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Movement under uncertainty: The effects of the rubber-hand illusion vary along the
nonclinical autism spectrum.

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Abstract

Recent research has begun to investigate sensory processing in relation to nonclinical variation in traits associated with the autism spectrum disorders (ASD). We propose that existing accounts of autistic perception can be augmented by considering a role for individual differences in top-down expectations for the precision of sensory input, related to the processing of state-dependent levels of uncertainty. We therefore examined ASD-like traits in relation to the rubber-hand illusion: an experimental paradigm that typically elicits crossmodal integration of visual, tactile, and proprioceptive information in an unusual illusory context. Individuals with higher ASD-like traits showed reduced effects of the rubber-hand illusion on perceived arm position and reach-to-grasp movements, compared to individuals with lower ASD-like traits. These differences occurred despite both groups reporting the typical subjective experience of the illusion concerning visuotactile integration and ownership for the rubber hand. Together these results suggest that the integration of proprioceptive information with cues for arm position derived from the illusory context differs between individuals partly in relation to traits associated with ASD. We suggest that the observed differences in sensory integration can be best explained in terms of differing expectations regarding the precision of sensory estimates in contexts that suggest uncertainty.

Keywords

Rubber hand illusion; sensory integration; uncertainty; expected sensory precision; movement; autistic traits.

1. Introduction

Autism spectrum disorders (ASD) frequently involve atypical sensory processing in both childhood and adulthood (reviewed in Iarocci & McDonald, 2006; Marco, Hinkley, Hill, & Nagarajan, 2011; Simmons et al., 2009). The upcoming fifth edition of the Diagnostic and Statistical Manual of Mental Disorders will for the first time include sensory dysfunction as a diagnostic criterion for ASD (i.e., “hyper- or hyporeactivity to sensory input or unusual interest in sensory aspects of the environment,” American Psychiatric Association, 2013), calling attention to the need to advance our understanding in this area. To understand the nature of ASD and to throw light on individual differences in perception more generally, it is also important to explore the extent to which the relevant underlying sensory mechanisms vary in the general population.

This broader focus of research originates from evidence that ASD-like traits vary meaningfully amongst nonclinical individuals, with those meeting a clinical diagnosis of ASD situated at the extreme end of a spectrum that encompasses the population at large (reviewed in Happé, Ronald, & Plomin, 2006; Mandy & Skuse, 2008). The distribution of scores typically found for measures of ASD-like traits in large general population samples tends to be compatible with this hypothesis (e.g., Constantino & Todd, 2003; Posserud, Lundervold, & Gillberg, 2006), and correlations between ASD-like traits and sensory task performance in non-clinical samples are consistent with sensory differences seen in clinically-diagnosed ASD (e.g., Donohue, Darling, & Mitroff, 2012; Walter, Dasonville, & Bochsler, 2009). A similar technique used to investigate phenomena related to ASD is the group comparison of nonclinical individuals scoring high on trait measures of ASD to those scoring lower. This approach has also revealed sensory differences (Grinter, Maybery, et al., 2009; Grinter, Van Beek, Maybery, & Badcock, 2009) and neurophysiological response characteristics (Puzzo, Cooper, Vetter, & Russo, 2010) associated with ASD-like traits consistent with that seen in clinically-diagnosed ASD, and this method is employed in the present study.

Contemporary theories of perception in ASD propose fundamental differences in the processing of sensory information to account for a complex pattern of strengths and weaknesses observed across different perceptual-cognitive tasks and contexts (e.g., Brock, Brown, Boucher, & Rippon, 2002; U. Frith, 1989; Happé & U. Frith, 2006; Mottron, Dawson, Soulières, Hubert, & Burack, 2006; Plaisted, O'Riordan, & Baron-Cohen, 1998). A theme underlying parts of this discussion, in particular the weak central coherence theory (U. Frith, 1989; Happé & U. Frith, 2006), is the neurocognitive distinction between the contribution of bottom-up sensory processing to perception (relating most directly to sensory input) and the top-down modulation of input based on endogenous factors such as prior knowledge and attention (C. Frith & Dolan, 1997; Gilbert & Sigman, 2007; Kveraga, Ghuman, & Bar, 2007). More recent Bayesian accounts develop this point in relation to ASD explicitly: for example, Pellicano and Burr (2012) suggest that prior expectations regarding the state of the world may have diminished influence on perception in ASD, increasing reliance on bottom-up signals (for discussion and related proposals, see Brock, 2012; Friston et al., 2013; Hohwy, in press; Mitchell & Ropar, 2004; Paton et al., 2012; van Boxtel & Lu, 2013).

An important challenge for these accounts is the uneven landscape of enhanced and compromised perceptual performance in ASD, which does not cohere clearly with a general bias in top-down processes. For example, for visual illusions, some, but not all, studies have suggested less susceptibility (that is, increased veridical perception) in ASD (Bölte, Holtmann, Poustka, Scheurich, & Schmidt, 2007; Happé, 1996; Hoy, Hatton, & Hare, 2004; Ropar & Mitchell, 1999, 2001; Walter et al., 2009). Similarly, whereas a general impairment in top-down modulation would seem to predict diminished multisensory integration in ASD, studies do not unequivocally support this, even though there are a number of intriguing underlying differences (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012; Kwakye, Foss-Feig, Cascio, Stone, & Wallace, 2011; Paton, Hohwy, & Enticott, 2012; reviewed in Marco et al., 2011).

We reasoned that uneven performance could relate to differences in the way context determines the *expected levels of sensory precision*, which is an aspect of top-down modulation that has only recently been described (Feldman & Friston, 2010) and

linked to ASD in the context of predictive coding models of perception (Friston, Lawson, & C. Frith, 2013; Paton et al., 2012). Conceptually, expectations regarding the precision of sensory input are of importance to the relative weighting of bottom-up and top-down perceptual processes in response to state-dependent (i.e., changing) levels of uncertainty. This proposal therefore predicts that differences will become apparent in contexts and experimental set-ups where changing conditions suggest changing levels of uncertainty in the sensory signal. In particular, individuals with ASD, as well as nonclinical individuals with ASD-like traits, may be less sensitive than individuals with few ASD-like traits to contexts that suggest increased uncertainty. This would predict that in contexts that suggest low uncertainty (i.e., high precision of sensory input) there would be less difference between the groups, but that in contexts that suggest higher uncertainty (i.e., suggests low precision of sensory input) differences would begin to emerge. Sometimes these differences would give rise to enhanced performance of the ASD and ASD-like groups, namely when the expectation for high precision input leads to increased sensory sampling and less integration under prior expectations relevant to the context. Sometimes this would lead to compromised performance for these groups, namely when expectation for high precision leads to blindness to underlying patterns of hidden, influencing factors.

We therefore explore this proposal in relation to the rubber-hand illusion (Botvinick & Cohen, 1998), a well-studied experimental paradigm involving multisensory interactions in relation to the neural representation of body location. Here, repetitive tactile stimulation is applied synchronously to the participant's hand (hidden from view) and a fake rubber hand (that lies in view). This pattern of sensory input typically induces the illusory sensation that touch is felt on the surface of the rubber hand, as well as a heightened sense of ownership for the rubber hand (see Ehrsson, 2012, for review). The integration between visual and tactile sensory inputs is also associated with a measurable drift in perceived hand location towards the rubber hand (Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005) and subtle changes in subsequent reaching movements performed with the stimulated hand (e.g., Kammers, Kootker, Hogendoorn, & Dijkerman, 2010). Importantly, these phenomena tend to exist specifically when the seen and felt touch are applied synchronously, and are reduced for asynchronous stimulation. This paradigm therefore involves both sensory

integration under different global causal models and, also, a highly unusual, uncertainty-inducing context of experiencing touch on a rubber hand.

As described above, the rubber-hand illusion should be expected to trigger differences in expected precisions of visual, tactile and proprioceptive sensory input. Our previous study of this illusion (Paton et al., 2012) compared a clinical ASD group with healthy controls and found differences in proprioception and motor parameters on a reach task. Following the results of this study, we expect that participants will experience the typical subjective effects of the illusion (e.g., that touch is mislocated to the rubber hand) regardless of their level of ASD-like traits, and thus rate the strength of these effects, as assessed via questionnaire, stronger during synchronous than asynchronous stimulation. We further predict that individuals with ASD-like traits will show less sensitivity to the presence of the illusion in their perceived arm position than individuals low on ASD-like traits (i.e., less of a difference in proprioceptive drift between synchronous and asynchronous stimulation conditions). This hypothesis is based on the notion of lower sensitivity to state-dependent uncertainty in individuals with ASD-like traits, and coheres with the previous finding of more accurate proprioception in individuals with ASD compared to controls (Paton et al., 2012).

In addition, it is predicted that reaching movements performed subsequent to the illusion will reflect the uncertainty suggested by the unusual illusory content. This latter hypothesis is based on the idea that expectations regarding the precision of sensory (proprioceptive) input occurring as movement unfolds affect how smoothly movement is performed. In short, if proprioceptive imprecision is expected, movement should be uncertain, exploratory, and tentative (*cf.* Friston, Daunizeau, Kilner, & Kiebel, 2010). Specifically, we expect that individuals with low ASD-like traits will exhibit less smooth movement after experiencing the illusion than individuals with high ASD-like traits. Higher order temporal derivatives of position (e.g., jerk) are of interest to this hypothesis due to their relationship with movement smoothness. Our previous study, which found differences between clinical ASD and control participants in the acceleration of reaching movements performed following the illusion, was unable to assess comprehensively differences in movement (such as

smoothness) due to limits of the tracking technique used. The current study therefore extends previous findings to a nonclinical sample of individuals with and without ASD-like traits and asks, in particular, whether the differences in motor parameters could pertain to differences in expected precisions.

2. Method

2.1. Participants

Twenty-four right-handed individuals ($M = 28.96$, $SD = 11.16$ years; 13 female) completed the experiment. Volunteers were recruited via advertisements distributed to the general Monash University population. Participants were separated into two groups based on a median-split of their scores on the Autism-Spectrum Quotient (AQ, described below; whole sample: $M = 116.33$, $SD = 14.47$; low AQ group: $M = 104.58$, $SD = 8.95$; high AQ group: $M = 128.08$, $SD = 7.5$). Note that, while the present study used Likert scoring for the AQ, values for the AQ using binary scoring are as follows: whole sample, $M = 21.33$, $SD = 6.83$; low AQ group, $M = 16$, $SD = 3.84$; high AQ group, $M = 26.67$, $SD = 4.56$. Each group contained 12 participants (low AQ group: $M = 32.42$, $SD = 13.98$ years, 7 female; high AQ group: $M = 25.50$, $SD = 6.26$ years, 6 female). The study was approved by the Monash University Human Research Ethics Committee. All participants provided written informed consent.

2.2. Materials and Procedure

Participants were seated in accordance with the experimental set-up illustrated in Figure 1.

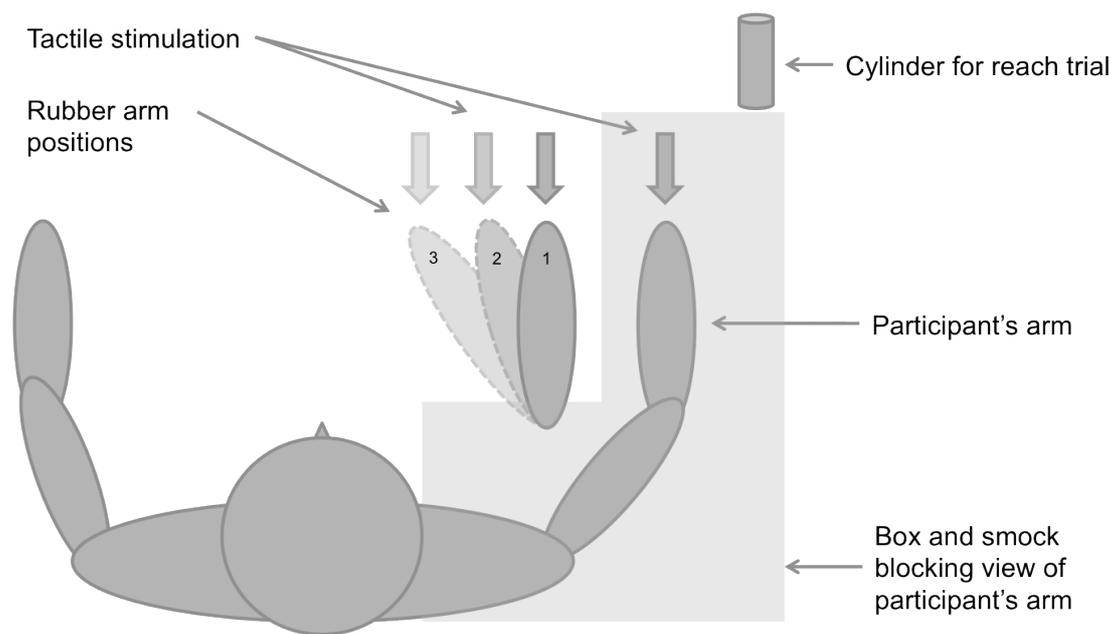


Fig. 1 Experimental set-up. The rubber arm and participant's right arm were placed in separate compartments. A prosthetic right limb was used with a high degree of visual similarity to a human limb regarding physical dimensions, skin detail, and compression to touch. A semi-silvered mirror lid enabled the experimenter to control the participant's vision into either compartment via adjustment of the lighting inside. Participants were able to see the rubber arm only during the stimulation phase of each trial. The participant's own arm was occluded from view throughout the experiment. The cylindrical reach target was only visible during the reaching phase of each trial.

2.2.1. Independent variables

The position of the rubber arm was varied between three positions across trials. Synchronous and asynchronous tactile stimulation was delivered independently for each position of the rubber arm. Trials were conducted in two blocks, each comprised of a single trial for each of the six conditions. Participants therefore completed two trials for each of the six conditions, and dependent measures were averaged across

these two trials. To control for order effects, trial order was randomised for each block across participants. The duration of the experiment was 90–120 min.

2.2.1.1. Stimulation type. An experimenter seated opposite to the participant manually applied repetitive tactile stimulation to anatomically corresponding locations of the participant's right hand and the rubber arm. Stimulation was applied at approximately 1–2 Hz for 3 min in each trial with a pair of small paintbrushes (2–2.5 x 0.5 cm brush area). Trials involved either synchronous or asynchronous stimulation for the entire period. Asynchronous tactile stimulation is typically used as a control condition in rubber-hand illusion studies, as temporal synchronicity between the seen and felt touch is associated with significantly stronger perceptual effects (Botvinick & Cohen, 1998; estimated as best within approximately 300 ms, Shimada, Fukuda, & Hiraki, 2009). Stimulation during the asynchronous condition was both temporally and spatially asynchronous. Participants were directed to attend to the rubber hand during the stimulation period.

2.2.1.2. Rubber arm position. The participant's arm rested in the same position for every condition. The rubber arm was varied between three positions such that the horizontal distance separating the middle finger of each hand was 20 cm, 25 cm, or 30 cm (numbered 1–3 in in Fig 1, and referred to as positions 1–3 henceforth). The orientation of the rubber arm changed between each position such that the end proximal to the participant always entered the box in line with the participant's right shoulder. This was intended to maintain anatomical plausibility for ownership of the rubber arm across conditions, which is a known constraint on illusion induction (Ehrsson et al., 2004; Pavani et al., 2000; Tsakiris & Haggard, 2005). The orientation of tactile stimulation on the rubber hand was adjusted across positions to maintain congruency in the direction of stimulation applied to the real and rubber hands in a hand-centred reference frame (see Costantini & Haggard, 2007, for an investigation of orientation mismatch in hand-centred versus external space reference frames).

Anatomical congruence between the placement of the rubber arm and the position of the real arm has been shown to influence the strength of the rubber-hand illusion (Costantini & Haggard, 2007; Ehrsson, Spence, & Passingham, 2004; Ide, 2013;

Lloyd, 2007; Pavani, Spence, & Driver, 2000; Tsakiris & Haggard, 2005; see also White & Aimola Davies, 2011). These findings may relate to expected precisions, in as much as different positions of the (real) arm have been shown to have different proprioceptive precisions (van Beers et al., 1998). The effects of manipulating rubber arm position is of interest in relation to examining the influence of top-down processes on the illusory experience; for example, top-down processes comparing expectations regarding body position to that of the rubber arm (Tsakiris & Haggard, 2005). Increasing the distance of the rubber arm from the real arm was expected to decrease the self-rated strength of the illusion, as has been found previously in a nonclinical sample (Lloyd, 2007). We further hypothesised that individuals with stronger ASD-like traits may be less sensitive to changes in the anatomical congruence between the real and rubber arms than individuals with lower ASD-like traits, due to a lesser influence of top-down processes on perception. We therefore expected the latter group to be more likely to show differences in self-rated illusion strength and proprioceptive drift between the rubber arm positions during synchronous stimulation.

2.2.2. Dependent measures

Several dependent measures were collected in each trial to capture perceptual and sensorimotor effects of the rubber-hand illusion. Estimates of arm location were recorded directly before and after each stimulation period. A reach-to-grasp movement was conducted following the post-stimulation estimate of arm location. At the end of each trial, participants completed a questionnaire related to their subjective experience of the illusion. A psychological inventory designed to assess ASD-like traits (the AQ) was completed during a break midway through the twelve trials of the rubber hand illusion.

2.2.2.1. Illusion ratings. Participants completed a short questionnaire to report on their experiences during tactile stimulation. This consisted of 11 items displayed in Table 1, adapted from Botvinick and Cohen (1998; I1–I3, C2, C4, C5), Longo, Schuur, Kammers, Tsakiris, and Haggard (2008; C6, C7), Petkova and Ehrsson (2008; C3), and Hohwy and Paton (2010; C1, C8). Three items (I1–I3) were

statements describing the content of the illusion typically reported in the literature. Eight items (C1–C8) were included to control for response biases, and described possible experiences that were not expected to differ consistently between synchronous and asynchronous stimulation. Each item was rated on a 20 cm horizontal visual analogue scale with left and right endpoints marked as *strongly disagree* and *strongly agree*, respectively. The centre of the scale was labelled *very unsure whether agree or disagree*. Participants could mark the scale anywhere along its length, and markings were scored to the nearest millimetre. Greater values indicated stronger agreement with the statement. Items were presented in a fixed order across trials and in pen-and-paper format. Participants were required to remove their right arm from the box when completing this measure to help disrupt the effects of the illusion between trials.

Table 1 Self-rated illusion questionnaire.

Item type	No.	Text
Illusion	I1	It seemed as if I was feeling the touch of the paintbrush in the location where I saw the rubber hand being touched.
	I2	It seemed as though the touch I felt was caused by the paintbrush I could see touching the rubber hand.
	I3	It felt as if the rubber hand was my hand.
Control	C1	It felt as if my (real) hand was getting cold.
	C2	It seemed as if I might have more than one right hand or arm.
	C3	It seemed as if I was in two different locations at the same time.
	C4	It felt as if my (real) hand was turning 'rubbery'.
	C5	The rubber hand began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.
	C6	I found the touch of the paintbrush on my hand was pleasant.
	C7	I found myself liking the rubber hand.
	C8	I felt the room temperature change during the experiment.

2.2.2.2. *Proprioceptive drift*. Participants were asked to estimate the position of their visually occluded right hand directly before and after each period of stimulation. For this procedure the experimenter slid a plexiglass marker across a rail that ran

horizontally with respect to the participant along the top of the box. The participant verbally indicated when a vertical line on the marker was judged as being directly above the centre knuckle of their right hand. The location of the marker was recorded to the nearest millimetre via a fixed ruler (only visible to the experimenter) that spanned the length of the rail. Participants were unable to see either the rubber arm or their own arm during this stage of each trial, and were asked to keep their arm still to limit proprioceptive feedback. A measure of *proprioceptive drift* was calculated for each trial by subtracting the participant's pre-stimulation estimate of hand location from their post-stimulation estimate. Positive values indicate that the estimate of hand location was closer to the rubber arm following stimulation. As with questionnaire ratings, proprioceptive drift is a common measure of illusion induction (e.g., Botvinick & Cohen, 1998; Tsakiris & Haggard, 2005). There is evidence distinguishing the neural substrates (Brozzoli, Gentile, & Ehrsson, 2012; Ehrsson et al., 2004; Fiorio et al., 2011; Kammers, Verhagen, et al., 2009) and behavioural coincidence (Holmes, Snijders, & Spence, 2006; Rohde, Di Luca, & Ernst, 2011) of these measures, however, suggesting a distinction between the mechanisms underlying changes in perceived hand location and the subjective experience of ownership and tactile mislocation induced in the rubber-hand illusion set-up.

2.2.2.3. Reach-to-grasp movement. Following the post-stimulation estimate of hand location, participants were asked to reach out and grasp a cylinder with the hand involved in the stimulation period. The cylinder measured 4.5 cm diameter by 18 cm height and was located within the box 13 cm in front and 5 cm to the right of the participant's hand. Participants were able to see approximately the upper 2 cm of the cylinder during this phase of the experiment while both their arm and the rubber arm were occluded from view. Participants were instructed that they were not required to minimise their reaction time or maximize their speed of movement.

Hand trajectories were recorded using an electromagnetic tracker (Ascension Technology Corporation 3DGuidance trakSTAR with mid-range transmitter; 1.4 mm and 0.5 degrees static accuracy in an optimal environment). The six dimensions of translation and rotation were recorded via a magnetic sensor attached to the centre of the dorsal surface of the participant's right hand. These data were filtered with a 50

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Hz notch filter to remove AC line noise and a third order zero-phase low-pass Butterworth filter with a cutoff at 20 Hz.

Participants were instructed to begin the movement when a light was switched on to allow vision of the target object. Position data were recorded continuously (60 Hz sample rate) for 5 seconds following this point. In an adaptation of the method used by Kammers, de Vignemont, Verhagen, and Dijkerman (2009) and Kammers, Verhagen, et al. (2009), movement onset was defined as when velocity first exceeded 20 mm/s continuously for 0.05 seconds. Movement offset was defined as when velocity first exceeded 20 mm/s for 0.05 seconds when proceeding retrograde through the time series. Twelve trials were discarded due to recording malfunction or on account of the participant failing to execute the movement as instructed.

The kinematic parameter of primary interest was the normalised integrated jerk of the reaching movement. Jerk is the derivative of acceleration with respect to time (i.e., the third derivative of position, mm/s^3), and is commonly employed as a measure of movement smoothness (Hogan & Sternad, 2009). In the present study, integrated jerk was calculated as the area under the curve of the Euclidean jerk vector obtained from the three linear axes. Following previous research that has studied the jerk of voluntary movements in clinical populations, the integrated jerk for each trial was normalised for both movement extent and movement duration before undergoing analysis (Hogan & Sternad, 2009; Nobile et al., 2011; Romero, Van Gemmert, Adler, Bekkering, & Stelmach, 2003; Teulings, Contreras-Vidal, Stelmach, & Adler, 1997).

The present study also analysed several other kinematic parameters that have been examined in previous studies of reaching movement in the rubber-hand illusion (Kammers, de Vignemont, et al., 2009; Paton et al., 2012; Zopf, Truong, Finkbeiner, Friedman, & Williams, 2011). Movement duration is the time between movement onset and offset as defined above. Mean velocity is the mean of Euclidean velocity across the time series. Peak velocity is the maximum instantaneous Euclidean velocity recorded across the time series. Relative time to peak velocity is the time between movement onset and when peak velocity is achieved, as a percentage of total movement duration. Integrated acceleration was calculated from the recorded

trajectories as the area under the curve of the Euclidean acceleration vector. Peak horizontal displacement is the maximum of displacement in the horizontal dimension (with respect to the participant) in the direction towards the reach object and away from the rubber arm. Following Zopf et al. (2011), the angle of initial movement was calculated from the instantaneous velocity at the time point when 10% of the Euclidean displacement towards the end point was achieved. These latter two measures of hand displacement are of particular interest given that the rubber-hand illusion affects perceived hand position, which may be expected to influence the initial displacement of subsequent reaching movements towards a fixed target (Heed et al., 2011; Newport, Pearce, & Preston, 2010; Zopf et al., 2011). Hence, by analysing both displacement measures and other parameters (such as integrated jerk and movement duration) we hoped to distinguish to an extent between an effect of proprioceptive drift on subsequent reaching movements and other potential effects of the rubber-hand illusion on reaching movements.

2.2.2.4. *AQ*. The AQ is a self-administered and non-diagnostic 50-item questionnaire, designed to measure traits associated with ASD in adults (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001). The psychometric properties of this scale have received support for use in non-clinical participants with normal IQ (e.g., Baron-Cohen et al., 2001; Hurst, Mitchell, Kimbrel, Kwapil, & Nelson-Gray, 2007; Stewart, Watson, Allcock, & Yaqoob, 2009). Each item consists of a statement; for example, "I prefer to do things the same way over and over again". Participants rate their level of agreement with each statement on a 4-point Likert scale ('definitely agree', 'slightly agree', 'slightly disagree', 'definitely disagree') and responses are summed with 26 items reverse scored. The range of possible scores is 50–200, with higher scores indicating greater similarity to traits of ASD. This approach to scoring differs from the binary system used by Baron-Cohen et al. (2001). Likert scoring is preferred in the current study to increase sensitivity to individual differences between nonclinical participants. This method of scoring has been used previously for the AQ (e.g., Stewart et al., 2009), and there is evidence that Likert scoring is associated with improved psychometric properties compared to binary scoring for personality questionnaires (Muñiz, García-Cueto, & Lozano, 2005). In the present study, a pen-and-paper version of this scale was administered.

2.3. Statistical analyses

The present study employed a mixed factorial design. The within-subjects factors were questionnaire item type (illusion items vs. control items), stimulation type (synchronous stimulation vs. asynchronous stimulation), and rubber arm position (position 1 vs. position 2 vs. position 3). The between-subjects factor was AQ group (low AQ group vs. high AQ group). Mixed between-within subjects ANOVAs were conducted for each dependent measure to assess for main and interaction effects across conditions. Normalised integrated jerk values were non-normally distributed in the present study (as has been found previously in the literature; Teulings et al., 1997). The nonparametric Wilcoxon signed-rank test was therefore used to examine for differences in jerk between the two stimulation conditions separately for each AQ group. Post-hoc tests were performed using Bonferroni correction to control for Type I error. Effect sizes are reported here using Cohen's *d*.

3. Results

3.1. Illusion ratings

A 2x2x2x3 mixed ANOVA was performed for illusion ratings with Group (Low AQ vs. High AQ) as a between-subjects factor and Item Type (Illusion vs. Control), Stimulation Type (Synchronous vs. Asynchronous) and Rubber Arm Position (Position 1 vs. Position 2 vs. Position 3) as within-subjects factors.

A main effect was found for Item Type, indicating that illusion items ($M = 10.00$, $SD = 2.81$) were rated higher than control items ($M = 7.20$, $SD = 2.94$), $F(1, 22) = 34.70$, $p < .001$, Cohen's $d = 0.97$. A main effect was also found for Stimulation Type, indicating that item ratings were higher following synchronous stimulation ($M = 10.80$, $SD = 2.48$) than following asynchronous stimulation ($M = 6.40$, $SD = 3.27$), $F(1, 22) = 79.81$, $p < .001$, Cohen's $d = 1.52$. Importantly, an interaction effect was found between Item Type and Stimulation Type, $F(1, 22) = 76.93$, $p < .001$.

Interaction effects were also found between Stimulation Type and Group, $F(1, 22) = 4.53$, $p < .05$, and between Item Type, Stimulation Type, and Group, $F(1, 22) = 6.64$, $p < .05$. There were no other significant main or interaction effects ($p > .05$).

As expected, post-hoc tests indicated that synchronous stimulation ($M = 13.79$, $SD = 2.96$) was associated with higher illusion item ratings than asynchronous stimulation ($M = 6.21$, $SD = 4.00$), $t(23) = 8.78$, $p < .001$, Cohen's $d = 2.15$ (see Fig. 2). Furthermore, synchronous stimulation was associated with significantly higher ratings on illusion items ($M = 13.79$, $SD = 2.96$) than control items ($M = 7.80$, $SD = 3.18$), $t(23) = 8.09$, $p < .001$, Cohen's $d = 1.95$. In contrast, there was no significant difference between ratings for illusion and control items for asynchronous stimulation, $t(23) = -0.72$, $p = .48$, Cohen's $d = -0.11$. Together these results indicate that synchronous stimulation induced the phenomenological features of the illusion typically reported in the literature more strongly than asynchronous stimulation. Further post-hoc analyses are presented in the Supplementary Material.

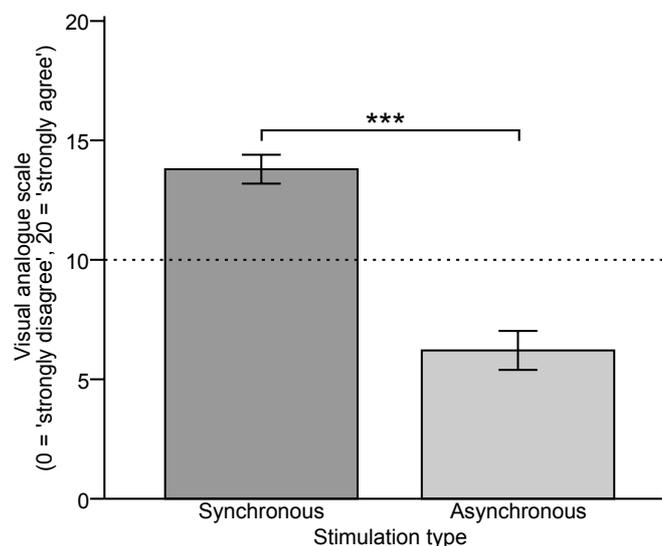


Fig. 2 Ratings of illusion items across stimulation type conditions. Error bars indicate ± 1 standard error. (***) $p < .001$.

3.2. Proprioceptive drift

A 2x2x3 mixed ANOVA was performed for proprioceptive drift with Group (Low AQ vs. High AQ) as a between-subjects factor and Stimulation Type (Synchronous vs. Asynchronous) and Rubber Arm Position (Position 1 vs. Position 2 vs. Position 3) as within-subjects factors.

A significant main effect of Group was found for proprioceptive drift, $F(1, 22) = 4.99$, $p < .05$, Cohen's $d = 0.91$. The low AQ group displayed greater proprioceptive drift across conditions ($M = 1.36$, $SD = 1.72$) compared to the high AQ group ($M = -0.04$, $SD = 1.31$). A significant main effect of Stimulation Type was found for proprioceptive drift, $F(1, 22) = 10.92$, $p < .01$, Cohen's $d = 0.73$, indicating that synchronous stimulation ($M = 1.38$, $SD = 2.19$) was associated with greater drift in perceived arm position towards the rubber arm than asynchronous stimulation ($M = -0.07$, $SD = 1.73$). There was no significant interaction between Stimulation Type and Group ($p > .05$); however, a significant three-way interaction was found between Stimulation Type, Rubber Arm Position, and Group, $F(2, 44) = 3.28$, $p < .05$. No other main or interaction effects were found for this variable ($p > .05$).

To clarify the three-way interaction effect, two-way repeated-measures ANOVAs were conducted separately for each AQ group, with Stimulation Type and Rubber Arm Position as factors. A significant Stimulation Type by Rubber Arm Position interaction effect was found for the low AQ group, $F(2, 22) = 6.05$, $p < .01$, but not the high AQ group, $F(2, 22) = 0.19$, $p = .83$. Further one-way ANOVAs for the low AQ group indicated a significant main effect of Rubber Arm Position for synchronous stimulation, $F(2, 22) = 5.20$, $p < .05$, but not asynchronous stimulation, $F(2, 22) = 0.89$, $p = .43$. Post-hoc tests for the low AQ group during synchronous stimulation indicated that significantly greater drift was observed for position 3 (30 cm separation between participant's arm and the rubber arm; $M = 2.95$, $SD = 2.85$) compared to position 1 (20 cm separation; $M = .94$, $SD = 2.44$; $p < .01$, Cohen's $d = 0.76$). To summarise, the degree of drift in arm position towards the rubber arm following synchronous stimulation was influenced by the distance of the rubber arm from the

participant's arm, but only for the group of participants who scored lower on the AQ (see Fig. 3).

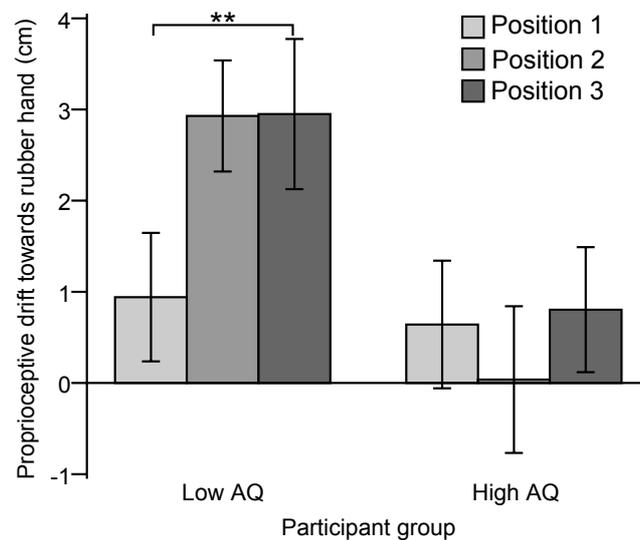


Fig. 3 Proprioceptive drift towards the rubber hand across rubber arm position conditions following synchronous stimulation. Error bars indicate ± 1 standard error. (** $p < .01$).

3.3. Integrated acceleration

A 2x2x3 mixed ANOVA was performed for integrated acceleration with Group (Low AQ vs. High AQ) as a between-subjects factor and Stimulation Type (Synchronous vs. Asynchronous) and Rubber Arm Position (Position 1 vs. Position 2 vs. Position 3) as within-subjects factors.

A significant main effect of Group was found for integrated acceleration, $F(1, 21) = 8.19$, $p < .01$, Cohen's $d = 1.19$. The low AQ group displayed greater integrated acceleration across conditions ($M = 31.36$, $SD = 7.66$) than the high AQ group ($M = 23.84$, $SD = 4.63$; see Fig. 4). Consistent with our previous examination of the acceleration of reaching movements in the rubber-hand illusion (Paton et al., 2012), a significant main effect of Stimulation Type was found for integrated acceleration, $F(1,$

21) = 6.19, $p < .05$, Cohen's $d = 0.47$. However, contrary to the direction of our previous finding for nonclinical participants, synchronous stimulation ($M = 29.70$, $SD = 10.50$) was associated with greater integrated acceleration in subsequently performed reach-to-grasp movements than asynchronous stimulation ($M = 25.82$, $SD = 4.99$; see Fig. 5). This inconsistency between studies may reflect the difference in the acceleration variables used previously (recorded via an accelerometer) and in the current study (recorded via a 6-dimensional tracker, and derived specifically from the linear axes, thus controlling for rotational changes that occur throughout the movement). This previous study also contained a number of independent variables not included in the present study, potentially contributing to a difference between studies in the stimulation-type comparison. No other main or interaction effects were found for this variable ($p > .05$).

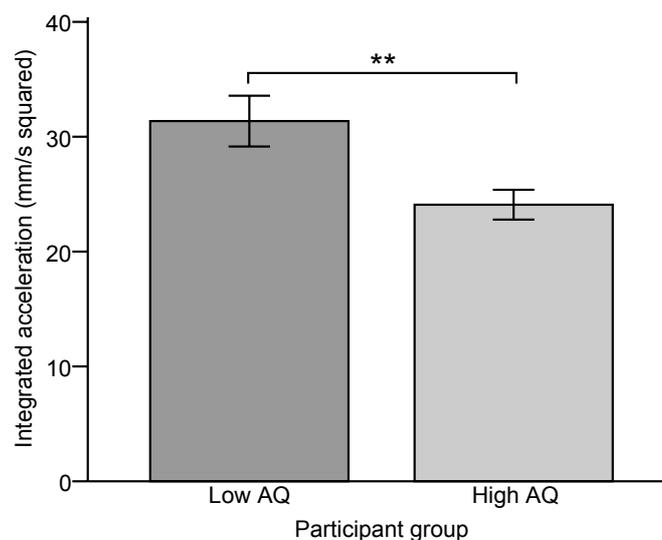


Fig. 4 Integrated acceleration of reach-to-grasp movements between participant groups separated by AQ scores. Error bars indicate ± 1 standard error. (** $p < .01$).

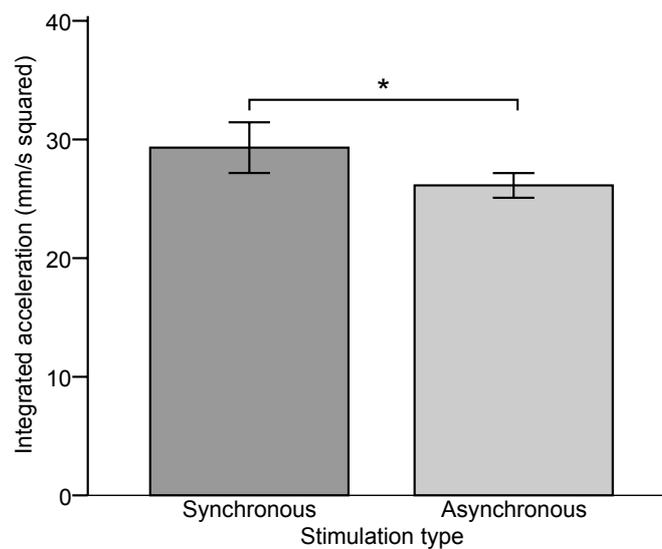


Fig. 5 Integrated acceleration of reach-to-grasp movements between stimulation types. Error bars indicate ± 1 standard error. ($*p < .05$).

3.4. Normalised integrated jerk

Differences in integrated jerk between the two stimulation conditions were examined separately for each AQ group using the nonparametric Wilcoxon signed-rank test. For the low AQ group, the integrated jerk of reaching movements was significantly greater following synchronous stimulation ($M = .66$, $SD = .49$) than when following asynchronous stimulation ($M = .32$, $SD = .21$), $z = -2.28$, $p < .05$, Cohen's $d = 0.89$. In contrast, integrated jerk did not differ significantly between stimulation conditions for the high AQ group, $z = -0.24$, $p = .81$, Cohen's $d = -0.16$ (see Fig. 6). Similarly, post-hoc correlational analyses conducted to further elucidate this effect indicated that AQ scores shared a significant negative correlation with integrated jerk following synchronous stimulation ($r_s = -.47$, $p < .05$, two-tailed), but not asynchronous stimulation ($r_s = -.11$, $p = .63$, two-tailed; see Fig. 7). These findings therefore indicate that the integrated jerk of reach-to-grasp movements was increased by the presence of the illusion for participants who scored lower on the AQ, but was not significantly different across stimulation types for participants who scored higher on the AQ.

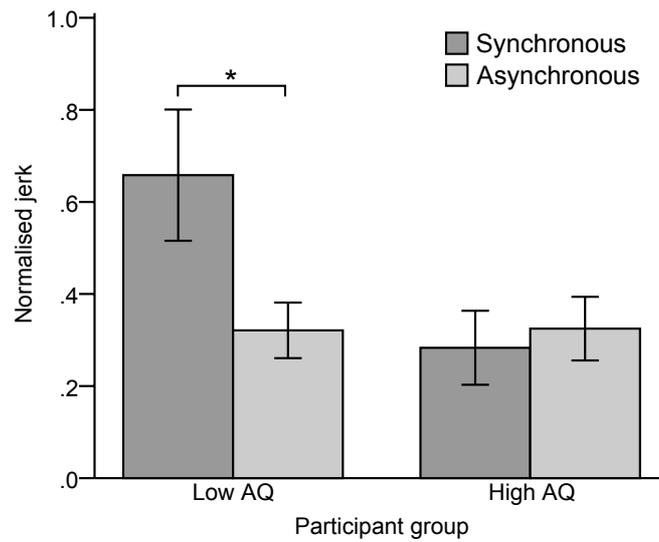


Fig. 6 Normalised integrated jerk of reach-to-grasp movements across AQ groups and stimulation types. Error bars indicate ± 1 standard error. ($*p < .05$).

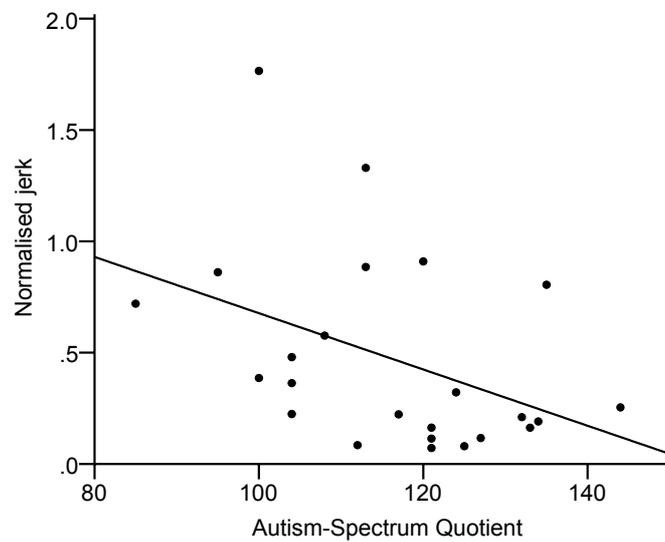


Fig. 7 A significant correlation was observed between AQ scores and the normalised integrated jerk of reach-to-grasp movements following synchronous stimulation. ($r_s = -0.47$, $p < .05$, two-tailed; linear least squares regression line of best fit: $y = -0.013x + 1.941$, $R^2 = .18$, $t = -2.17$, $p < .05$).

3.5. Movement duration

For movement duration, a 2x2x3 mixed ANOVA was performed with Group (Low AQ vs. High AQ) as a between-subjects factor and Stimulation Type (Synchronous vs. Asynchronous) and Rubber Arm Position (Position 1 vs. Position 2 vs. Position 3) as within-subjects factors. A significant two-way interaction between Stimulation Type and Group was found, $F(1, 22) = 4.48, p < .05$. No other main or interaction effects were found for this variable ($p > .05$).

Post hoc tests comparing movement duration between stimulation conditions did not reach significance, however, for either the low AQ group (synchronous stimulation: $M = 1.71, SD = 0.37$; asynchronous stimulation: $M = 1.53, SD = .40$; $t(11) = 2.14, p = .06$, Cohen's $d = 0.46$) or the high AQ group (synchronous stimulation: $M = 1.55, SD = 0.50$; asynchronous stimulation: $M = 1.62, SD = .41$; $t(11) = -0.94, p = .37$, Cohen's $d = -0.13$).

3.6. Further reach measures

For each of the remaining reach measures, a 2x2x3 mixed ANOVA was performed with Group (Low AQ vs. High AQ) as a between-subjects factor and Stimulation Type (Synchronous vs. Asynchronous) and Rubber Arm Position (Position 1 vs. Position 2 vs. Position 3) as within-subjects factors. No significant differences were found across conditions or groups for mean velocity, peak velocity, or maximum horizontal displacement ($p > .05$). Significant differences observed for relative time to peak velocity and angle of initial movement are reported in Supplementary Material. Means and standard deviations for each reach measure are shown in Table S1 in Supplementary Material.

4. Discussion

The present study supports the hypothesis that proprioceptive and sensorimotor characteristics of ASD, as reflected in the multimodal effects of the rubber-hand illusion, vary together with ASD-like traits in the general population. Nonclinical adults scoring higher on ASD-like traits showed reduced effects of the illusion on perceived arm position compared to those scoring lower on ASD-like traits (as indicated by a lesser influence of the position of the rubber arm on estimated arm position during synchronous stimulation). Individuals with higher ASD-like traits also demonstrated reduced sensitivity to the presence of the illusion in their reaching movements. These effects occurred despite both groups reporting the typical subjective effects of the illusion, concerning referral of touch and a heightened sense of ownership for the rubber hand. This pattern of intact subjective effects but diminished proprioceptive and sensorimotor effects resembles that found previously for the rubber-hand illusion in a sample of adults diagnosed with ASD (Paton et al., 2012). The present findings are also consistent with a study of the rubber-hand illusion in children diagnosed with ASD, which reports intact subjective effects of the illusion but delayed proprioceptive effects (Cascio et al., 2012). While ASD-like traits are most commonly defined in terms of social difficulties and unusual repetitive behaviours and interests, the present study adds to recent research that has found sensory differences associated with ASD to vary together with other aspects of this condition in the general population (e.g., Donohue et al., 2012; Grinter, Maybery, et al., 2009; Grinter, Van Beek, et al., 2009; Walter et al., 2009). This research is therefore consistent with the continuum hypothesis of ASD (Happé et al., 2006; Mandy & Skuse, 2008), and highlights the relevance of sensory characteristics in defining a broader autistic phenotype.

To characterise the proprioceptive and sensorimotor differences associated with ASD-like traits in the present study, we need to emphasise a distinction between different levels of sensory integration in the rubber-hand illusion. Visuotactile integration in the illusion is dependent upon the close temporal synchrony of repetitive tactile and

visual inputs (Botvinick & Cohen, 1998; Shimada et al., 2009), a signal that is conveyed precisely during illusion-induction by continuous tactile and visual stimulation. In contrast, we can hypothesise that changes in perceived arm position induced by the illusion reflect integration between sensory (proprioceptive) estimates of arm position and predictions for arm position derived from the illusory context. This context would, for example, include the visual presence of the rubber arm and the (illusory) location of felt touch. The evidence that proprioceptive differences occurred despite a typical subjective experience of the illusion in each group suggests that enhanced proprioceptive performance in the high AQ group reflects increased reliance on sensory (proprioceptive) input at the expense of the more global context. This distinction between visuotactile and proprioceptive mechanisms is consistent with a model of the rubber-hand illusion proposed by Makin, Holmes, and Ehrsson (2008), in which changes in perceived arm position occur subsequent to visual capture of the tactile input, based on evidence disassociating the co-dependence, time course, and spatial extent of these effects.

The enhanced proprioceptive performance of individuals with ASD-like traits in the present study (and in the ASD group in our previous rubber-hand illusion study; Paton et al., 2012) conflicts somewhat with a recent study examining limb proprioception in ASD outside of the context of sensory illusions (Fuentes, Mostofsky, & Bastian, 2011). In particular, no differences were found in this latter study in the accuracy and precision of proprioceptive estimates regarding arm position between individuals with ASD and healthy controls. As described in the preceding paragraph, enhanced performance in the present study can be explained in terms of a reduced tendency for taking the wider context, here provided by the rubber-hand illusion, into account. The more accurate proprioceptive performance in the high AQ group may then be serendipitous given the specific (illusion-based) task context used, rather than reflecting a superior capacity for accurate proprioception in ASD. The apparent conflict between the present findings and those of Fuentes et al. (2011) may therefore reflect a lack of a modulating context in the experimental set-ups used in the latter study, such that the hypothesised disregard for contextually-based models of sensory input in ASD-like perception did not cause a deviation in the performance of individuals with ASD from controls. The implication here is that group differences in

performance may vary across tasks depending on whether there is a more global model of sensory input suggested by the specific task context, and whether this task-specific context aids or misleads accurate performance. Integrating proprioceptive sensory information into a more global model (as we suggest occurs for the low AQ group in the rubber-hand illusion) is likely to be beneficial to accuracy in some contexts but not others.

Within a predictive coding framework of perception, the degree of precision that is expected from the sensory input in a given context determines the relative contribution of (top-down) relatively global hypotheses regarding the state of the world and (bottom-up) sensory input (Feldman & Friston, 2010; Friston & Stephan, 2007). The former are more likely to mediate an influence of contextual information on perception. We can therefore speculate that the group differences observed in the present study reflect individual variation in the expected levels of sensory precision (Friston et al., 2013; Hohwy, in press; Paton et al., 2012; see also Brock, 2012; Pellicano & Burr, 2012). In particular, the greater tendency of the low AQ group to draw on the illusory context to estimate arm position, as suggested by greater proprioceptive drift when the distance between the real and rubber arms was increased in the synchronous stimulation condition, may reflect an expectation for low precision of bottom-up sensory (proprioceptive) estimates within the unusual context of the illusion. Similarly, the enhanced proprioceptive performance of the high AQ group may reflect an expectation for high precision in sensory input, leading to a lessened influence of global models that take into account the illusory context when estimating arm position. This would explain why these participants specifically show diminished proprioceptive effects of the illusion rather than reduced effects of the illusion in general. The latter could otherwise be explained by a general bias concerning global integration.

A group difference was also found in the effect of the rubber-hand illusion on the smoothness of reach-to-grasp movements performed with the stimulated hand following illusion-induction. In particular, we found that individuals lower in ASD-like traits executed movements less smoothly following synchronous stimulation (as indicated by increased normalised integrated jerk) compared to the asynchronous

stimulation control condition. The high AQ group, in contrast, showed uniform movement smoothness across conditions, at a level similar to that of the asynchronous condition for the low AQ group. This is partially consistent with our previous study (Paton et al., 2012), which observed differences in the integrated acceleration of reach-to-grasp movements following the rubber-hand illusion between a clinical ASD group and a nonclinical control group. This previous clinical study did not assess movement smoothness, however, and there was no group difference in integrated acceleration in the present study involving nonclinical participants – so a direct comparison between reaching movements found for clinical ASD and nonclinical ASD-like traits is a task for further studies.

The reach effects in the present study can also be interpreted in terms of group differences in expectations for sensory precision, which we brought to bear on the proprioceptive drift findings above. Again, given that individuals with higher ASD-like traits report experiencing the typical subjective effects of the illusion, the lack of difference in reaching movements across stimulation conditions seems best explained by insensitivity to the context of the illusion when executing movement rather than a general resistance to the illusion itself. Explicating this notion of context-insensitivity within the framework of predictive coding, we can hypothesise that a less smooth movement would be performed when the individual expects imprecision in their proprioceptive and kinaesthetic feedback for the planned movement. This could occur due to difficulty coordinating movement when the trajectory required to reach the target is uncertain, or, similarly, could reflect the introduction of exploratory movements to elicit proprioceptive and kinaesthetic feedback. In contrast, a more confident, or smoothly executed, movement may be likely to occur when the individual assumes high precision in their estimate of initial arm position and predicts high precision in their proprioceptive and kinaesthetic feedback once the movement is underway. Quantifying this in terms of differences of higher order temporal derivatives (e.g., jerk) is useful because one may assume that since such derivatives encompass relatively long time-scales they are encoded at higher cortical levels, consistent with the idea of more high-level, relatively global context modulation (in essence, trying to anticipate the overall smoothness of the movement given levels of expected uncertainty; *cf.* Friston et al., 2010, p.235).

An alternative explanation is that the observed differences in reaching movements for the low AQ group are directly related to group differences in the magnitude of drift in arm location induced by the illusion. Specifically, the reduced smoothness of movement following the synchronous stimulation condition for the low AQ group could reflect the increased tendency for proprioceptive drift that this group demonstrates. Counter to this interpretation, however, is the lack of difference found in the displacement measures of the reach-to-grasp movements. If the shift in perceived arm location towards the rubber arm contributed significantly to the subsequent reaching movements, we would expect this to manifest as a difference in the angle of initial movement or peak horizontal displacement of the reach trajectories. For example, a shift in perceived arm location to the left would mean that the subsequent arm trajectory would have a sharper angle of movement to the right and greater deviation to the right than that really required to reach the target. This logic is adopted in Newport et al. (2010), Zopf et al. (2011), and Heed et al. (2011), who each report differences in reach displacement induced by the rubber-hand illusion (see also Kammers, de Vignemont, et al., 2009, who report no differences in the displacement of reaching movements following the illusion; Kammers, Longo, Tsakiris, Dijkerman, & Haggard, 2009; Kammers, Verhagen, et al., 2009). Given that we did not see differences in displacement parameters in the present study, the observed effect of the illusion on movement smoothness may not merely reflect the increased proprioceptive drift experienced by the low AQ group.

The interpretation of the reach data that we favour leads to an interesting implication regarding movement impairments that commonly occur in ASD (e.g., Mari, Castiello, Marks, Marraffa, & Prior, 2003; Nazarali, Glazebrook, & Elliott, 2009; Rinehart, Bradshaw, Brereton, & Tonge, 2001; Rinehart et al., 2006; see Fournier, Hass, Naik, Lodha, & Cauraugh, 2010, for meta-analysis). If, as we suggest in the preceding paragraphs, the lack of differences in reaching movements for the high AQ group across synchronous and asynchronous stimulation conditions reflects insensitivity to the context-specific inducements of expectations for imprecision in the sensory estimates used to guide reaching movements, then a tendency to disregard context in this manner in ASD may lead to overconfident movement in contexts that would

usually suggest imprecision. Difficulties in movement coordination might then be partly explained in terms of movement errors caused by overconfident movement execution, and would be specifically expected to occur in contexts that advise for tentative movement execution. In other words, we suggest that a lesser sensitivity to, and urge to resolve, ambiguity in body position may contribute to uncoordinated movement in ASD. It might therefore be useful to further examine the effects of the rubber-hand illusion on movement execution with respect to clinical measures of motor coordination in ASD.

In summary, the present study examined individual differences in the relative contribution of sensory input and contextual factors to perception. Working within a Bayesian (prediction error minimisation) framework, we reasoned that ASD-like sensory integration involves a tendency to ignore contextual information that suggest imprecision, and predicted that this entails high estimations of sensory precision across contexts, leading to an increased reliance on lower-level sensory estimates and a decreased tendency to subsume input under higher-level expectations. The finding that, following synchronous stimulation, nonclinical individuals high in ASD-like traits show reduced sensitivity to the position of the rubber hand in their proprioceptive estimates and show less sensitivity to uncertainty while executing reaching movements, despite reporting the subjective experience of the illusion, is consistent with this hypothesis. The ability to modulate expected levels of sensory precision in response to contextual information suggesting varying uncertainty may lead to a better understanding of the complex constellation of compromised and enhanced perceptual performance in autism, as well as of individual differences in perception in the general population.

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