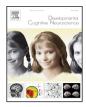
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Observing and participating in social interactions: Action perception and action control across the autistic spectrum

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ABSTRACT

Autism is a developmental condition, characterized by difficulties of social interaction and communication, as well as restricted interests and repetitive behaviors. Although several important conceptions have shed light on specific facets, there is still no consensus about a universal yet specific theory in terms of its underlying mechanisms. While some theories have exclusively focused on sensory aspects, others have emphasized social difficulties. However, sensory and social processes in autism might be interconnected to a higher degree than what has been traditionally thought. We propose that a mismatch in sensory abilities across individuals can lead to difficulties on a social, i.e. interpersonal level and vice versa. In this article, we, therefore, selectively review evidence indicating an interrelationship between perceptual and social difficulties in autism. Additionally, we link this body of research with studies, which investigate the mechanisms of action control in social contexts. By doing so, we highlight that autistic traits are also crucially related to differences in integration, anticipation and automatic responding to social cues, rather than a mere inability to register and learn from social cues. Importantly, such differences may only manifest themselves in sufficiently complex situations, such as real-life social interactions, where such processes are inextricably linked.

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1. Autism: is it a social or a sensory condition?

Autism is a pervasive developmental condition, which is characterized by difficulties in social interaction and communication, as well as restricted interests and repetitive behaviors. This short definition already suggests that autism's cardinal characteristics fall into two broad categories, first, a collection of social aspects

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and, second, a group of non-specifically or less social (hereafter, for simplicity, non-social) aspects (e.g. Huerta et al., 2012; Fitzgibbon et al., 2013). Indeed, the vast majority of hypotheses during the last decades have mainly focused on facets either belonging to the one or the other of these two categories.

For instance, on the non-social side, the *weak central coherence* hypothesis considers autism as a different, detailed-oriented cognitive and perceptual style (Frith, 1989; Happé and Frith, 2006). More precisely, it claims that people with an autism spectrum disorder (ASD) tend to process information locally, rather than globally. According to this idea, people with ASD perceive the world differently in a number of aspects such as visual and auditory infor-

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mation. Similarly, the executive dysfunction hypothesis (e.g. Hill, 2004) focuses on difficulties that people with ASD face when it comes to executive functions, i.e. problems with functions such as planning, flexibility, inhibition and working memory. On the other hand, one of the first theories focusing on specifically social aspects of the condition, the Theory of Mind hypothesis (Baron-Cohen et al., 1985) proposed that individuals with autism lack a specific meta-representational capacity, namely a "theory of mind", which prevents them from inferring other people's mental states, such as beliefs, emotions or desires. Later, it was suggested that implicit and spontaneous mechanisms of mentalizing might be the ones that are primarily linked to relevant difficulties in autism, rather than explicit processes as initially believed, which might be more easily compensated for through strategic learning (Senju et al., 2009; Schilbach et al., 2011). A second theory focusing on the social dimension emphasizes a special category of neurons, which are thought to be active both when an action is performed and observed (Di Pellegrino et al., 1992; Rizzolatti and Craighero, 2004). This broken mirror neuron hypothesis of autism proposes that impaired social skills in autism are related to dysfunctions in the putative human mirror neuron system making it difficult for individuals with autism to simulate and thus understand others' behavior (MNS; Altschuler et al., 2000; Ramachandran and Oberman, 2006). Some studies have offered supportive evidence for the involvement of the MNS (e.g. Perkins et al., 2010). However, both the validity of a broken MNS and a direct, causal relationship between the MNS and social skills in autism, have been challenged by other reports (e.g. Southgate and Hamilton, 2008). Differences in MNS activation between neurotypical individuals and persons with an ASD could be alternatively traced back to potential modulatory effects of the so called "mentalizing system", a set of brain regions known to subserve explicit mental state attribution (e.g. Wang and Hamilton, 2012; Cook and Bird, 2012; Dumas et al., 2014a). Yet again, the social motivation (SM) hypothesis focuses on motivational rather than cognitive aspects (Chevallier et al., 2012). It proposes that people with autism lack the social drive inherent to non-autistic individuals, which would assist them in exploiting the necessary learning opportunities in social interactions in order to develop relevant expertise in social cognition. More precisely, this hypothesis is settled upon the fact that the propensity to initiate social contacts, social orienting, social seeking and liking, appears to be diminished in ASD. This idea, however, is brought into question by evidence, which suggests that individuals with autism are in fact interested in social interaction and exchange, but only when the interaction is structured in such a way that it suits their needs (Wing and Gould 1979; Schilbach 2016a).

In short, several important theories on autism have advanced our understanding in crucial facets of the condition; however, there is still no established unified account, which could explain social and sensory aspects of autism in the context of their inherent interrelationship. In fact, it has even been suggested that a single theory might be intractable (Happé, 2003; Happé et al., 2006; Gallagher and Varga, 2015). However, recent developments centered around the idea of the human brain organized around principles of Bayesian inference and predictive coding have recently refueled interest in a unifying account of autism: For instance, Pellicano and Burr (2012), adopted a standpoint to argue that non-social features of autism might be explained in reference to attenuated Bayesian priors (so-called hypo-priors), which suggests that previous experiences might be less important when processing current sensory input for individuals with autism. This hypothesis predicts the more accurate and acute perception in autism, driven primarily by perceptual evidence as opposed to prior knowledge, as well as the sense of being overwhelmed by this information, which is commonly reported by individuals with autism. The hypopriors hypothesis was then reformulated (Friston et al., 2013; Van

Boxtel and Lu, 2013) within the predictive coding scheme, a more specific Bayesian account (Mumford, 1992; Friston, 2005; Friston, 2008; Clark, 2013), while considering social aspects of cognition and behavior as well (Lawson et al., 2014; Van de Cruys et al., 2014).

The predictive coding framework relies on the idea that sensory information is processed hierarchically in levels of increasing abstraction. In this setting, prediction errors (i.e. the discrepancy between predictions and incoming information) ascend the processing hierarchy for optimizing neural configuration in generating accurate predictions, which descending the hierarchy, are contrasted to sensory input. More concretely, higher levels of the hierarchy produce predictions, which are tested against the input information of the immediate lower levels. Propagating only the prediction error and not the actual incoming information to higher levels is an efficient and resource-oriented way of reducing the bandwidth of the processed information. The neural processes and computations needed to extract regularities in the environment can be described in terms of Bayesian inference. In this regard, the brain is thought to represent information accessed via the sensory organs in the form of probability densities; these probabilities are maintained via a combination of already gained experience (socalled priors) and newly sensed information (evidence). The more confidence (precision) is placed on the validity of experience the less the latter is updated in the face of new incoming information. The ultimate goal of such a predictive system is the effective minimization of the prediction error, through perception, learning and action (for a comprehensive review of traditional theories and a future integrative direction in autism research see Bolis et al., under review)

Such endeavors of developing a more unified account of autism are further supported by evidence that social and non-social domains are not as independent as once might have been assumed in research practice. For instance, Linkenauger et al. (2012) showed that deficits of individuals with autism in relating information about their own bodies' action capabilities to visual information specifying the environment, strongly predicted the degree of social and communicative difficulties. Additionally, MacDonald et al. (2013) demonstrated that children with autism that showed weaker motor skills had greater social communicative skill difficulties. Moreover, Leekam et al. (2007) linked the distinct sensory processing in autism with higher-level social processes. Having said that, focusing on 'internal' (i.e. within individual brains) dynamics has, indeed, yielded informative insights, such as providing insights into the relevance of a dysbalance of inhibitory/excitatory neurotransmission in autism (e.g. Robertson et al., 2016). Additionally, considering 'external' (i.e. collective socio-cultural) dynamics, such as the role of collaborative morality (Spikins et al., 2016) or social expectations of others (Jensen et al., 2016), can prove to be crucial in achieving a comprehensive account of autism. However, studying 'internal' and 'external' dynamics in isolation and thus neglecting the dialectics between the individual and the collective (Vygotsky, 1930–1935/1978; views of Vygotsky and colleagues in Dafermos, 1930–1935/2002), which are inherently intertwined across multiple temporal scales (i.e. from evolutionary and cultural to developmental and daily learning processes), might result in misconstruing the essence of a condition such as autism (Bolis et al., under review).

More specifically, Vygotsky and colleagues argued that the development of the human mind has its origin at the interaction between the individual and society, viewing culture and social interaction as the major developmental driving forces (e.g. Vygotsky, 1934/2008; 1930–1935/1978). When it comes to children with certain "disabilities", one of the main propositions of the so-called cultural historical approach was the recognition of primary and secondary difficulties. It was suggested that it is not the primary difficulties, which are directly linked to the physi-

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