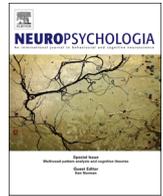




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Movement under uncertainty: The effects of the rubber-hand illusion vary along the nonclinical autism spectrum

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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.

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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 nonclinical samples are consistent with sensory differences seen in clinically diagnosed ASD (e.g., Donohue, Darling, & Mitroff, 2012; Walter, Dassonville, & 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; Frith, 1989; Happé &

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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 (Frith, 1989; Happé & 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 (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, Lawson, & Frith, 2013; Hohwy, 2013; Mitchell & Ropar, 2004; Paton, Hohwy, & Enticott, 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 et al., 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 et al., 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

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