task.

Nevertheless, as atypicalities in predictive control appear context-sensitive, autism-related attenuations in the use of prior knowledge may be contingent on specific trial conditions. Recent Bayesian perspectives argue that it is this hierarchical, situation-dependent scaling of predictive processing that is atypical in ASD (e.g., Lawson *et al.*, 2017; Palmer *et al.*, 2017). Accordingly, we explored whether any *context-sensitive* relationships between autistic-like traits and sensorimotor prediction were present in our data. Specifically, we calculated baseline-subtracted fingertip force profiles for the ‘small-heavy’ (pGFR underestimation) and ‘large-heavy’ objects (pGFR overestimation), before examining correlations with AQ scores. Here, no significant relationships were found between pGFR overestimation and AQ scores ( $r = .20$ ;  $p = .08$ ,  $BF_{10} = 0.62$ ), suggesting that participants comparably increased force rate for larger test objects. Results did, however, provide anecdotal support for an inverse relationship between AQ and pGFR underestimation values ( $r = -.25$ ,  $BF_{10} = 1.47$ ), although such effects were non-significant when accounting for multiple comparisons ( $p = .03$ , Table 1). *Supplementary Analysis 1* suggests that inverse correlations between AQ and underestimation scores were evident in both our kinematic data and in pre-existing SWI data (Buckingham *et al.*, 2016; available at: <https://osf.io/2cmdu/>). Therefore, though evidence is clearly inconclusive, it would be premature to rule out any context-sensitive relationships between autistic-like traits and sensorimotor prediction at this point.

## **Experiment Two: predictive sensorimotor control in autistic people.**

In Experiment two, we examined how predictive sensorimotor control manifests in individuals with a clinical diagnosis of ASD, using the same object lifting protocol as in Experiment one. As expected, the ASD group displayed significantly higher self-reported autistic-like traits than their NT counterparts on the shortened version of the Social Responsiveness Scale (SRS-S; Sturm *et al.*, 2017;  $t(56) = 12.32$ ,  $p < .001$ ,  $BF_{10} = 2.33 \times 10^{14}$ ), and there were no group differences for age or handedness (Table 2). As two autistic participants were unable to verbally report perceived heaviness, they and their matched NT controls were excluded from analyses of these outcomes (remaining  $n = 54$ ). Furthermore, two participants displayed extreme PGFR and pLFR values ( $> 3.29$  SD; remaining  $n = 54$ ) and three participants showed poor quality

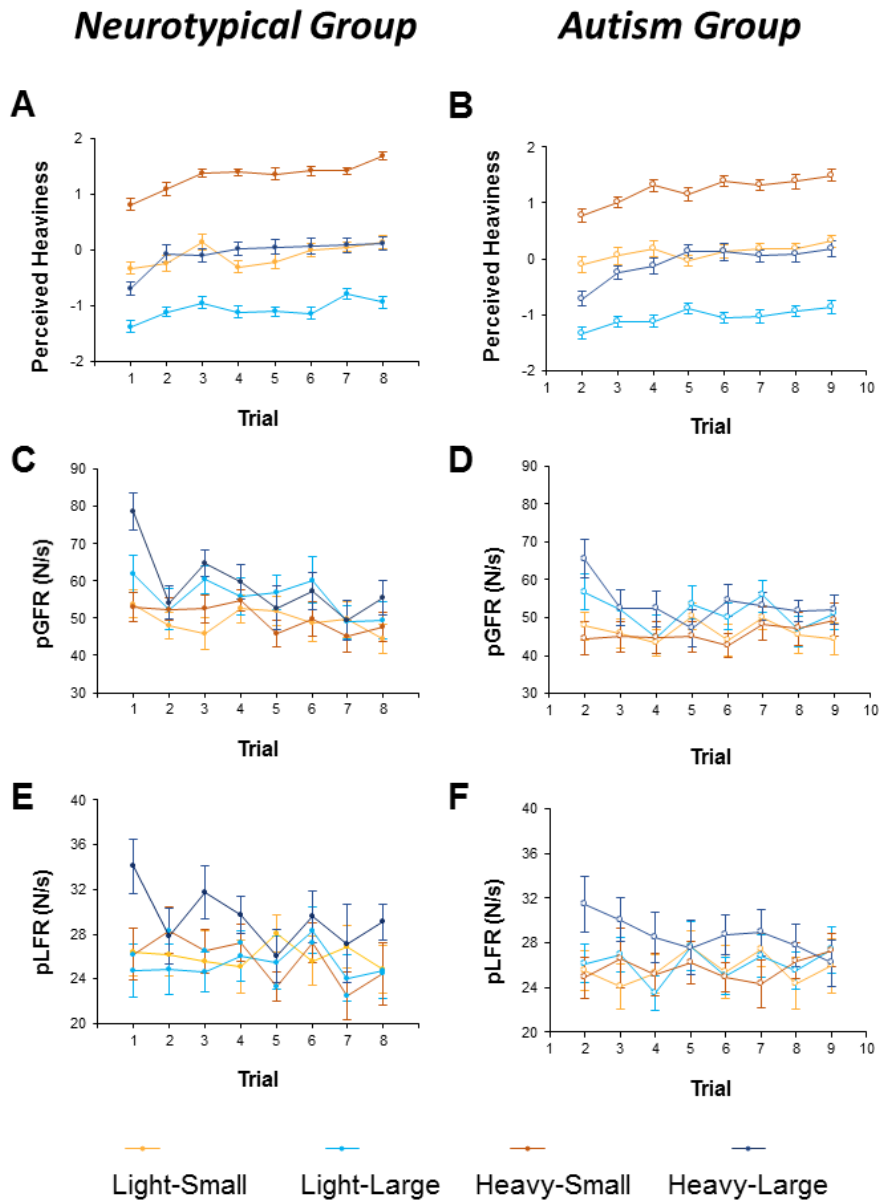
gaze data (remaining  $n = 52$ ), leading to the subsequent exclusion of these cases, and their matched controls, from the separate analysis procedures. Remaining data showed no statistical violations relating to normality, homoscedasticity, or linearity.

To firstly assess whether groups made similar cognitive predictions about object weight *prior to* their lifting trials, participants provided numerical ratings for how heavy they predicted each object would be, based on their visual appearance. A mixed-model ANOVA revealed a significant main effect of size for these scores, with larger objects predicted to be heavier than equally-weighted smaller ones ( $F(1.69, 84.69) = 61.03, p < .001, \eta p^2 = .55, BF_{10} = 1.61 * 10^{21}$ ). Importantly, there was no significant ‘group-by-size’ interaction effects ( $F(1.69, 84.69) = .79, p = .46, \eta p^2 = .02, BF_{10} = 0.26$ ), and ratings were unrelated to both SCQ ( $r = .23, p = .27, BF_{10} = 0.44$ ) and SRS-S scores ( $r = -.10, p = .49, BF_{10} = 0.22$ ), suggesting that groups had equivalent prior expectations of object weight. To then assess whether these predictions influenced perception comparably across both groups, we analysed perceived heaviness ratings (as in Experiment one). As before, ANOVA revealed significant effects of size ( $F(1, 52) = 537.70, p < .001, \eta p^2 = .91, BF_{10} = 2.19 * 10^{26}$ ) and weight ( $F(1, 52) = 426.77, p < .001, \eta p^2 = .89, BF_{10} = 8.59 * 10^{21}$ ). However, no ‘group-by-size’ interaction effects were observed ( $F(1, 52) = 0.17, p = .69, \eta p^2 = .003, BF_{10} = 0.18$ ), with both groups rating small objects as heavier than larger ones (Figure 3A-B). Similarly, no ‘group-by-mass’ effects emerged ( $F(1, 52) = 1.73, p = .20, \eta p^2 = .03, BF_{10} = 0.26$ ), and relationships between autistic-like traits and SWI scores were non-significant (SRS-S:  $r = -0.10, p = .49, BF_{10} = 0.22$ ; SCQ:  $r = -0.16, p = .47, BF_{10} = 0.33$ ).

To examine the *use* of these sensorimotor predictions, we compared pGFR and pLFR values between groups from the first lift of each test object. ANOVA showed significant effects for both size (pGFR:  $F(1,52) = 61.05, p < .001, \eta p^2 = .54, BF_{10} = 2.98 * 10^8$ ; pLFR:  $F(1,52) = 12.14, p = .001, \eta p^2 = .19, BF_{10} = 8.35$ ) and mass (pGFR:  $F(1,52) = 6.07, p = .02, \eta p^2 = .11, BF_{10} = 1.30$ ; pLFR:  $F(1,52) = 12.75, p < .001, \eta p^2 = .20, BF_{10} = 11.42$ ). However, between-group comparisons revealed that pGFRdiff ( $t(52) = 0.47; p = .64; BF_{10} = 0.30$ ) and pLFRdiff ( $t(52) = 0.25; p = .80; BF_{10} = 0.28$ ) were not significantly different (Table 2), suggesting that NT and ASD groups scale fingertip forces equivalently according to prior expectations of object mass (Figure 3C-F). Furthermore, analysis generally showed no significant associations between autistic-like traits and either pGFRdiff (SRS-S:  $r = -.14, p = .31, BF_{10} = 0.28$ ; SCQ:  $r = -.33, p = .12, BF_{10} = 0.25$ ) or pLFRdiff (SRS-S:  $r = -.002, p = .99, BF_{10} = 0.17$ ). Similarly, though Bayes Factors provided moderate evidence for an inverse correlation between pLFRdiff



and SCQ scores ( $BF_{10} = 3.23$ ; as in Buckingham *et al.*, 2016), Pearson's correlation coefficient was non-significant when accounting for multiple comparisons ( $r = -.47, p = .02$ ).



**Figure 3.** Trial-by-trial averages ( $\pm$  SEM) for normalised perceived heaviness ratings (A-B), peak grip force rate (pGFR; C-D), and peak load force rate (pLFR; E-F) in *Experiment Two*. Filled circles represent neurotypical (NT) values, empty circles represent autistic group (ASD).

Interestingly, there were no significant group differences in either pGFR overestimation ( $t(52) = 1.91, p = .06, BF_{10} = 1.20$ ) or underestimation ( $t(52) = 1.38; p = .17; BF_{10} = 0.60$ ; Table 2). These findings were unsurprising, given the inconclusive nature of our earlier analysis, and are reinforced by null correlations between pGFR underestimation and SRS-S scores ( $r = -.24; p = .23; BF_{10} = 0.48$ ). However, analysis did provide moderate evidence for a correlation between pGFR underestimation and current SCQ scores ( $r = -.52, p = .01, BF_{10} = 6.62$ ), and it is likely that the low NT group underestimation values ( $8.84 \pm 18.93$  N/s) are obscuring any autism-related group differences that may exist in this dataset (see Jarrold & Brock, 2004 for discussion of “floor effects” in matched-group ASD research). Therefore, it remains unclear whether underestimation profiles differ from NT values in our clinically-diagnosed ASD sample, and further investigation is required.

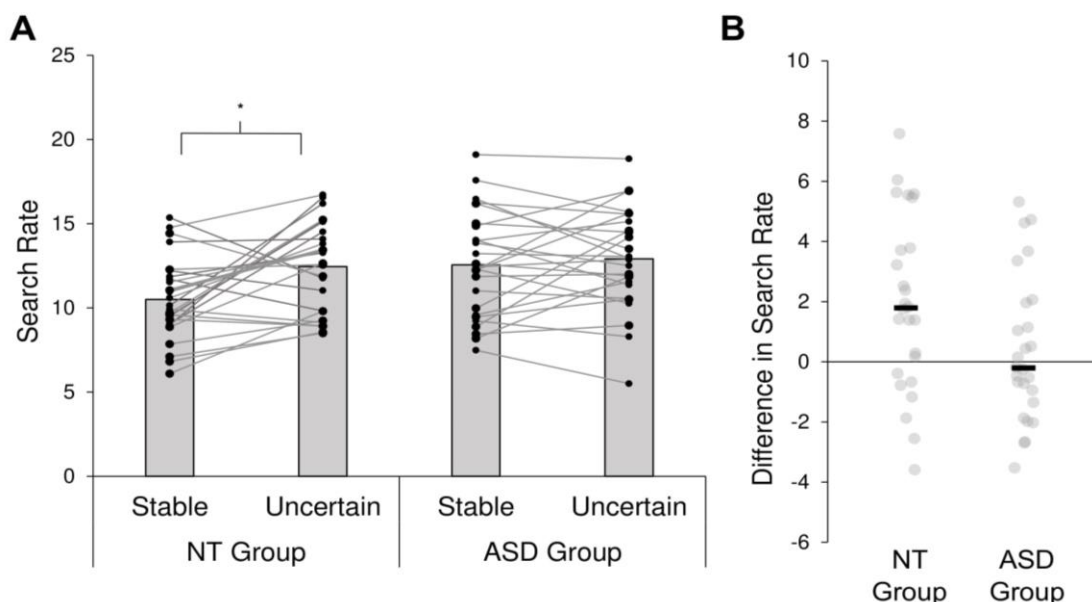
**Table 4.** Group Averages (SD) in Experiment Two.

	<i>ASD Group</i>	<i>NT Group</i>
<b><i>Demographic Measures</i></b>		
Age	21.28 (3.63)	21.31 (3.30)
SRS-S Total	19.03 (6.24)	3.86 (0.24)*
<b><i>Perceptual Measures</i></b>		
Predicted Weight Score	1.31 (1.07)	1.52 (0.94)
SWI Score	1.24 (0.41)	1.18 (0.35)
<b><i>Sensorimotor Measures</i></b>		
pGFRdiff (N/s)	29.73 (29.18)	33.54 (30.31)
pLFRdiff (N/s)	7.19 (16.15)	6.22 (11.80)
pGFR Underestimation (N/s)	16.18 (20.00)	8.85 (18.93)
pGFR Overestimation (N/s)	4.88 (22.40)	16.71 (23.23)

SRS-S: Social Responsiveness Scale- shortened; SWI: Size-Weight Illusion; pGFR: peak Grip Force Rate; pLFR: peak Load Force Rate; \*denotes significant between-group difference.

To initiate this enquiry, we probed the degree to which participants’ adjusted visual sampling behaviours under uncertain trial conditions. Under these conditions, NT observers tend to increase the frequency of gaze fixations towards uncertain, goal-related stimuli (Tong *et al.*, 2017). Such uncertainty-driven adjustments in visual sampling are regulated by context-sensitive processing mechanisms (e.g., precision modulation, volatility representations), and

are recently hypothesised to be atypical in ASD (Palmer *et al.*, 2017). Therefore, we specifically compared changes in gaze search rate between the final four ‘baseline’ trials (i.e., where objects were familiar and unexpected outcomes were unlikely) and the first lifts of each ‘test’ object (i.e., where such environmental statistics were more uncertain; as in Arthur *et al.*, 2019). ANOVA revealed a significant ‘group-by-uncertainty’ interaction ( $F(1,50) = 4.62, p = .04, \eta p^2 = .09, BF_{10} = 6.38$ ). As expected, NT participants showed significant increases in search rate between ‘baseline’ and ‘test’ trials ( $t(25) = 3.42, p = .002, BF_{10} = 17.48$ ), an effect primarily driven by an increase in the number of short, object-driven fixations (*Supplementary Analysis II*). Corresponding changes in the ASD group were not significantly different from zero ( $t(25) = .74, p = .47, BF_{10} = 0.27$ ), and appeared minimal in these individuals (Figure 4). Nevertheless, these changes in search rate were only marginally related to self-reported autistic-like traits (SRS-S scores:  $r = -.30; p = .03, BF_{10} = 1.56$ ) and did not significantly correlate with SCQ scores ( $r = .35, p = .11, BF_{10} = 0.89$ ). Therefore, though data provides cautious, preliminary evidence for a reduced distinction between stable and uncertain environmental conditions in ASD, further empirical scrutiny is required.



**Figure 4.** Changes in gaze search rate between stable (Baseline lifts 2–5) and uncertain (initial ‘test’ lifts) trial conditions for Neurotypical (NT) and Autism (ASD) groups. Bars represent group averages, lines and circles represent individual cases. \*denotes significant difference between conditions ( $p < 0.01$ ).

## Discussion

We investigated the aetiology of sensorimotor difficulties in ASD using a multi-modal object lifting paradigm. We first explored associations between predictive sensorimotor control and autistic-like traits in a non-clinical population (Experiment one), before assessing how specific movement-related mechanisms differ in autistic individuals (Experiment two). In both experiments, participants' actions were strongly driven by prior expectations, and the generic employment of these sensorimotor predictions did not appear implicated in ASD.

Specifically, contrary to simple Bayesian theories of ASD (e.g., Pellicano & Burr, 2012; Sinha *et al.*, 2014; Van de Cruys *et al.*, 2014) and evidence of abnormal fronto-cerebellar functioning in the disorder (e.g., Fatemi *et al.*, 2002; Allen & Courchesne, 2003), we did not find any chronic autism-related attenuations in the use of prior information. Instead, autistic participants appeared to both *make* typical predictions about an object's likely mass, and then *use* these computations to control their actions. For example, when lifting heavy-looking objects, both autistic and neurotypical participants showed equivalent increases in fingertip force rates (Figure 2) and comparable movement kinematics (Table 2). These results align with the null trait-based effects observed in experiment one (Table 1) and in previous non-clinical object lifting research (Arthur *et al.*, 2019). They also add to various studies which have highlighted typical, or even enhanced, prediction-related functions in autistic people (e.g., Mostofsky *et al.*, 2004; Gidley-Larson *et al.*, 2008; Tewolde *et al.*, 2018).

Such findings are noteworthy, from a conceptual perspective, as they suggest that autism is unlikely to be characterised by generic impairments in the ability to make and/or use 'predictive' action models. These observations are clearly at odds with proposals of chronically-diminished priors (Pellicano & Burr, 2012) and inflexible weighting of prediction errors (Van de Cruys *et al.*, 2014) in the disorder. Indeed, according to these 'simple' Bayesian perspectives, one would have expected autism-related atypicalities to emerge consistently across sensorimotor systems, since predictions about object weight are shown to influence perception, motor activity, visual sampling behaviours, and action kinematics (Johansson & Westling, 1988; Gordon *et al.*, 1991; Johansson *et al.*, 2001; Buckingham, 2014). However, it was clear that such effects did not occur in our study, where broad expectation-driven action and sampling behaviours were consistently displayed by autistic participants (e.g., see Figure 3). These null findings may have significant applied implications, as various motor skill interventions rest on an individual's ability to develop, refine, and automate self-generated

action models (Körding *et al.*, 2007; Haker *et al.*, 2016). Given the substantive impact that sensorimotor difficulties are likely to have on autistic people's independence (Jasmin *et al.*, 2009), social activities (Brandwein *et al.*, 2015), and health-related behaviours (e.g., Scharoun *et al.*, 2017), our findings offer potentially fruitful avenues for both researchers and practitioners in the field.

Conversely, though, results do correspond with wide-ranging clinical evidence that autism-related atypicalities in sensorimotor prediction are *context-dependent* (e.g., von Hofsten *et al.*, 2009; Tewolde *et al.*, 2018). Notably, although no broad processing impairments were displayed by autistic participants in our study, anticipatory motor atypicalities *have* previously been observed in various related object interaction tasks (e.g., bimanual lifting; Schmitz *et al.*, 2003). Such contextual irregularities have been the focus of recent Bayesian hypotheses, which argue that autism is characterised by atypicalities in how predictive processing is *adjusted* under different conditions (Lawson *et al.*, 2017; Palmer *et al.*, 2017). According to these perspectives, such between- and within-study inconsistencies would be expected, as any atypicalities are contingent upon highly-variable environmental statistics (e.g., uncertainty, volatility; Palmer *et al.*, 2017). This is cautiously supported by our own data, where autism-related tendencies to over- but not under-estimate pGFR were inconsistently displayed (see *Supplementary Analysis I*). However, given the inconclusive nature of these interpretations, further empirical scrutiny is required.

Recent neurological evidence suggests that sensorimotor difficulties are caused by differences in the regulation, or 'connectivity', of neurobiological networks (Villalobos *et al.*, 2005; Mostofsky *et al.*, 2009; Fournier *et al.*, 2010; Gowen & Hamilton, 2013). From a computational perspective, this research supports context-sensitive, hierarchical models of autism, which posit that predictive atypicalities in the disorder may stem from aberrant neuromodulatory functioning (e.g., see Friston *et al.*, 2013; Lawson *et al.*, 2014). According to these perspectives, autism-related atypicalities will be more frequent under uncertain task conditions, where ambiguous prior information is typically down-regulated relative to more-reliable sensory evidence (e.g., from visual feedback and proprioception; Maloney & Zhang, 2010; Tong *et al.*, 2017). Indeed, these 'typical' content-sensitive patterns of behaviour were apparent in Experiment two, where NT participants exhibited marked changes in gaze search rate (i.e., visual sampling) under more uncertain trials (Figure 4; *Supplementary Analysis II*). Interestingly, such distinctions were not displayed by the ASD group, suggesting that autistic

participants display reduced, uncertainty-related adjustments in sensorimotor control (see also Palmer *et al.*, 2015).

However, these preliminary findings must be interpreted with caution at this stage, as visual sampling atypicalities could implicate various interrelated cognitive and attentional mechanisms. Indeed, despite being a key tenet of predictive processing theories (e.g., Palmer *et al.*, 2017), it is entirely possible that the precise, context-sensitive differences in gaze behaviour observed in *Experiment two* are indicative of wider autism-related atypicalities (e.g., in Executive Functioning: Ozonoff & McEvoy, 1994; Attentional styles: Happé & Frith, 2006; Anxiety: White *et al.*, 2009). Therefore, it currently remains unclear how prior inputs are mechanistically integrated with sensory and environmental information in ASD. Though we consistently observed that the use of prior information does not appear to be *chronically* attenuated in autism, and we were able to qualitatively discern trials where prior uncertainty was relatively low or high in our task, future studies should aim to statistically-compute and/or experimentally manipulate the uncertainty and reliability of sensory cues (Maloney & Zhang, 2010). To do this, researchers should focus on outcomes relating to sensorimotor *integration*, as context-sensitive representations of prior and sensory uncertainty are said to modulate the ‘connectivity’ of neurobiological action systems (Friston *et al.*, 2013). Specifically, studies could employ complex, multi-system movement tasks, such as interceptive motor skills, where prediction-related visuomotor patterns are both well-established (see Fiehler *et al.*, 2019) and integral to successful performance (Fooker & Spering, 2019).

In conclusion, we have provided evidence that autistic people typically control their lifting actions according to predictions about an object’s weight. These ‘predictive’ profiles are implemented across various sensorimotor systems (e.g., cognition, gaze patterns, motor control), and are shaped by an individual’s prior knowledge and experience. Future research is required to examine how these prediction-related mechanisms are integrated and altered under different probabilistic conditions, to help us better understand and manage sensorimotor difficulties in autism.

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## **Competing Interests**

The authors report no competing interests.

## Supplementary Material

### Supplementary Analysis I

Given the inconclusive, anecdotal relationships highlighted between AQ scores and pGFR underestimation (Table 1), we reanalysed Buckingham *et al.*'s (2016) existing force data (available online at: <https://osf.io/2cmdu/>). Specifically, we explored whether their previously-observed associations between AQ scores and pGFRdiff were driven by chronic attenuations in the use of prior knowledge (as previously proposed), or context-specific processing atypicalities (i.e., attenuations in *either* pGFR underestimation or overestimation). Although there were no 'baseline' trials in this previous study, the authors included a 400g medium-sized object (diameter: 7.5 cm) in the SWI protocol which could be compared with equally-weighted small (diameter: 5 cm) and large (diameter: 10 cm) cylinders. As such, we extracted pGFR and pLFR data from initial trials of each object, and computed index scores for underestimation and overestimation profiles respectively. As in experiment one, underestimation scores were calculated by subtracting 'small' from 'medium' force rate values, while first-lift values from the 'medium' object were subtracted from those of the 'large' object to index overestimation. Again, higher values would signify greater tendencies to under- or overestimate forces.

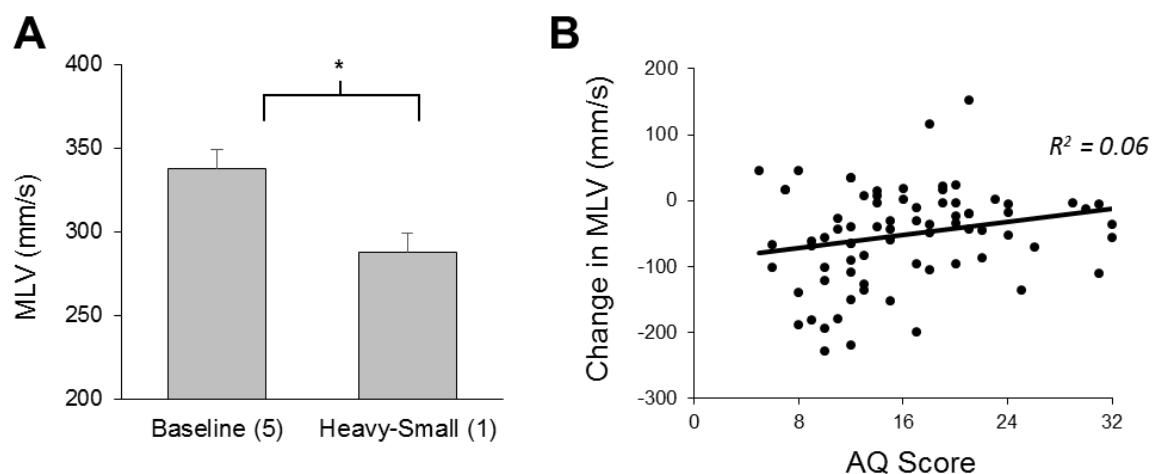
Notably, Bayesian correlation analysis provided only anecdotal support for the previously-reported relationships between high AQ scores and attenuated sensorimotor prediction (pGFRdiff:  $r = -0.24$ ,  $BF_{10} = 1.23$ ; pLFRdiff:  $r = -0.24$ ,  $BF_{10} = 1.23$ ). Furthermore, there was a lack of relationships between AQ and overestimation tendencies in this dataset (pGFR:  $R = 0.11$ ,  $BF_{10} = 0.22$ ; pLFR:  $R = 0.07$ ,  $BF_{10} = 0.16$ ). Interestingly, though, analyses highlighted strong, context-specific associations between AQ scores and pGFR underestimation tendencies ( $r = -.37$ ,  $BF_{10} = 34.89$ ), and moderate evidence in favour of trait-based pLFR underestimation effects ( $r = -.32$ ,  $BF_{10} = 8.73$ ).

To further scrutinise these context-specific effects, we next examined whether they were present in our kinematic data; since any underestimation of required lifting force tends to result in a marked 'slowing' of movement (Jenmalm *et al.*, 2006). Here, using the same approach employed in our force analyses, MLV values from initial lifts of the 'small-heavy' object were subtracted from those in the final 'baseline' trial, to provide an underestimation score. As expected, participants generally displayed slower lifting movements in this initial, unexpectedly-heavy trial (Supplementary Figure 1A). Notably, these kinematic



underestimation profiles were inversely related to AQ scores (Supplementary Figure 1B), although support was only anecdotal in this data ( $r = -.24$ ,  $p = .04$ ,  $BF_{10} = 1.14$ ).

Together, this analysis lends support for the notion that autism-related atypicalities in sensorimotor prediction may be context-dependent (e.g., Lawson *et al.*, 2017; Palmer *et al.*, 2017). Although participants with greater autistic-like traits display typical, prediction-related increases in force rate when lifting large (heavy-looking) objects, they appear less likely to decrease pGFR when lifting small (lighter-looking) ones. These associations are driving the weak effects that were previously observed by Buckingham and colleagues (2016), and appear to emerge in both our clinical and non-clinical datasets. Although the precise causes of these discrepancies can only be speculated at this point, it is likely that the persistently-elevated pGFR profiles shown by high-AQ participants represents a compensatory strategy, aimed at minimising the risk of error. Here, increased grip ‘safety margins’ can reduce the likelihood of performance-based errors (i.e., slips and drops; Cashaback *et al.*, 2017), meaning that they are often deployed under high-uncertainty conditions (Hadjiosif & Smith, 2015). Such an argument lends support for proposed associations between autism and volatility processing (Lawson *et al.*, 2017), however further research is evidently required (see *main discussion*).



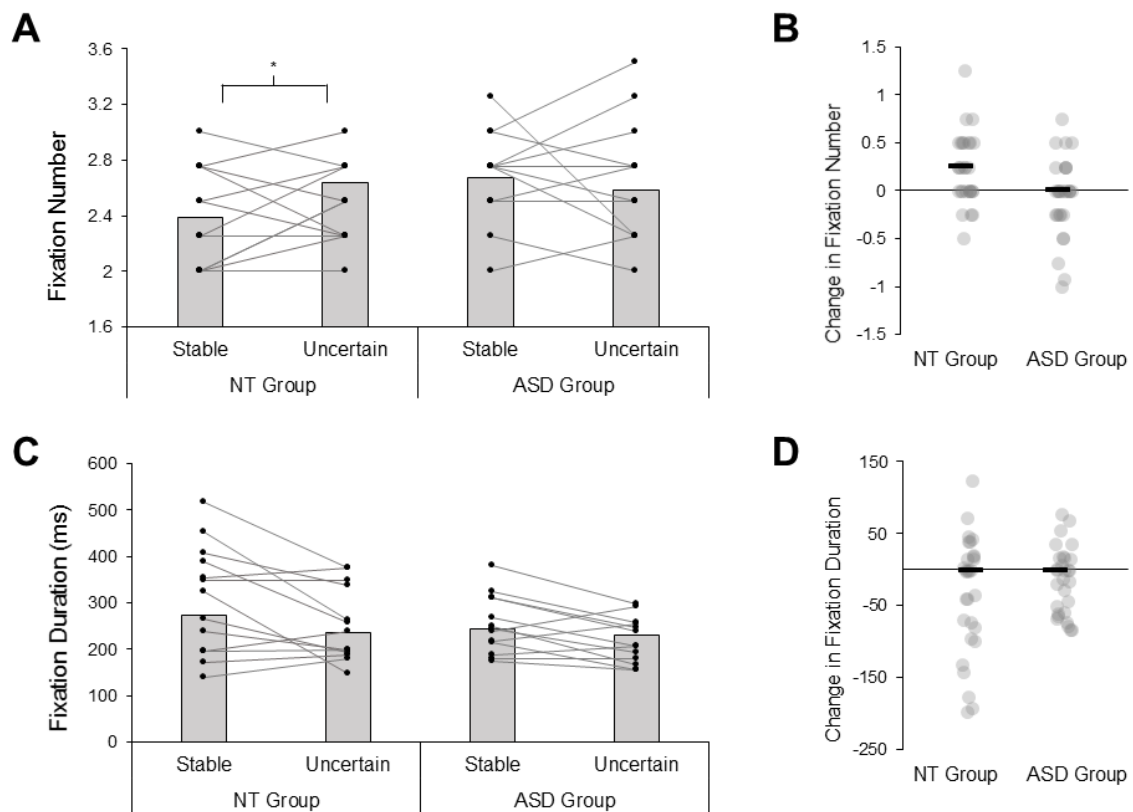
**Supplementary Figure 1.** Changes in Maximum Lift Velocity (MLV; **A**) from the final ‘Baseline’ trial to the initial ‘Heavy-Small’ trial, and scatter plot highlighting the relationship between Autistic Quotient scores and the magnitude of these changes (**B**). \*Denotes significant difference between trials ( $t(73) = 6.30$ ,  $p < .001$ ,  $BF_{10} = 6.11 \times 10^5$ ).

## Supplementary Analysis II

In *Experiment two*, the ASD group appeared to display reduced uncertainty-related increases in gaze search rate compared to their matched NT counterparts (Figure 4). Such gaze adjustments also correlate with levels of autistic-like traits in both general (Arthur *et al.*, 2019) and clinically-diagnosed populations (Experiment two). Therefore, although these context-sensitive visual sampling effects should currently be interpreted with caution (see *main discussion*), they reinforce recent calls for future investigation (Palmer *et al.*, 2017).

To assist in future research development, we inspected the raw fixation data obtained in Experiment two, examining whether observed changes in search rate resulted from: a) an increase in fixation frequency and/or b) a shortening of fixation durations. Separate ANOVA's were conducted, with both fixation number and duration entered as dependent variables. Significant group-by-condition interaction effects occurred for fixation number ( $F(1,50) = 7.73$ ;  $p = .01$ ;  $\eta p^2 = .13$ ;  $BF_{10} = 4.03$ ) but not duration ( $F(1,50) = 1.20$ ;  $p = .28$ ;  $\eta p^2 = .02$ ;  $BF_{10} = 0.61$ ). As illustrated in Supplementary Figure 2, NT participants showed significant increases in the number of fixations between 'stable' and 'uncertain' trials ( $p = .003$ ;  $BF_{10} = 15.03$ ), whereas minimal changes were displayed by ASD participants ( $p = .46$ ;  $BF_{10} = 0.27$ ).

These increases in fixation frequency likely reflect an increased sampling of object-specific information, as this represented a goal-relevant, uncertain stimuli in this task. This assumption was reinforced upon visual inspection of the gaze data, where almost all fixations were directed towards goal-relevant cues (i.e., the object and lifting platform; *Supplementary Video II*). However, to specifically test this hypothesis, we examined the proportion of fixations made to the object and platform in each trial. Such analysis was performed for the NT group only (using Pupil Player software; Kassner *et al.*, 2014), with any task-irrelevant fixation trials (0.02%) excluded. As predicted, NT subjects showed greater object-directed fixations between stable and uncertain trials ( $t(25) = 3.32$ ;  $p = .003$ ,  $BF_{10} = 14.04$ ), but non-significant differences for platform-directed fixations ( $t(25) = .23$ ;  $p = .82$ ,  $BF_{10} = 0.21$ ).



**Supplementary Figure 2.** Changes in average gaze fixation number (A, B) and duration (C, D) between stable (Baseline lifts 2–5) and uncertain (initial ‘test’ lifts) trial conditions for Neurotypical (NT) and Autism (ASD) groups. Bars represent group averages, lines and circles represent individual cases. \*denotes significant difference between conditions ( $p < 0.01$ ).

Together, this analysis illustrates the divergent visual sampling behaviours shown between NT and ASD participants in Experiment two. Specifically, while ASD participants did not distinguish between ‘stable’ and ‘uncertain’ trials in their gaze behaviours, NT participants showed an increase in the number of short, object-directed fixations. This adaptation may reflect an increased sampling of uncertain sensory information, and should thus be examined further in future investigations.

## References

- Adams RA, Shipp S, Friston KJ. Predictions not commands: active inference in the motor system. *Brain Structure and Function* 2013; 218: 611-643.
- Allen G, Courchesne E. Differential effects of developmental cerebellar abnormality on cognitive and motor functions in the cerebellum: an fMRI study of autism. *American Journal of Psychiatry* 2003; 160: 262-273.
- Arthur T, Vine S, Brosnan M, Buckingham G. Exploring how material cues drive sensorimotor prediction across different levels of autistic-like traits. *Experimental Brain Research* 2019; 237: 2255–2267.
- Association AP, editors. *Diagnostic and statistical manual of mental disorders (DSM-V)*. Washington DC: American Psychiatric Association; 2013.
- Baron-Cohen S, Wheelwright S, Skinner R, Martin J, Clubley E. The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders* 2001; 31: 5-17.
- Berument SK, Rutter M, Lord C, Pickles A, Bailey A. Autism screening questionnaire: diagnostic validity. *The British Journal of Psychiatry* 1999; 175: 444-451.
- Brandwein AB, Foxe JJ, Butler JS, Frey H-P, Bates JC, Shulman LH, et al. Neurophysiological indices of atypical auditory processing and multisensory integration are associated with symptom severity in autism. *Journal of Autism and Developmental Disorders* 2015; 45: 230-244.
- Brayanov JB, Smith MA. Bayesian and “anti-Bayesian” biases in sensory integration for action and perception in the size–weight illusion. *Journal of Neurophysiology* 2010; 103: 1518-1531.
- Buckingham G. Getting a grip on heaviness perception: a review of weight illusions and their probable causes. *Experimental Brain Research* 2014; 232: 1623-1629.
- Buckingham G, Goodale MA. Size matters: a single representation underlies our perceptions of heaviness in the size-weight illusion. *PLoS One* 2013; 8: e54709.
- Buckingham G, Michelakakis EE, Rajendran G. The influence of prior knowledge on perception and action: relationships to autistic traits. *Journal of Autism and Developmental Disorders* 2016; 46: 1716-1724.

- Cashaback JG, McGregor HR, Pun HC, Buckingham G, Gribble PL. Does the sensorimotor system minimize prediction error or select the most likely prediction during object lifting? *Journal of Neurophysiology* 2017; 117: 260-274.
- Charpentier A. Analyse experimentale de quelques elements de la sensation de poids. *Archive de Physiologie Normale et Pathologiques* 1891; 3: 122-135.
- Chouinard PA, Leonard G, Paus T. Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *Journal of Neuroscience* 2005; 25: 2277-2284.
- Dichter GS, Felder JN, Bodfish JW. Autism is characterized by dorsal anterior cingulate hyperactivation during social target detection. *Social Cognitive and Affective Neuroscience* 2009; 4: 215-226.
- Ewbank MP, Rhodes G, von dem Hagen EA, Powell TE, Bright N, Stoyanova RS, et al. Repetition suppression in ventral visual cortex is diminished as a function of increasing autistic traits. *Cerebral Cortex* 2014; 25: 3381-3393.
- Fatemi SH, Halt AR, Realmuto G, Earle J, Kist DA, Thuras P, et al. Purkinje cell size is reduced in cerebellum of patients with autism. *Cellular and Molecular Neurobiology* 2002; 22: 171-175.
- Fiehler K, Brenner E, Spering M. Prediction in goal-directed action. *Journal of Vision* 2019; 19: 10-10.
- Fooken J, Spering M. Eye movements as a readout of sensorimotor decision processes. *bioRxiv* 2019: 785832.
- Foster NC, Bennett SJ, Causer J, Elliott D, Bird G, Hayes SJ. Getting off to a shaky start: specificity in planning and feedforward control during sensorimotor learning in autism spectrum disorder. *Autism Research* 2019: 10.1002/aur.2214.
- Fournier KA, Hass CJ, Naik SK, Lodha N, Cauraugh JH. Motor coordination in autism spectrum disorders: a synthesis and meta-analysis. *Journal of Autism and Developmental Disorders* 2010; 40: 1227-1240.
- Friston K. The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience* 2010; 11: 127-138.
- Friston KJ. A theory of cortical responses. *Philosophical transactions of the Royal Society B: Biological sciences* 2005; 360: 815-836.
- Friston KJ, Lawson R, Frith CD. On hyperpriors and hypopriors: comment on Pellicano and Burr. *Trends in Cognitive Sciences* 2013; 17: 1.

- Gidley-Larson JC, Bastian AJ, Donchin O, Shadmehr R, Mostofsky SH. Acquisition of internal models of motor tasks in children with autism. *Brain* 2008; 131: 2894-2903.
- Gidley Larson J, Mostofsky S. Motor deficits in autism. In: editors. *Autism: A neurological disorder of early brain development*. London: Mac Keith Press; 2006. 231-247.
- Gordon AM, Forssberg H, Johansson RS, Westling G. Visual size cues in the programming of manipulative forces during precision grip. *Experimental Brain Research* 1991; 83: 477-482.
- Gowen E, Hamilton AFdC. Motor abilities in autism: a review using a computational context. *Journal of Autism and Developmental Disorders* 2013; 43: 323-344.
- Hadjiosif AM, Smith MA. Flexible control of safety margins for action based on environmental variability. *Journal of Neuroscience* 2015; 35: 9106-9121.
- Haker H, Schneebeli M, Stephan KE. Can Bayesian theories of autism spectrum disorder help improve clinical practice? *Frontiers in Psychiatry* 2016; 7: **1-17**.
- Happé F, Frith U. The weak coherence account: detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders* 2006; 36: 5-25.
- Hayhoe MM, Matthis JS. Control of gaze in natural environments: effects of rewards and costs, uncertainty and memory in target selection. *Interface focus* 2018; 8: 20180009.
- Hollander E, Anagnostou E, Chaplin W, Esposito K, Haznedar MM, Licalzi E, et al. Striatal volume on magnetic resonance imaging and repetitive behaviors in autism. *Biological Psychiatry* 2005; 58: 226-232.
- Holm S. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 1979: 65-70.
- Jarrold C, Brock J. To match or not to match? Methodological issues in autism-related research. *Journal of Autism and Developmental Disorders* 2004; 34: 81-86.
- Jasmin E, Couture M, McKinley P, Reid G, Fombonne E, Gisel E. Sensori-motor and daily living skills of preschool children with autism spectrum disorders. *Journal of Autism and Developmental Disorders* 2009; 39: 231-241.
- Jenmalm P, Schmitz C, Forssberg H, Ehrsson HH. Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. *Journal of Neuroscience* 2006; 26: 9015-9021.
- Johansson RS, Westling G. Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research* 1988; 71: 59-71.

- Johansson RS, Westling G, Bäckström A, Flanagan JR. Eye–hand coordination in object manipulation. *Journal of Neuroscience* 2001; 21: 6917-6932.
- Kassner M, Patera W, Bulling A. (2014). *Pupil: an open source platform for pervasive eye tracking and mobile gaze-based interaction*. Paper presented at the Adjunct Proceedings of the 2014 ACM International Joint Conference on Pervasive and Ubiquitous Computing (UbiComp).
- Körding KP, Beierholm U, Ma WJ, Quartz S, Tenenbaum JB, Shams L. Causal inference in multisensory perception. *PLoS one* 2007; 2: e943.
- Kwon O-S, Knill DC. The brain uses adaptive internal models of scene statistics for sensorimotor estimation and planning. *Proceedings of the National Academy of Sciences* 2013; 110: E1064-E1073.
- Land MF. Vision, eye movements, and natural behavior. *Visual Neuroscience* 2009; 26: 51-62.
- Landry O, Chouinard PA. Why we should study the broader autism phenotype in typically developing populations. *Journal of Cognition and Development* 2016; 17: 584-595.
- Lawson RP, Mathys C, Rees G. Adults with autism overestimate the volatility of the sensory environment. *Nature Neuroscience* 2017; 20: 1293-1299.
- Lawson RP, Rees G, Friston KJ. An aberrant precision account of autism. *Frontiers in Human Neuroscience* 2014; 8: 302.
- MacDonald M, Lord C, Ulrich D. The relationship of motor skills and adaptive behavior skills in young children with autism spectrum disorders. *Research in Autism Spectrum Disorders* 2013; 7: 1383-1390.
- Maiello G, Paulun VC, Klein LK, Fleming RW. The sequential-weight illusion. *i-Perception* 2018; 9.
- Maloney LT, Zhang H. Decision-theoretic models of visual perception and action. *Vision Research* 2010; 50: 2362-2374.
- Mosconi MW, Luna B, Kay-Stacey M, Nowinski CV, Rubin LH, Scudder C, et al. Saccade adaptation abnormalities implicate dysfunction of cerebellar-dependent learning mechanisms in autism spectrum disorders (ASD). *PLoS One* 2013; 8: e63709.
- Mostofsky SH, Bunoski R, Morton SM, Goldberg MC, Bastian AJ. Children with autism adapt normally during a catching task requiring the cerebellum. *Neurocase* 2004; 10: 60-64.

- Mostofsky SH, Powell SK, Simmonds DJ, Goldberg MC, Caffo B, Pekar JJ. Decreased connectivity and cerebellar activity in autism during motor task performance. *Brain* 2009; 132: 2413-2425.
- Murray NP, Janelle CM. Anxiety and performance: A visual search examination of the processing efficiency theory. *Journal of Sport and Exercise Psychology* 2003; 25: 171-187.
- Organisation WH, editors. *The ICD-10 Classification of Mental and Behavioural Disorders - Clinical Descriptions and Diagnostic Guidelines*. . Geneva: WHO; 2012.
- Ozonoff S, McEvoy RE. A longitudinal study of executive function and theory of mind development in autism. *Development and Psychopathology* 1994; 6: 415-431.
- Palmer CJ, Lawson RP, Hohwy J. Bayesian approaches to autism: Towards volatility, action, and behavior. *Psychological Bulletin* 2017; 143: 521.
- Palmer CJ, Paton B, Kirkovski M, Enticott PG, Hohwy J. Context sensitivity in action decreases along the autism spectrum: a predictive processing perspective. *Proceedings of the Royal Society B: Biological sciences* 2015; 282: 1-9.
- Pellicano E, Burr D. When the world becomes ‘too real’: a Bayesian explanation of autistic perception. *Trends in Cognitive Sciences* 2012; 16: 504-510.
- Ruzich E, Allison C, Smith P, Watson P, Auyeung B, Ring H, et al. Measuring autistic traits in the general population: a systematic review of the Autism-Spectrum Quotient (AQ) in a nonclinical population sample of 6,900 typical adult males and females. *Molecular autism* 2015; 6: 1-12.
- Sasson NJ, Elison JT, Turner-Brown LM, Dichter GS, Bodfish JW. Brief report: Circumscribed attention in young children with autism. *Journal of Autism and Developmental Disorders* 2011; 41: 242-247.
- Sasson NJ, Turner-Brown LM, Holtzclaw TN, Lam KS, Bodfish JW. Children with autism demonstrate circumscribed attention during passive viewing of complex social and nonsocial picture arrays. *Autism Research* 2008; 1: 31-42.
- Schanding GT, Nowell KP, Goin-Kochel RP. Utility of the social communication questionnaire-current and social responsiveness scale as teacher-report screening tools for autism spectrum disorders. *Journal of Autism and Developmental Disorders* 2012; 42: 1705-1716.
- Scharoun SM, Wright KT, Robertson-Wilson JE, Fletcher PC, Bryden PJ. Physical Activity in Individuals with Autism Spectrum Disorders (ASD): A Review. In: editors. *Autism-Paradigms, Recent Research and Clinical Applications*. InTech; 2017.



- Schmitz C, Martineau J, Barthélémy C, Assaiante C. Motor control and children with autism: deficit of anticipatory function? *Neuroscience letters* 2003; 348: 17-20.
- Schuwerk T, Sodian B, Paulus M. Cognitive mechanisms underlying action prediction in children and adults with autism spectrum condition. *Journal of Autism and Developmental Disorders* 2016; 46: 3623-3639.
- Shipp S, Adams RA, Friston KJ. Reflections on agranular architecture: predictive coding in the motor cortex. *Trends in Neurosciences* 2013; 36: 706-716.
- Simonoff E, Pickles A, Charman T, Chandler S, Loucas T, Baird G. Psychiatric disorders in children with autism spectrum disorders: prevalence, comorbidity, and associated factors in a population-derived sample. *Journal of the American Academy of Child & Adolescent Psychiatry* 2008; 47: 921-929.
- Sinha P, Kjelgaard MM, Gandhi TK, Tsourides K, Cardinaux AL, Pantazis D, et al. Autism as a disorder of prediction. *Proceedings of the National Academy of Sciences* 2014; 111: 15220-15225.
- Stevenson IH, Fernandes HL, Vilares I, Wei K, Körding KP. Bayesian integration and non-linear feedback control in a full-body motor task. *PLoS Computational Biology* 2009; 5: e1000629.
- Sturm A, Kuhfeld M, Kasari C, McCracken JT. Development and validation of an item response theory-based Social Responsiveness Scale short form. *Journal of Child Psychology and Psychiatry* 2017; 58: 1053-1061.
- Sutera S, Pandey J, Esser EL, Rosenthal MA, Wilson LB, Barton M, et al. Predictors of optimal outcome in toddlers diagnosed with autism spectrum disorders. *Journal of Autism and Developmental Disorders* 2007; 37: 98-107.
- Tewelde FG, Bishop DV, Manning C. Visual motion prediction and verbal false memory performance in autistic children. *Autism Research* 2018; 11: 509-518.
- Tong MH, Zohar O, Hayhoe MM. Control of gaze while walking: task structure, reward, and uncertainty. *Journal of Vision* 2017; 17: 28-28.
- Van de Cruys S, Evers K, Van der Hallen R, Van Eylen L, Boets B, de-Wit L, et al. Precise minds in uncertain worlds: Predictive coding in autism. *Psychological Review* 2014; 121: 649.
- Villalobos ME, Mizuno A, Dahl BC, Kemmotsu N, Müller R-A. Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. *Neuroimage* 2005; 25: 916-925.

- von Hofsten C, Uhlig H, Adell M, Kochukhova O. How children with autism look at events. *Research in Autism Spectrum Disorders* 2009; 3: 556-569.
- White SW, Oswald D, Ollendick T, Scahill L. Anxiety in children and adolescents with autism spectrum disorders. *Clinical Psychology Review* 2009; 29: 216-229.
- Wilson MR, Miles CA, Vine SJ, Vickers JN. Quiet eye distinguishes children of high and low motor coordination abilities. *Medicine & Science in Sports & Exercise* 2013; 45: 1144-1151.
- Wolpert DM, Landy MS. Motor control is decision-making. *Current Opinion in Neurobiology* 2012; 22: 996-1003.
- Yu A, Dayan P. Uncertainty, neuromodulation, and attention. *Neuron* 2003; 46: 681-692.

## Figure Legends

**Figure 1.** The experimental set-up for object lifting trials (a), the four ‘test’ objects lifted by participants (b), and a schematic overview of the testing session (c). Objects were concealed by a manual clapper-board prior to each trial. Following an auditory tone (trial onset), participants reached and lifted objects with their thumb and forefinger to a comfortable height above the table. Objects were held steady until hearing a second auditory tone (trial offset), before being placed back on the platform. These procedures were repeated for ‘baseline’ and subsequent ‘test’ trials, where various prediction-related sensorimotor measures were obtained. See Supplementary Video 1 for illustration of this protocol (available at: <https://osf.io/p52h8/>).

**Figure 2.** Scatter plots highlighting associations between autistic-like traits (AQ scores) and the magnitude of the perceptual Size-Weight Illusion (SWI; **A**), prediction-related differences in peak Grip Force Rate (pGFR; **B**) and peak Load Force Rate (pLFR; **C**) in Experiment one. No significant relationships emerged (all  $p > 0.05$ ).

**Figure 3.** Trial-by-trial averages ( $\pm$  SEM) for normalised perceived heaviness ratings (A-B), peak grip force rate (pGFR; C-D), and peak load force rate (pLFR; E-F) in *Experiment Two*. Filled circles represent Neurotypical (NT) values, empty circles represent autistic group (ASD) values.

**Figure 4.** Changes in gaze search rate between stable (Baseline lifts 2–5) and uncertain (initial ‘test’ lifts) trial conditions for Neurotypical (NT) and Autism (ASD) groups. Bars represent group averages, lines and circles represent individual cases. \*denotes significant difference between conditions ( $p < 0.01$ ).