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The rubber hand illusion reveals proprioceptive and sensorimotor differences in autism spectrum disorders

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Abstract

Autism spectrum disorder (ASD) is characterised by differences in unimodal and multimodal sensory and proprioceptive processing, with complex biases towards local over global processing. Many of these elements are implicated in versions of the rubber hand illusion (RHI), which were therefore studied in high-functioning individuals with ASD and a typically developing control group. Both groups experienced the illusion. A number of differences were found, related to proprioception and sensorimotor processes. The ASD group showed reduced sensitivity to visuotactile-proprioceptive discrepancy but more accurate proprioception. This group also differed on acceleration in subsequent reach trials. Results are discussed in terms of weak top-down integration and precision-accuracy trade-offs. The RHI appears to be a useful tool for investigating multisensory processing in ASD.

Keywords: High-functioning autism spectrum disorder, rubber hand illusion, multimodal sensory integration, local processing bias

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Abstract

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The role and nature of sensory processing in autism spectrum disorders (ASD) is not

fully understood, even though there is agreement that differences in sensory processing are

important for understanding ASD (Iarocci & McDonald, 2006; Rogers & Ozonoff, 2005;

Ben-Sasson et al., 2009; Dakin & Frith, 2005; Frith, 1989; Mottron et al., 2006).

Much research of this issue in ASD contrasts local and global sensory processing.

Local processing, such as visual search, detail recognition, and complex pattern learning, tend

to show heightened sensitivity (Mottron et al., 2006; Dakin & Frith, 2005; Simmons et al.

2009). It is more difficult to interpret findings in more global, context-dependent processing,

such as visual grouping and motion coherence, but it appears processing in ASD is more

problematic in these domains, with a bias towards local over global processing (Happé &

Frith, 2006).

Aspects of the local-global processing distinction can be operationalised in terms of

unimodal versus multimodal sensory processing (Iarocci & McDonald, 2006). It seems that

unimodal processing may be enhanced in ASD, for example in pitch discrimination (Bonnel

et al., 2003), and vibration and thermal pain (but not light touch) (Cascio et al., 2008).

Multimodal integration tends to factor in broader context (for example, it depends on

assessing the prior probability of co-location of auditory and visual stimuli), and may rely on

integration of one or more local estimates with each other (e.g., auditory and visual (Alais &

Burr, 2004), or visual and proprioceptive (van Beers et al., 2002; van Beers et al., 1999)) or

with more global top-down expectations (for example, integrating prior estimates about

movement with ambiguous bottom-up signals from the otoliths of the vestibular system

(Schwabe & Blanke 2008)).

Relatively few studies have looked at multimodal sensory integration in ASD but there is some evidence for subtle issues in this area. Audiovisual integration appears to function well albeit within a longer than normal temporal window (Foss-Feig et al., 2010). Temporal synchrony in audiovisual integration has been found to be worse for linguistic stimuli in children with ASD than in children with other developmental disabilities (Bebko et al., 2006), and individuals with ASD benefit less from added visual information in audiovisual lip-reading than controls (Smith & Bennetto, 2007). Proprioception (perceived limb position) has been implicated as a central element in sensorimotor disturbances in ASD (Masterton & Biederman, 1983). Specifically, internal models of action demonstrate an increased association in ASD between self-generated movement and proprioceptive feedback in learning tasks such that there seems to be an increased reliance on proprioception at the expense of visual input (Haswell et al., 2009).

Unimodal and multimodal sensory processes are often studied with illusions, and there is some uncertainty about the sensitivity in ASD to visual illusions with some but not all studies showing decreased sensitivity (Happé, 1996; Walter et al., 2009; Ropar & Mitchell, 1999, 2001; Hoy et al., 2004; Bölte et al., 2007). Most studies have focused on unimodal processing but illusions are also useful for the study of multimodal processing. Audiovisual integration, for example, is well-described using the ventriloquist effect (Alais & Burr, 2004) and a variant of this effect used in ASD showed subtle differences in temporal modulation of audiovisual integration (Foss-Feig et al., 2010; Kwakye et al., 2011). Illusions can also be used to gauge proprioceptive and sensorimotor processing in ASD and there is evidence that children with autism, though less posturally stable than typically developed children, are less posturally reactive to illusory visual environmental stimuli (Gepner et al., 1995; Gepner & Mestre, 2002).

The overall picture is thus that, beyond reasonably well-established increased unimodal sensitivity, the sensory differences in ASD revolve around global, context-dependent aspects of multimodal sensory integration involving sensory and proprioceptive processes. It will therefore be useful to investigate more complex but otherwise well-studied examples of multimodal sensory integration involving these factors. Therefore, the rubber hand illusion (RHI) (Botvinick & Cohen, 1998), which is an example of visuotactile integration that depends on proprioceptive processing, is here explored in a group of individuals with high-functioning ASD and a non-clinical control group.

In the RHI, synchronous rather than asynchronous touch on a real, hidden hand and on a visible rubber hand tend to induce the experience of a touch located on the rubber hand. There is now a large of body of research on the RHI and various permutations of it, and a number of different independent measures of it have been developed (Ehrsson, 2007; Moseley et al.; Lenggenhager et al., 2007; Tsakiris, 2010; Giummarra et al., 2008; Makin et al., 2008). The illusion has also been studied in some clinical populations such as schizophrenia (Peled et al., 2003; Peled et al., 2000) and anorexia nervosa (Mussap & Salton, 2006). The present study incorporated a number of these more recent developments, which have relevance for the mentioned aspects of ASD. The RHI is thought to reflect modulation of body ownership relating to the surprising ease with which non-body objects like rubber hands can seemingly be incorporated into the body image, due to illuded multisensory integration. As such the RHI adds further value to the study of multisensory integration and may be of specific value to the study of ASD. For example, differences in body ownership and body image processing could potentially relate to differences in imitation, which require on-line mapping of the body images of self and other (Rogers et al., 2005). In so far as the RHI affects the body schema, thought to be implicated in motor planning and control, it could

also help throw light on observed differences in sensorimotor processes in ASD (Rinehart et al., 2001; Mari et al., 2003; Nazarali et al., 2009; Rinehart et al., 2006).

In the control group, we expected the RHI to be stronger when there is little proprioceptive discrepancy between the real hand and the rubber hand, and we expected the illusion to be weakened for versions of the RHI where the rubber hand is replaced with a non-hand object or where the touch is performed with a machine rather than the experimenter's finger; finally we expected few if any sensorimotor aftereffects of the RHI on a subsequent reach trial. Recent studies of multisensory integration in ASD (Kwakye et al., 2011) suggest intact ability but with underlying differences, so we expected the ASD group to experience a RHI to some degree and with some underlying differences. For the RHI specifically, we expected these differences to reflect proprioceptive estimates being weighted differently (Haswell et al., 2009), as well as reflect less sensitivity to the global context of hands rather than non-hand objects being touched, and being touched by people rather than machines (Happe & Frith, 2006); further, such sensory differences might have an effect on subsequent sensorimotor processes (Nazarali et al., 2009; Nayate et al., 2005).

Method

Participants

Participants were 17 individuals (3 female) diagnosed with a high-functioning ASD (either DSM-IV autistic disorder or Asperger's disorder) (mean age: 32.06 [$SD = 12.43$]; 3 left handed; mean Autism Spectrum Quotient: 33.44 [$SD = 7.54$]) and a control group of 17 (5 female) healthy volunteers (mean age: 27.06 [$SD = 6.20$]; 1 left handed). Individuals with ASD were recruited via the [name deleted for blind review] participant database, which is comprised of clinically diagnosed individuals who have previously taken part in research and

have agreed to be contacted in relation to future projects. All clinical participants had a clinical diagnosis (DSM-IV) of either autistic disorder or Asperger's disorder, as confirmed via diagnostic report or with the diagnosing clinician (psychiatrist, psychologist, or paediatrician) and their status as "high-functioning" was derived from their performance on a standardised cognitive assessment (IQ $\geq$ 70). Control participants were recruited from advertisements placed within [deleted for blind review]. The study was approved by the human research ethics committees of [deleted for blind review] and [deleted for blind review], according to the ethical standards of the Declaration of Helsinki, 1964. All adult participants provided written informed consent, while a parent of child participants provided written informed consent.

Procedure

The rubber hand illusion is an example of visuotactile integration that centrally involves proprioception and relies on temporal perception. When there is visual input only of a rubber hand and not the participant's real hand, synchronous rather than asynchronous touch on both induces the illusion that the touch is felt on the rubber hand.

The present study incorporated a number of more recent developments of the RHI. It was thus a mixed design with one between subjects factor, *Group* (ASD or Control) and 5 within subjects factors: *Synchrony* (Synchronous or Asynchronous Touch), *Goggles* (Goggles or No Goggles), *Item* (Rubber hand or Cardboard Box), *Stimulation* (Manual Touch or Machine Touch), and *Statement* (Participants rate agreement with a number of illusion statements gauging aspects of the RHI as well as a number of control statements; see Table 1). These factors are described in the below sections.

Participants were seated at a table and their right hand was occluded in a large wooden box with a towel draped over their shoulder to conceal their upper arm. Their left hand was placed on the left side of the table. A rubber hand, or in some conditions a cardboard box, was placed in front of them. Participants would experience the RHI wearing video goggles or without wearing goggles (counterbalanced). Touch was performed in synchrony or asynchrony (*ca.* 1 touch/sec) delivered on the dorsal aspect of the second phalanx of subject's middle finger on the real hand and on the rubber hand, and on the middle of the cardboard box by either a human experimenter or a computer controlled machine (Figures 1 and 2). These conditions were all counterbalanced. See further details of procedure below.

Factors

Synchrony: Synchronous vs. asynchronous touch. In all conditions, participants are touched either synchronously or asynchronously. Each trial consists of a 3 min touch period, followed by a number of tasks to assess the RHI (see below). The touch period consists of three repetitions of 45s tapping plus 15s break in which no taps are delivered (to allow for skin temperature measurement, see below). Synchronous touch is the basic element of RHI, which normally greatly facilitates visuotactile integration on the rubber hand.

Goggles: Video goggles vs. no video goggles. In the classic version of the RHI, there is proprioceptive discrepancy between the seen rubber hand where touch is felt as located, and the true, felt position of the unseen real hand. A recently described variation of RHI (Hohwy and Paton 2010) uses video goggles to overlap the seen location of the rubber hand with the felt location of the real hand. This minimises proprioceptive discrepancy and appears

to facilitate illusion onset. Differences between ASD participants and control participants between the standard no goggles RHI and the goggles RHI could thus reveal differential roles in proprioceptive integration, which as mentioned has been implicated in ASD. All conditions were thus repeated with and without these goggles (stereoscopic OLED head mounted display (eMagin Z800) connected to a colour CCD camera (Sony CCD sensor, 520 Lines) mounted on a tripod). In the no goggles condition, the middle finger of the rubber hand would be placed approximately at midline and the real right hand placed 28cm to the right behind a cover; in the goggles condition, the real right hand would be placed approximately at midline and the rubber hand visible in the goggles at midline too, see Figure 1a-b.

Item: Touch on rubber hand vs. non-hand cardboard box. There is ongoing debate about whether the RHI can be induced on objects that do not look like hands, such as table tops or cardboard boxes. Early reports suggest this is possible (Armel & Ramachandran, 2003) but later reports have failed to fully replicate this (Tsakiris & Haggard, 2005; Haans et al., 2008; Tsakiris et al., 2010). At best, weaker versions of the illusion seem to be induced, and RHI on non-hand objects seems to work best with prior induction of the illusion on a hand-like object (Hohwy & Paton, 2010). Given differential processing by the mirror neuron system (MNS) of hand and non-hand objects and their goal directedness (Enticott et al., 2010) it is possible that individuals with ASD, for whom a still widely debated MNS deficit has been posited (Williams et al., 2001; Oberman et al. 2005; Iacoboni & Dapretto, 2006; Gallese & Goldman, 1998; Enticott et al., In press), would show a different response than controls to the RHI for non-hand objects. The link from MNS to ASD suggests that observation of hand vs. non-hand objects should differ for ASD and control groups, in particular when the observed hand is, as it in the RHI, viewed in the egocentric rather than allocentric perspective

(Théoret et al., 2005). The RHI creates an ambiguous situation concerning whether the seen hand is self or not-self, which could put demands on proper functioning of the MNS, in particular as it relates motor planning: during synchronous touch it should be more like observing one's own hand, leading representation to be on-line and ready for action execution whereas during asynchrony it would be more like observing someone else's hand, leading representation to be on-line. For touch on objects like cardboard boxes there is also ambiguity but it would be less related to visual observation of hands and so activating MNS less. Thus MNS processing should be involved in explaining the differences in the RHI for hand and non-hand objects in typically developing individuals. If there are issues with MNS processing in ASD, then it is conceivable that there would be less difference in their RHI experiences for hand and non-hand objects. Participants were thus exposed to synchronous and asynchronous touch on both types of object (a rubber hand and a small, white cardboard box) (Figure 2a-b).

Stimulation: Manual touch vs. machine touch. Versions of the RHI normally use manual touch by a human finger or a paint brush but a few versions have used machine produced touch (e.g., Rohde et al., 2011). Though there is as yet little concrete evidence of differences to the RHI experience from manipulating the method of touch delivery, we have anecdotal suggestions from our own lab that machine touch can be less engaging and creates a somewhat weaker RHI in typically developing individuals; if such a differential effect could be substantiated it might relate to machine touch being more precise and hence more predictable, and it could also relate to it grabbing attention less than when touch is delivered by another human. Individuals with ASD seem to be less sensitive than typically developing controls to biological movement than non-biological movement (Kaiser & Pelphrey, In press); this could influence processing of the RHI under human vs. machine touch. Also, ASD is

characterised by differences in empathy (Baron-Cohen & Wheelwright, 2004), which could possibly engender differential experiences of, or responses to, the RHI for human vs. machine touch. To explore these potential group differences, synchronous and asynchronous touch was delivered by either a human experimenter's index finger or a foam tipped touch machine (twin computer controlled stepper motors) (Figure 2c-d).

Dependent Measures

Four purported measures of the RHI were employed. After the touch period, participants first were tested for proprioceptive drift (in the no goggles condition only), then they performed a reach trial (all conditions) and finally they filled in a computer questionnaire (all conditions). Additionally, skin temperature was measured on both hands throughout breaks in the touch periods. These dependent measures are described in detail below.

Questionnaires: After each trial, and after the drift and reach tasks described below, the experience of the RHI was measured via the type of questionnaire that is commonly used in RHI studies, adapted for this particular study, see Table 1. A selection of statements from Botvinick & Cohen, 1998 (S1, S2, S3, S5, S7, S8), Longo et al., 2008 (S9, S10, S12), Petkova & Ehrsson, 2008 (S6), and Hohwy & Paton, 2010 (S4, S11) were used. Changes to wording were made to reflect our specific experimental paradigm (e.g., goggles vs. no goggles, manual vs. machine touch, and rubber hand vs. cardboard box). Statements S1-3 are central for the specific experience of the RHI: for each condition, S1 asks about the felt location of the touch, S2 asks about the felt cause of the touch, and S3 as about whether it feels as if the hand or box is one's own. Here we first follow the procedure of Guterstam et

al., 2011, such that averaged responses to S1-S3 are expected to differ from averaged responses to the remaining statements. In particular, responses to S1-3 during synchrony should be higher than answers to S4-11 during synchrony (S12 gauges whether the participant is continually finding the experience enjoyable and is consistently rated highly; it is therefore excluded from analysis). The reasoning behind this method is that, before responses to the three target statements are compared across conditions, it should be established that these statements, which purportedly relate specifically to the rubber hand experience, in fact do elicit a specific pattern of responses under conditions of synchronous touch thought to induce the RHI. The responses should thus differ from the pattern of responses to a series of control statements that are designed to ask about things that are as unusual as the RHI experience but would relate to phenomena that are either thought not to occur or that relate to more general aspects of the experimental set-up and overall situation. If someone did not experience the RHI, then it would be expected that there would be little difference in the pattern of responses to target and control questions during synchrony specifically (on the assumption that people respond roughly in the same way to statements about unusual experiences they do not have or to general aspects of the experimental set-up and overall situation). Target and controls statements, respectively, are averaged in this part of the analysis because the item of interest is the difference in patterns of responses to groups of statements rather than the individual statements themselves.

Statements were presented in randomised order on a computer screen out of sight of the experimenter. Participants used their right hand to indicate their response with a computer mouse (the cursor was hidden until participants moved the mouse). Participants were asked to indicate their degree of agreement with each statement in the questionnaire with a mouse click on a computerized, horizontal, 20cm visual analogue scale (VAS). The left end of the

scale was marked with "strongly disagree", the right end with "strongly agree". No other points were marked. This procedure differs from most other studies in the RHI literature where 7 point Likert scales are commonly used. Some studies have used several-point VAS (e.g., Ionta et al., 2011) however we felt the subtle differences between points might be interpreted differently between groups. A computer program scaled the VAS from 1-100 and statement responses were subsequently outputted and analysed on this scale.

Proprioceptive drift. Proprioceptive drift is a common RHI measure (Ehrsson et al., 2004; Tsakiris & Haggard 2005), though exactly how it is related to the RHI experience is disputed (Rohde et al., 2011). After inducing the illusion, participants were asked to indicate where it feels as if their real middle finger is, and the illusion is normally indicated by increased drift towards the rubber hand during synchrony (in order to ease the burden of this taxing experimental paradigm no proprioceptive drift measure was taken prior to illusion induction). Measurements are taken by blinding the participant's view of the entire set up with a board. The experimenter then slides a finger, starting either from the left or the right, along the edge of the board and instructs the participant to say "stop" when the finger is where they feel their real middle finger is located. The experimenter notes the centimetre reading of this location on a ruler on the edge of the board that is not visible to the participant. The actual locations of the participant's middle finger and the rubber hand/cardboard box were kept constant (distance 28cm). This measure is important for ASD as it relates to integration of proprioceptive estimates with other, visuotactile estimates. This measure is only taken in the no goggles condition as there is no proprioceptive discrepancy in the goggles condition.

Reach trial. There is conflicting evidence concerning the ability of the RHI to influence movement. Even though participants experience a touch on the rubber hand, and have proprioceptive drift towards it, the illusion does not seem to influence subsequent ballistic pointing trials (Kammers et al., 2009). There is however evidence for more subtle kinds of influence in grip aperture and peak velocity for RHI (Kammers et al., 2010; Zopf et al., 2011), as well as influences from passive versus active illusion induction (Kammers et al., 2009). Given evidence for differences for motor planning and reprogramming in ASD (Rinehart et al., 2001; Mari et al., 2003; Nazarali et al., 2009; Rinehart et al., 2006), as well as the mentioned overreliance on proprioception (Haswell et al., 2009), a reach trial was included. After indicating proprioceptive drift, a cylindrical object was placed between and approximately 20 cm in front of the real hand and the rubber hand (or cardboard box); see Figure 1. In the no goggles condition it was thus placed to the left of the real hand and to the right of the rubber hand/box. In the goggles condition it was placed to the right of the location of the rubber hand as perceived in the goggles. Participants were asked to reach for it and an accelerometer (3 axis, accuracy 10 mg_0 [10 one thousandths of a standard gravity], 125 Hz sample rate) strapped to their wrist recorded the overall acceleration (in units of standard gravity, $g_0 = 9.80665$ m/s^2) of their movement. The accelerometer records acceleration in three spatial dimensions, but does not measure yaw, pitch and roll. Measurement began as participants were asked to move and ended 5 s later. A Euclidian acceleration vector was derived for each trial based on the three axes of acceleration. The area under the curve for each of these Euclidian acceleration vectors was taken as the measure of interest. All participants succeeded in reaching the target object.

Skin temperature. There is some recent evidence that there are skin temperature differences on the right, experimental hand between synchronous and asynchronous touch, and between the left hand and the right experimental hand during synchronous touch (Moseley et al., 2008). This has been replicated for the RHI using a goggles paradigm, but not for other variations of the RHI (Hohwy & Paton, 2010). Whether this cooling signals a kind of dis-ownership of the body part is debated, as are the precise conditions under which cooling obtains (Moseley et al., In print), including the direction of causation with evidence that prior cooling of the hand facilitates the RHI (Kammers et al., 2011). A temperature measure is included here to gain further insight into this phenomenon and because there is some evidence of temperature differences in some disorders, specifically schizophrenia (Chong & Castle, 2004). To our knowledge, no data exist on skin temperature in ASD. Temperature was measured using an infrared thermometer (0.01 °C accuracy, 2 Hz sampling rate, 90° field of view) mounted above the left and right hands. Temperature was measured during three 15s no-touch breaks in each touch period to avoid confounds due to the human experimenter's hand or the touch machine. Temperature measures are averaged over the entire field of vision for the thermometer, with some variation due to hand size and field of view.

Analysis

For each of the dependent measures a 2 (group: ASD vs. control) x 2 (synchrony: synchronous vs. asynchronous) x 2 (goggles: goggles vs. no goggles) x 2 (item: rubber hand vs. cardboard box) x 2 (stimulation: manual touch vs. machine touch) mixed-model ANOVA was performed using PASW Statistics 18. Bonferroni corrections were applied for all post-hoc tests as needed. Effect sizes were calculated with Cohen's *d*. The results are formatted

according to dependent variable with further division of results according to factor for clarity of presentation.

Results

Questionnaires

      Illusion statements vs. control statements. Averaged responses to S1-3 and to S4-11, respectively, were entered into a mixed model ANOVA with the factors being synchrony, goggles, stimulation, item as well as statement (illusion or control). As expected there was a main effect of synchrony, $F(1, 32) = 25.53$, $p < .01$, and of statement $F(1, 32) = 4.45$, $p = .043$. Crucially, there was an interaction between statement and synchrony $F(1, 32) = 42.49$, $p < .01$. Post hoc t-tests showed that during synchrony participants did give higher ratings to S1-3 ($M = 34.44$, $SD = 18.44$) than to S4-11 ($M = 27.71$, $SD = 13.50$), $t(33) = 3.64$, $p < .01$, Cohen's $d = .42$; and that their ratings to illusion and control statements during asynchrony did not differ significantly ($p = .71$). Hence, S1-3 did measure the RHI because there was the expected difference in the pattern, in the expected direction, of responses to the statements. S4-11 were excluded from further analysis and S1-3 entered as a 3-level statement factor in further analyses such that only they were compared across conditions.

      Synchrony (synchronous vs. asynchronous touch). There was a main effect of this factor, $F(1, 32) = 35.00$, $p < .01$, Cohen's $d = 0.42$, such that participants' ratings of the three statements were more affirmative during synchronous touch ($M = 34.44$, $SD = 18.73$) than during asynchronous touch ($M = 26.93$, $SD = 16.99$) (see Figure 3 and Figure S1). This suggests that irrespective of condition a RHI was experienced by both groups during synchronous touch and experienced to a lesser degree during asynchronous touch.

Goggles (no goggles vs. goggles). There was a main effect of this factor, F (1, 32) = 9.65, p < .01. There was a two-way interaction between this factor and group (control/ASD) F (1, 32) = 4.77, p = .04, and a three way interaction between those two factors and stimulation (manual/machine touch), F (1, 32) = 4.65, p = .04.

To test this three way interaction, two way repeated measures ANOVAs were performed for each group separately. The control group were more in agreement with the statements when wearing goggles than not wearing goggles, consistent with the prediction that the standard no-goggles version of the RHI requires overcoming proprioceptive discrepancy; main effect of goggles; F (1, 16) = 11.20, p < .01, Cohen's d = .61, with ratings for goggles (M = 35.92, SD = 16.24) larger than for no goggles (M = 25.97, SD = 16.22). For the control group, there was also a main effect of stimulation, F (1, 16) = 4.60, p = .05, Cohen's d = .27, with ratings for manual touch as expected somewhat higher (M = 32.03, SD = 14.58) than for machine touch (M = 27.87, SD = 15.74).

For the ASD group, in contrast, this separate two-way ANOVA showed no main effect of goggles. There was a main effect of stimulation, F (1, 16) = 4.91, p = .04, and a stimulation – goggles interaction, F (1, 16) = 6.55, p = .02. Further t-tests failed to reach significance after correction for multiple comparisons with the only trend, t(16) = 2.81, p = .013, Cohen's d = .24, being that when wearing goggles the RHI seems somewhat stronger during manual touch (M = 33.73, SD = 21.33) than machine touch (M = 28.85, SD = 19.72).

This complex picture suggests that (i) the control group but not the ASD group had the predicted overall response that wearing goggles intensifies the RHI (See Figure 4); though (ii) when wearing goggles the ASD participants trended towards being more sensitive to whether a human touched them or a machine.

Item (Touch on rubber hand vs. non-hand cardboard box). Results for this factor are given in the Appendix.

Stimulation (Manual touch vs. machine touch). Results for this factor are given in the Appendix.

Proprioceptive drift

There was no significant difference in drift between synchronous and asynchronous touch. There was a between subjects main effect: irrespective of condition, the control group had more proprioceptive drift towards the rubber hand (or box) than the ASD group, F (1, 31) = 5.46, p = .03, Cohen's d = 0.57. This suggests that seeing the rubber hand (or box) being touched, whether synchronously or asynchronously, while not seeing the real hand is associated with proprioceptive estimates in the direction of the rubber hand (or box) in controls (M = 3.72, SD = 3.68) but significantly less so in individuals with ASD (M = 1.60, SD = 3.80). In the context of visuotactile-proprioceptive conflict and occlusion of the real hand, ASD participants seem to have more accurate or less integrated proprioception than controls. See Figure 5.

Reach trial

The area under the curve (AUC) for the acceleration force vector for each 5s reach trial was calculated. No main effect for synchronous vs. asynchronous touch was found but there was an interaction between this factor and participant group, F (1, 32) = 5.69, p = .02, suggesting that controls and ASD participants had different reaching profiles during

synchrony and asynchrony. To investigate this further the 5s period was split into four periods of 1.25s duration each, based on the assumption that the elements of the movement (such as onset latency and peak acceleration) would differ over the course of the entire period. ANOVAs were performed for all four periods, and showed that the interaction in question survived multiple comparison correction (Bonferroni) for the second 1.25s period only, F (1, 32) = 11.59, $p < .01$.

Post-hoc t-tests were performed for the difference between synchrony and asynchrony in each group for this period. The control group had significantly *less* acceleration for synchronous touch than for asynchronous touch, $t(16) = -2.90$, $p = .01$, Cohen's $d = -.36$. For the ASD group it was the opposite pattern, they had significantly *more* acceleration in synchronous touch than in asynchronous touch $t(16) = 2.47$, $p = .025$, Cohen's $d = .37$, (see Figure 6). This suggests that acceleration was less for controls when they tended to experience the RHI than when tending to not experience it, and, conversely, that ASD participants had more acceleration in their reaching movement when they tended to experience the illusion than when tending to not experience it.

Skin temperature. There was no effect of any factor on skin temperature.

Discussion

Visual, tactile and proprioceptive elements have been implicated in findings on multisensory processing in ASD. This makes the rubber hand illusion (RHI) an interesting phenomenon to study in the context of ASD because the RHI involves a complex interplay of these elements. Here, different variants of the RHI were therefore explored in high-functioning ASD participants and healthy controls.

It was found that individuals with ASD do experience this rubber hand illusion to much the same degree as the control group. That is, they have a similar propensity for agreeing that they experience the touch sensation as being felt on the rubber hand. However, as expected this experimental paradigm revealed a number of underlying differences: (1) the ASD group did not have the same overall sensitivity to visuotactile-proprioceptive discrepancy between the rubber hand and the real hand as the control group. (2) The ASD group displayed less general proprioceptive drift towards the rubber hand than the control group did. (3) Patterns of acceleration in a reach trial reflected the presence of the illusion in both groups but the ASD group had the reverse pattern of acceleration from the control group.

A number of further measures gave no or inconclusive results (presented in the Appendix). The item factor (rubber hand vs. cardboard box) did show a group difference that seemed in the expected direction but was complicated by interaction with other factors. The stimulation factor (manual vs. machine touch) was significant in the expected direction but did not show any group differences. There was no significant result for the skin temperature measurement that was included in the experiment. Temperature changes have been associated, albeit with some variability, with the presence of the illusion but in the current paradigm did not indicate this. This may be because the illusion is relatively weak or because the touch did not occur for long enough. Alternatively, it may suggest that the temperature measure is not a reliable indicator of the illusion.

The findings listed as (1)-(3) above are discussed below in terms of precision, integration and prior assumptions for proprioceptive and visuotactile estimates.

The RHI was experienced either in the standard version, without goggles, or in a more recent version with video goggles (Hohwy & Paton, 2010) akin to studies of the full body illusion (Ehrsson, 2007). The key difference between these versions is the presence or

absence of visuotactile-proprioceptive discrepancy. In the standard version the touch is felt in a different location from where proprioception suggests the real hand is. In the goggles version, there is concordance in personal space between the seen location of the rubber hand and the felt location the real hand (Figure 1). It was hypothesised that the illusion would be rated higher when there is no proprioceptive discrepancy to overcome. This was found for the control group. The picture for the ASD group was more complex but suggests that, though the goggles are not wholly ineffectual, this group did not in general have a stronger illusion while wearing goggles. This indicates that in ASD as compared to controls, proprioceptive discrepancy or concordance does less to interfere with visuotactile integration of the touch sensation and the finger seen touching the rubber hand. This is consistent with the idea that whereas individuals with ASD experience fairly normal patterns of local, visuotactile integration, there are problems with integrating these estimates given estimations of a more global context (Happé & Frith, 2006; Simmons et al., 2009). The current finding leads to the more specific suggestion that this more global context may pertain to proprioception.

No significant effect of the presence of the illusion on proprioceptive drift was found in either group. This drift measure does not then distinguish synchronous from asynchronous touch in the current study. This is in contrast to a number of RHI findings (e.g., Longo et al., 2008). A contributing factor to this could be that, in contrast to other studies using proprioceptive drift (e.g., Tsakiris & Haggard, 2005), we did not obtain drift measures prior to inducing the illusion. This was omitted to minimise the burden on participants in this complex experimental design. However this prevents obtaining difference scores that normally enhance statistical power, given both trial to trial and person to person differences in proprioceptive biases towards the midline. Furthermore, there is now evidence that proprioceptive drift is not necessary to experience the RHI as the processes underlying drift

differ from the processes giving rise to the subjective experience (Ehrsson et al., 2004; Fiorio et al., 2011; Kammers et al., 2009; Rohde et al., 2011). Rohde et al., (2011), in particular, suggest that the difference in drift between synchronous and asynchronous touch requires continuous exposure to asynchronous touch; our touch sequences were not continuous but had frequent pauses very similar to those of Rohde et al., so this may also help explain why there was no drift difference. Finally we notice that though proprioceptive drift did not distinguish the two types of touch, reach acceleration, described here for the first time, did.

There is some evidence for general proprioceptive drift towards the midline during visual occlusion (Gross & Melzack 1978; Gross et al., 1974; Wann & Ibrahim, 1992; though see Desmurget et al., 2000) and consistent with this it is here found that, regardless of touch type (synchronous or asynchronous), the control group experienced general drift of their proprioceptive estimate towards the (midline) location of the rubber hand. In contrast, significantly less such general drift was seen in the ASD group. Thus when asked for a proprioceptive estimate of their right hand's location, individuals with ASD gave a more accurate estimate than controls. They seem less sensitive to the global context of the rubber hand and this finding can then be interpreted in terms of a bias, or enhanced sensitivity, towards local processing (Dakin & Frith, 2005; Simmons et al., 2009; Mottron et al., 2006; Rippon et al., 2007). Further study is needed to explore this but it may indicate a difference in the response to deprivation of visual input of the limb such that control participants default to a midline estimate as their proprioceptive estimates decay, whereas individuals with ASD do so to a lesser extent perhaps as a consequence of weaker top-down integration with more global context.

A difference in reach acceleration under different sensory inputs could be related to increased uncertainty leading to less confident movement, characterised with less

acceleration (Jeannerod, 1986; Rossetti et al., 1995; Kording & Wolpert, 2004; Sober & Sabes, 2003). Uncertainty can have multiple sources: uncertainty in prior assumptions, mismatch with expectations leading to prediction errors as movement unfolds, and lack of precision of sensory estimates (Bays & Wolpert, 2007). In the control group, uncertainty during synchronous touch could thus stem from prior assumptions about the trickery involved in the experimental set-up, prediction error generated when the rubber hand fails to move, and imprecision in the drifting proprioceptive estimate. During asynchronous touch reaching could be more confident because the visual input is deemed irrelevant and thus weighted less in visuotactile-proprioceptive integration (Sober & Sabes, 2005; Rohde et al., 2011).

The challenge then is to try to explain why the pattern of acceleration is reversed in the ASD group. The notion of a bias for local over global sensory processing in ASD (Happe & Frith, 2006; Ropar & Mitchell, 2002) suggests individuals with ASD may weight prior assumptions less against the ability to explain away sensory input. This would mean that uncertainty in the priors (e.g., the low prior probability of a disintegrated body schema) is not inherited as much in the posterior estimate, and would be less likely to curtail movement acceleration than it is in the control group. Also, the prior assumption which is being weighted less in ASD could be the one normally induced by the RHI: that seen and felt touch is located where one's hand is. Then the failure of the rubber hand to move would generate less prediction error and thus less uncertainty during movement.

More fundamentally, local processing bias, as well as enhanced sensory processing in ASD (Mottron et al., 2006) could be related to increased precision (i.e., less variance) of local sensory estimates. Such increased precision would impact on uncertainty and sensory integration (Ernst & Banks, 2002; van Beers et al., 1999; Bays & Wolpert, 2007). Briefly, overly precise estimates are less likely to gain much added precision in Bayesian integration,

and they are more likely to be represented confidently as discrete. Precision can thus stand in

the way of sensory integration. Given that sensory integration helps produce a more accurate

representation of complex states of affairs in the world, this means that increased precision of

local estimates can come at the cost of accuracy of more global estimates. However, the

precision and not the accuracy may be what drives movement parameters such as acceleration,

giving increased acceleration with increased precision of sensory estimates regardless of

whether these estimates are integrated in an accurate representation or not. In fairly simple

tasks there seem to be no difference in proprioceptive precision and accuracy for ASD

(Fuentes et al., 2010), however, it remains a possibility that these abilities are impaired in

ASD in more complicated, context-dependent scenarios such as the RHI, where

proprioception is processed in the context of a visible rubber hand.

In terms of predictions, it seems then that processing differences for the RHI give rise

to differences in the illusion's sensorimotor after effects and that other multisensory illusions

would also display after effect differences in ASD. There might be, for example, a decrease

in the rapidly induced auditory plasticity seen after experiencing the ventriloquist effect

(Recanzone, 1998).

Further studies are needed to explore these findings and the speculative

interpretations given of them here. Limitations of the current study that could be improved

upon in further studies include the relatively modest sample size as well as uncertainty about

the participants' subjective experience of the RHI. Participants may have interpreted the VAS

on which they rate illusion strength differently so it is difficult to say how strongly they each

experienced the RHI. It seems reasonable to claim it was a relatively weak version of the

illusion as responses tend to cluster around the middle of the VAS. Finally, to further

interpret the reach trial findings it would be desirable to have a more full record of movement

parameters that includes velocity, displacement and angular moment.

The findings presented here suggest that complex multisensory integration, such as

seen in the rubber hand illusion, is fertile ground for understanding the sensory processing

differences in autism spectrum disorder. In the wider perspective, these sensory differences

could be related to the broader range of symptoms in ASD for example by making it less

likely that individuals with ASD, in spite of precision of their sensory estimates, can benefit

fully from the accuracy normally afforded by multisensory integration. An example here

could be the way integration of voice and mouth movement in non-illusory situations

normally affords accurate estimates of what is said. For further studies of multisensory

processing in ASD, it may be of importance to separate the precision and accuracy of local

and global sensory and proprioceptive estimates. Finally, though based on sensory integration,

the RHI pertains to complex psychological and even philosophical issues of body ownership,

body image processing and conscious self-awareness. Little is known about these constructs

in individuals with ASD and further study of this specific illusion may therefore deepen our

understanding of this condition.

Conflicts of Interest

The authors declare that they have no conflict of interest.

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Appendix

Supplementary Results

Item (rubber hand vs. cardboard box). There was a main effect of this factor, F (1, 32) = 39.53, $p < .01$, a two-way interaction with participant group F (1, 32) = 4.92, $p = .03$, and a three way interaction with stimulation (manual/machine touch) F (1, 32) = 4.36, $p = .05$.

This interaction was explored in separate two way repeated measures ANOVAs for controls and ASD respectively. For control participants, as expected, there was a main effect for the item factor, F (1, 16) = 28.24, $p < .01$, Cohen's $d = .72$, such that they rated the illusion stronger when they observed the touch performed on a rubber hand ($M = 36.57$, $SD = 15.07$) than when the touch was done on a cardboard box ($M = 25.32$, $SD = 16.23$). The ASD group also had a main effect of this factor, F (1, 16) = 11.51, $p < .01$, Cohen's $d = .27$, such that they rated the illusion somewhat stronger when touch was done on the rubber hand ($M = 33.11$, $SD = 20.65$) than when there was touch on the cardboard box ($M = 27.73$, $SD = 19.17$).

In addition, in the ANOVAs for both groups there was a main effect of stimulation. For controls, F (1, 16) = 4.60, $p = .05$, Cohen's $d = .15$, suggesting controls rated manual touch somewhat higher ($M = 32.08$, $SD = 14.58$) than touch by the machine ($M = 29.87$, $SD = 15.74$). For ASD participants, F (1, 16) = 4.91, $p < .04$, Cohen's $d = .13$, suggesting the ASD participants rated manual touch somewhat higher ($M = 31.70$, $SD = 20.46$) than touch by the machine ($M = 29.15$, $SD = 19.11$).

Stimulation (Manual touch vs. Machine touch). There was the expected main effect of this factor F (1, 32) = 9.48, $p < .01$, with participants rating manual touch somewhat higher ($M = 31.82$, $SD = 17.77$) than machine touch ($M = 29.51$, $SD = 17.50$), Cohen's $d = 0.13$. There was a two-way interaction of this factor with the three-level statement factor F (2, 64)

= 4.28, *p* = .22. Post hoc analysis revealed that this interaction was mainly due to differences in responses to S1, *t* (33) = 3.09, *p* < .01, Cohen's *d* = .22, with responses to this statement being higher during human touch (*M* = 41.10, *SD* = 23.47) than during machine touch (*M* = 36.17, *SD* = 21.32). Differences in responses to S2 and S3 did not reach significance after correction for multiple comparisons.

Reach trial. Further analysis. Two further main effects were found for the full 5s period. There was a main effect for goggles, *F* (1,32) = 4.66, *p* = .04, Cohen's *d* = .42. Participants reached with more acceleration with goggles (*M* = 264.66, *SD* = 41.22) than without goggles (*M* = 249.01, *SD* = 32.84). A main effect here is to be expected since there is a difference between seeing the cylindrical target object on the screen in the goggles vs. seeing it without goggles and reach movement would reflect this difference. A main effect was also found for the item factor, *F* (1,32) = 5.23, *p* = .03, Cohen's *d* = .13. Participants' reaching acceleration was somewhat stronger when viewing the box (*M* = 258.67, *SD* = 30.47) than the rubber hand (*M* = 255.04, *SD* = 31.68). This may indicate that they were somehow influenced by the rubber hand and compensated for the size of it in their reaching and/or wrist movement.

Supplementary Figure

Figure S1

Figure Caption sheet

Fig 1 (a) Experimental set-up in the no goggles condition (standard rubber hand illusion with proprioceptive discrepancy between seen rubber hand and unseen real right hand). (b) Experimental set up in the goggles condition (virtual reality rubber hand without proprioceptive discrepancy between seen rubber hand and felt real right hand)

Fig 2 Variations of the rubber hand illusion. (a) manual touch on rubber hand, (b) manual touch on non-hand object, (c) machine touch on rubber hand, (d) machine touch on non-hand object

Fig 3 Ratings for statements S1-3 (averaged) during synchronous and asynchronous touch. Both control and ASD participants rate the statements higher during synchrony than asynchrony; (** : $p < .01$); see also Figure S1

Fig 4 Ratings for statements S1-3 (averaged) without and with goggles. Controls but not ASD participants rate the statements lower without goggles and higher with goggles; (** : $p < .01$)

Fig 5 Proprioceptive drift for control group vs. ASD group in synchronous vs. asynchronous touch conditions, as well as proprioceptive drift across all conditions. The ASD group shows less drift than the control group regardless of condition; (*: $p < .01$)

Fig 6 Area under the curve for the acceleration force vector (for the 2nd 1.25s time interval) in the reach trial. Acceleration during synchronous and asynchronous touch differ for both ASD and controls but in different directions; (** : $p < .01$; *: $p < .01$)

Fig S1 Ratings for statements each of S1-3 during synchronous and asynchronous touch.

Figure 1
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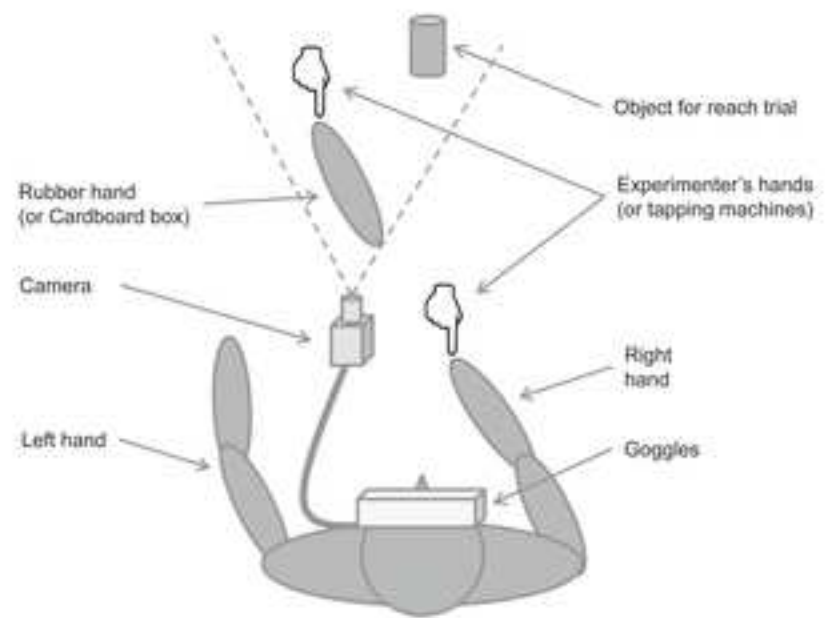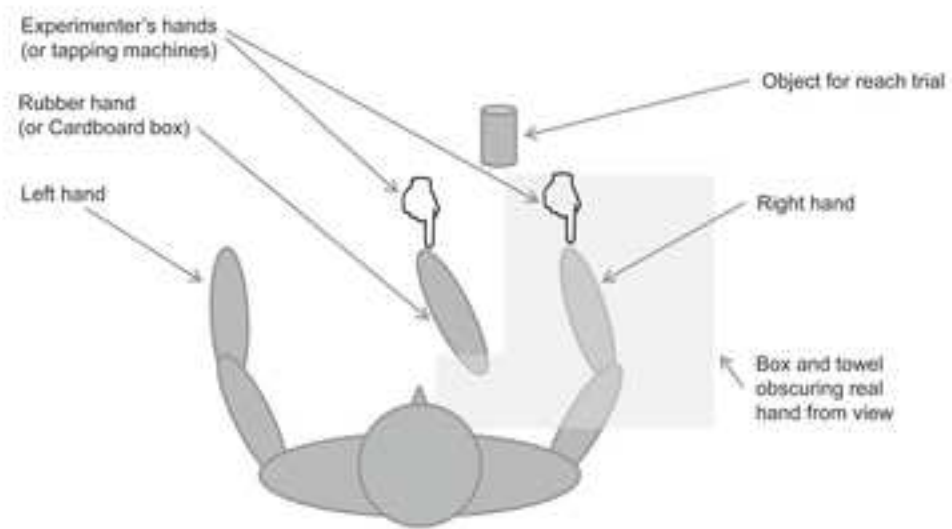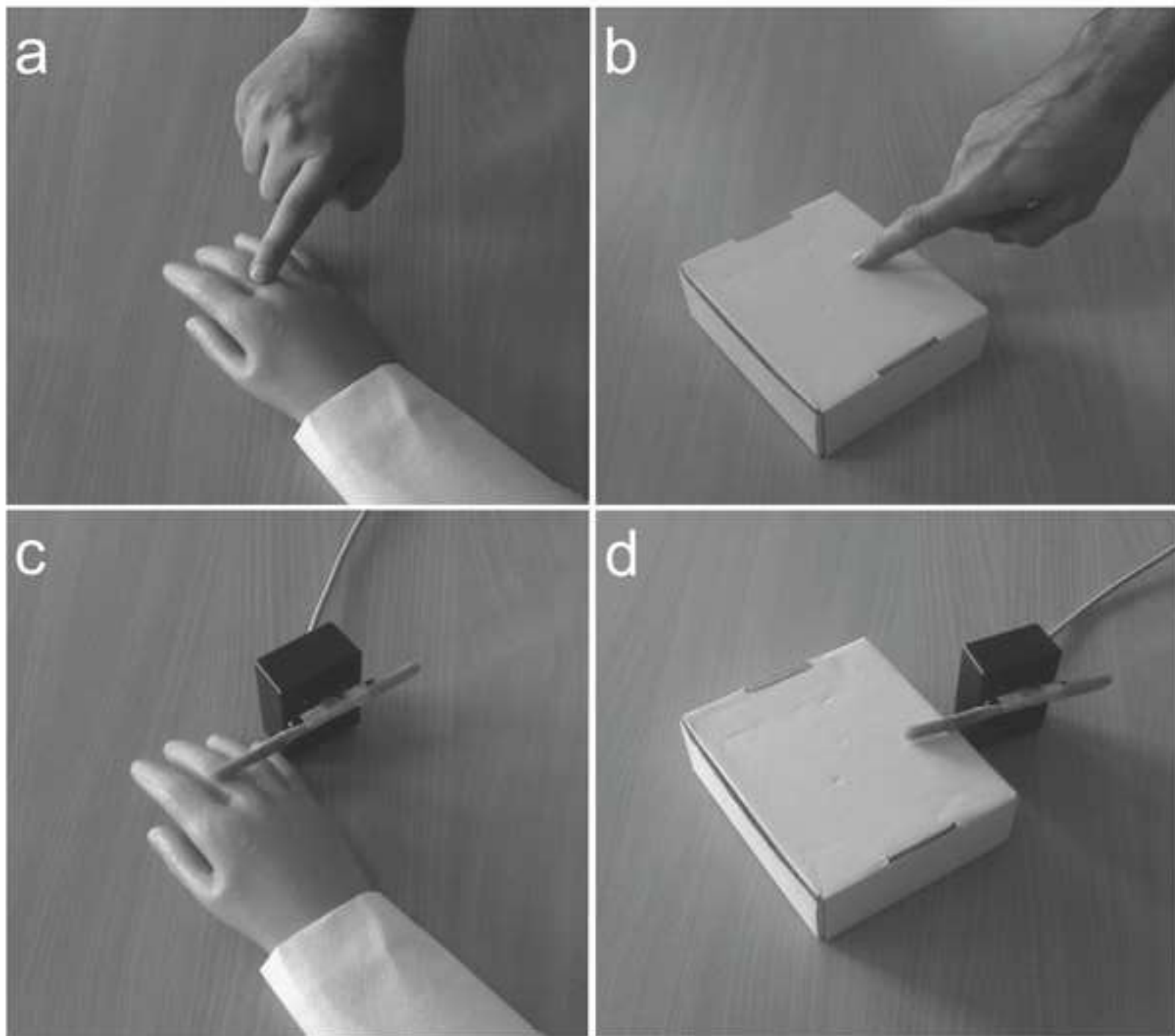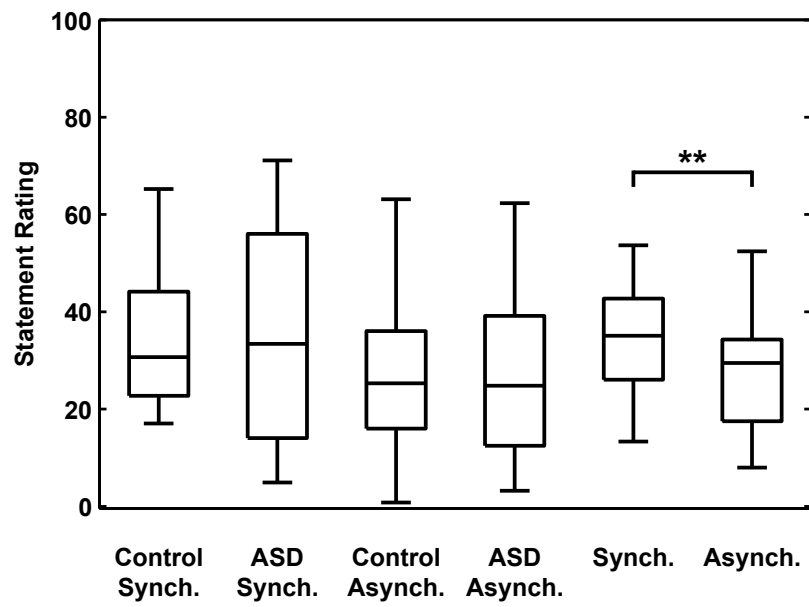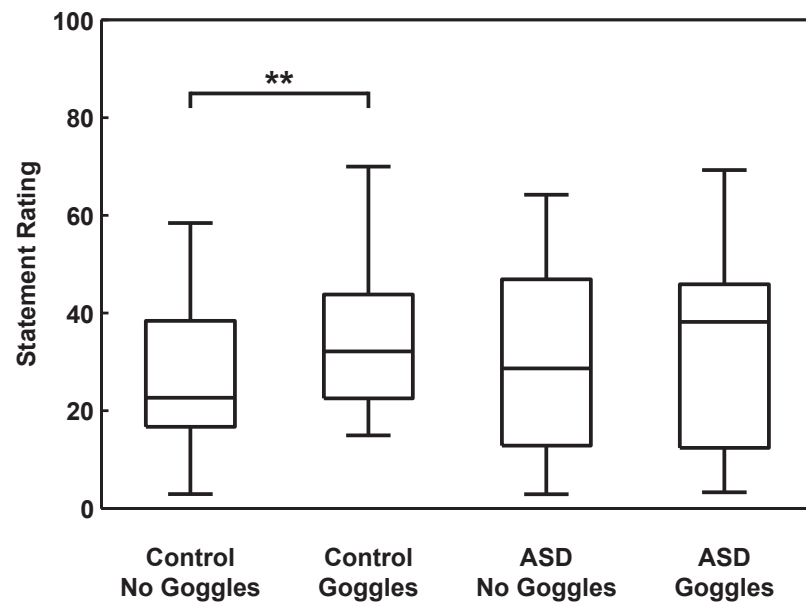
Figure 2
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Figure 3

Figure 4
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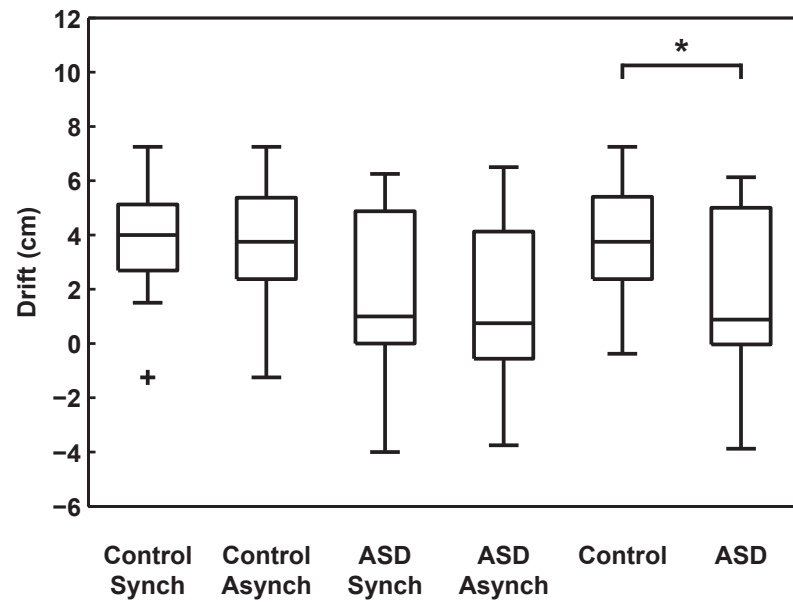
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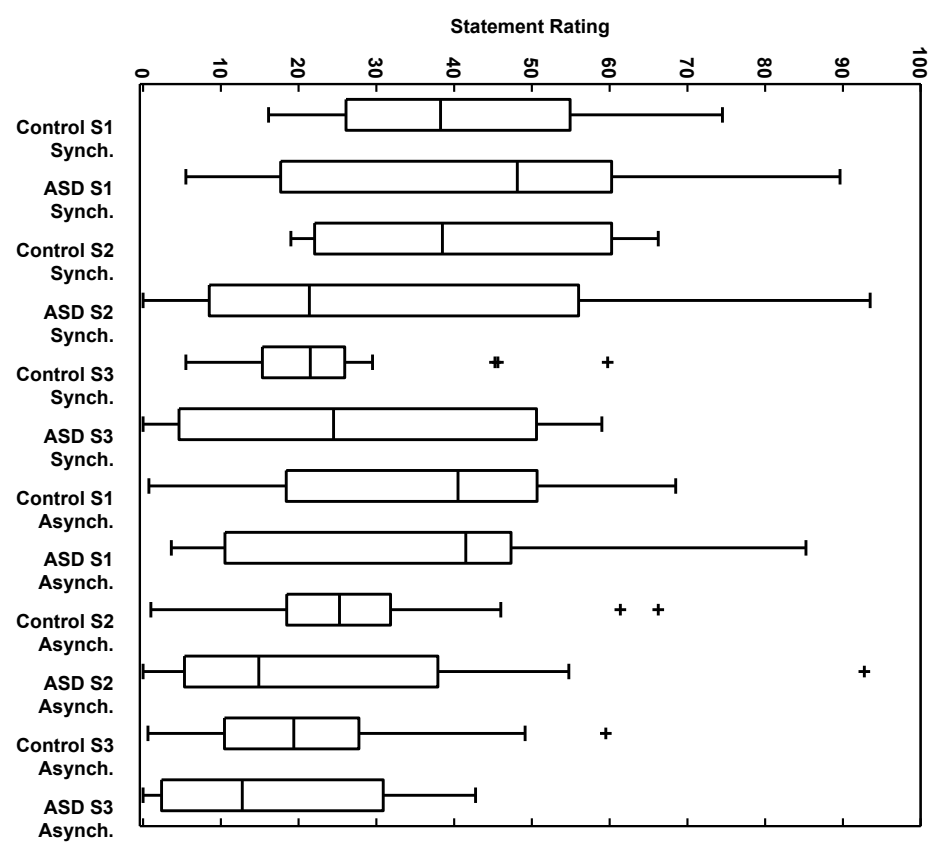Statement Rating
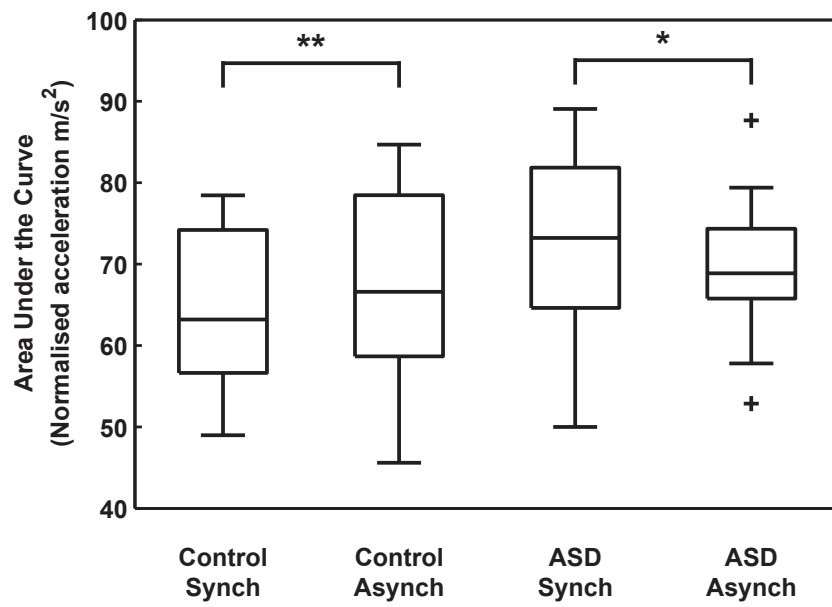
Statement No	Statement text (adjusted for trial variations)
S1	It seemed as if I was feeling the touch of the finger/piece of foam in the location where I saw the rubber hand/box being touched.
S2	It seemed as though the touch I felt was caused by the finger/piece of foam I could see touching the rubber hand/box.
S3	It felt as if the rubber hand/box was my hand.
S4	It felt as if my (real) hand was getting cold.
S5	It seemed as if I might have more than one right hand or arm
S6	It seemed as if I was in two different locations at the same time.
S7	It felt as if my (real) hand was turning 'rubbery'
S8	The rubber hand/box began to resemble my own (real) hand, in terms of shape, skin tone, freckles or some other visual feature.
S9	I found the touch of the finger/piece of foam on my hand was pleasant.
S10	I found myself liking the rubber hand/box.
S11	The room temperature changed during the experiment.
S12	I found that experience enjoyable.

Table 1 Computerised, randomised questionnaire presented after each trial; participants were asked to use a computer mouse to rate their agreement with each statement on a visual analogue scale marked at the ends with 'strongly disagree' and 'strongly agree'

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