

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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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 subservise 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 inter-relationship. 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 hypo-priors 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 (so-called 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-

cal condition, that are crucial to a child's development, but rather the secondary ones, which relate to an exclusion from sociocultural activities, which other children freely participate in. Different factors can contribute to this, such as unsuitable cultural and technological environment or social expectations of others. Interestingly, such lines of thought lend support to alternative avenues of research and intervention, which will not exclusively target the person of interest (i.e. an individual with autism in our case), but the social environment as well, e.g. via personalizing education (Vittorias et al., 2008) or facilitating communication between people (Bolis et al., under review), bringing focus back to social interaction (Schilbach et al., 2013).

Taken together, we suggest that it may be the coupling and the inextricable interplay of sensory and motor functions (within an individual) rather than selective deficits thereof – and whether or not a given partner in a social interaction is more or less similar to the autistic person (at the interpersonal level), which play an important role in the development and manifestation of cardinal characteristics of autism.

In this article, we, therefore, review evidence, that addresses the integration of sensory processing and individual as well as interpersonal aspects of action control to suggest that individuals with high autistic traits are not 'blind' to social information in the environment, but the extent to which they update their beliefs and they are, thus, influenced by this information when making decisions and executing actions is lower than in individuals with low autistic traits. Furthermore, we review findings to suggest that a more comprehensive understanding of autism (and other psychiatric disorders) will have to rely upon studying it in the context of ecologically valid real-time social interactions as social difficulties are known to be more pronounced (or may only manifest) under such conditions (Schilbach et al., 2013; Schilbach, 2016a). Here, we propose that a mismatch in autistic trait-related perceptual abilities across individuals can lead to difficulties on a social level and briefly describe a two-person experimental setup and avenues for future research to formally investigate this.

2. From action observation to interaction in autism

An important initial suggestion for understanding and studying the biological basis of autistic symptomatology has been to focus on the ability of individuals with autism to observe and interpret actions in others. With regard to general visual abilities and the idea of an *eagle eye hypothesis* some studies have provided evidence for superior performance of individuals with autism on visual tasks (Dakin and Frith, 2005). Furthermore, evidence has been found to document an increased reliance on visuospatial information by ASD individuals, which was related to increased parietal brain activation (e.g. DeRamus et al., 2014). Such differences in visuo-spatial processing have also been related to differences at the level of neurotransmission: binocular rivalry, a visual function that is thought to rely on the balance of excitation/inhibition in visual cortex, has been shown to be tightly linked to GABAergic signaling in healthy controls, while this link was shown to be completely and specifically absent in autism (Robertson et al., 2016). Also, alterations of serotonergic functioning have been discussed as a contributory factor in autism (e.g. Cook and Leventhal, 1996). Interestingly, serotonergic modulation is also known to change the balance between different sources of neural activity in sensory systems (Lottem et al., 2016).

With regard to visual processing of others' actions, disruptions in the visual perception of biological motion have been discussed as a potential hallmark of ASD (Kaiser and Pelphrey, 2012). Here, an impaired sensitivity for processing the actions of others (as compared to observing objects) has been demonstrated (e.g. Blake et al.,

2003; Kaiser et al., 2010). These findings were also paralleled by neuroimaging results indicative of atypical neural response patterns to biological motion perception with point-light stimuli (e.g. Herrington et al., 2007). Such point-light displays are created by attaching markers to a person's body and head and then recording that person's movements so that only the point-lights are visible (cf. Johansson, 1973). These stimuli are easily manipulated and predispositions to process their social aspects can be inferred by detecting enhanced behavioral sensitivity to displays of biological motion relative to animal (Pinto and Shiffrar, 2009), object (Kaiser et al., 2010) or other kinds of biological motions (Manera et al., 2010, 2011). Importantly, differential responses to point-light displays of human movement are already observed in typically developing infants (Yoon and Johnson, 2009), which has been taken to suggest that biological motion perception relies on an early emerging, evolutionary conserved brain system (Kaiser and Pelphrey, 2012). A large body of work has demonstrated responses of the so-called "social brain" to point-light displays of biological motion (for a review see Blake and Shiffrar, 2007). Here, the posterior superior temporal sulcus (pSTS) has been discussed as a key component of the neural system that supports social perception.

Studies of the visual perception of biological motion have, thus, been thought to provide a window into social dysfunction in ASD. This was based upon the idea that autism is related to an early and initial failure to develop the specialized brain mechanisms for social perception which, in turn, results in abnormal development and the phenotypic expression of ASD (Pelphrey et al., 2011). Consequently, different studies have investigated behavioral responses to point-light displays of biological motion in individuals with autism. While some studies do find impairments, the overall picture appears to be rather mixed. Interestingly, several studies have documented that when asked to verbally describe point-light displays of biological motion, children and adults with ASD exhibit impairments in emotion perception, but intact action perception (Hubert et al., 2007; Moore et al., 1997; Parron et al., 2008). Recently, Cusack et al. (2015) have systematically addressed this question by using an extensive test battery of point light displays in adult individuals with autism. Here, it was consistently shown that action perception is intact when autistic individuals are motivated to perform the relevant task under controlled conditions. This finding was replicated by von der Lühse et al. (2016), who demonstrated that, when prompted and explicitly asked to assess point-light displays of individual and even communicative actions between two agents, participants with autism do not perform worse than a group of matched controls. Only when the complexity of the task is increased, however, by including noise signals, do individuals with autism show an impairment of interpersonal action prediction, i.e. no modulation in behavioral sensitivity for the detection of a second agent in light of a first agent, who generates a communicative action, is found. Interestingly, this ability to predict action sequences across two agents shows an inverse relationship with increasing autistic traits across the entire spectrum (von der Lühse et al., 2016).

Apart from the ability to perceive the relevant aspects of the social environment and their interrelation, it is, of course, imperative to be able to quickly and adaptively generate adequate behavior to respond to it. In this respect, a recent suggestion has been that social perception and cognition may be fundamentally different when we are actively engaged in interaction with others as compared to merely observing others. This difference may be particularly relevant in autism and has been taken to suggest that interactive situations rely more heavily on the integration of perception- and action-based processes (Schilbach et al., 2013). While a vast literature exists on the behavioral and neural correlates of social observation, much less is known about the behavioral and neural mechanisms of social interaction (Schilbach, 2015).

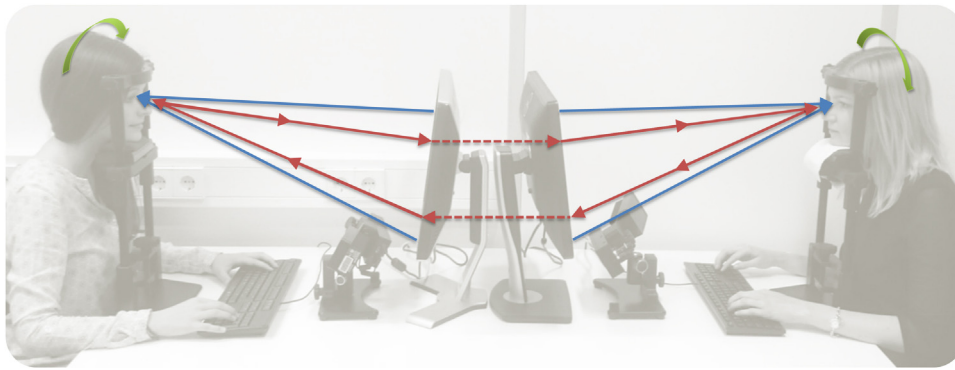


Fig. 1. Two-person psychophysiology setup: This setup allows for an investigation of the interrelation of sensory and social processes in direct, gaze-based social interaction between two persons (Person A, Person B); blue arrows: incoming sensory information from non-social stimuli; green arrows: intra-personal processes; red arrows: social interaction loop mediated by a micro-camera communication system. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In direct social interaction the unconscious imitation of the actions of others (often described as mimicry) is a powerful and ubiquitous behavior. Facial mimicry, for instance, is thought to be a form of “physiological linkage” or socio-emotional contagion between individuals (Dimberg, 1982; Dimberg et al., 2000) and assumed to be of considerable importance for interpersonal communication (Niedenthal et al., 2005; Schilbach, 2016b). Conversely, alterations of involuntary facial reactions (e.g. due to conditions resulting in facial paralysis) may have a detrimental effect on the quality of interpersonal communication (Cole, 2001; Oberman et al., 2007). In a series of studies, Schilbach and colleagues investigated the behavioral and neural correlates of facial mimicry by using anthropomorphic virtual characters that showed either self- or other-directed facial expressions (e.g. smiling) as compared to arbitrary facial movements (e.g. puckering; Schilbach et al., 2006; Mojzisch et al., 2006; Schilbach et al., 2008). In these studies, it was shown that attention allocation, as assessed by fixation duration, was specifically related to the perception of self-directed stimuli. EMG measurements demonstrated that facial activity was influenced by the perception of socially relevant facial expressions and showed spontaneous, involuntary facial responses irrespective of whether the facial expression was directed towards the observer or not (Mojzisch et al., 2006).

In a separate fMRI study, it was demonstrated that specific brain activations are related to the occurrence of involuntary facial movements in human observers in response to the perception of socially relevant facial expressions shown by perceived others. These activations comprise but extend beyond classical motor regions (i.e. face motor area) and include other regions of the social brain, such as the mentalizing system. While activity in motor cortex might help to generate a representation of the action which may, in fact, translate to mimicking that behavior oneself, involvement of the mentalizing system might contribute to social cognition by processing the differentiation of self and other. In dyadic interaction both mechanisms are crucially important as a facial expression might highlight someone else’s internal state, but could also refer to some object or might be expressive of the assessment of the vis-à-vis behavior or the process of interacting itself. Whether mimicry responses are abnormal in individuals with ASD has been subject of long-standing debate. Seminal studies by Heyes and colleagues have demonstrated that individuals with ASD, in fact, do show automatic imitative behavior (e.g. Bird et al., 2007; see also Southgate and Hamilton, 2008). More recently, Hamilton and co-workers (Forbes et al., 2016) showed that individuals with ASD also show mimicry, but they do not show an enhancement of mimicry responses in a gaze-based social context as neurotypical individuals do; hence providing support for the social top-down response mod-

ulation (STORM) model of mimicry in autism, in that the mimicry response is not top-down modulated by social context.

In another series of studies conducted by Schilbach et al. (2010, 2011), an action control paradigm was used, which required that participants performed spatially congruent or incongruent button presses to respond to an unpredictable change in the visual stimulus. In order to investigate the effect of social context on behavioral and neural mechanisms of action control, the stimulus type was varied to include both social (face stimulus) and non-social (geometric shape) stimuli. Using this paradigm it was shown that the so-called incongruity costs, i.e. longer reaction times necessary to generate a spatially incongruent as compared to a congruent response, were significantly smaller for the social as compared to the non-social stimulus in healthy controls. At the neural level this effect reflected by a differential increase of neural activity in subcortical structures relevant for the habitual performance of actions (caudate nucleus) as well as regions involved in action monitoring (ACC), action preparation (IFG) and social cognition (dorsomedial prefrontal cortex). These findings indicate that even a minimal, gaze-based social context significantly and automatically changes the neural networks relevant for action control, which might explain the effortless and prompt behavioral adaptations that non-autistic individuals make in the presence of others. As expected, a group of individuals with high-functioning autism did show incongruity effects, but those were not modulated by the social context.

While the above described studies are informative, they do not provide an account of the computational mechanisms that may underlie differences in behavior and brain activity. As described in the introduction, recent developments in cognitive neuroscience have embraced a perspective that describes the brain as a “prediction machine” whose ultimate goal it is to construct a model of the environment in order to predict the causes of sensory input, to anticipate future states and to minimize the resulting ‘prediction error’. Specific theoretical commitments aside, all these accounts tend to agree in suggesting that perception in individuals with ASD may be more strongly driven by perceptual evidence as compared to prior knowledge. This may explain a stronger reliance on perceptual input, but may render ambiguous situations, in which sensory input is not sufficient to disambiguate, problematic, because they may require stronger reliance on prior knowledge. Consequently, such accounts can be seen to align with suggestions made by Wang and Hamilton (2012) that autistic symptomatology may result from difficulties in the context-sensitive, top down modulation of perceptual processing. In order to test, whether autistic traits are, in fact, related to differences in Bayesian inference, Sevgi et al. (2016) used computational modeling to investigate autistic trait-related

differences in the weighting of social and non-social information during reward-based learning and decision-making. In this study, it was shown that individuals with higher autistic traits are not 'blind' to social information in the environment and, in fact, do learn about it, but the extent to which they update their beliefs and are, thus, influenced by this information when making decisions is lower than in individuals with lower autistic traits. This again emphasizes that what might be different in autism is not merely the ability to process social information, but a propensity to actually use this information when generating actions oneself.

Until today, no consistent neurochemical, neurophysiological, or neuroanatomical abnormality has been detected that could be directly used to inform the diagnosis of ASD. Based on the above described findings, it may be important in future research to assess the neural mechanisms of how sensory processing reaches cortical hubs and influences decision-making and action control (Sepulcre et al., 2015) in more ecologically valid social situations (Schilbach, 2015, 2016a,b). Here, it will also be important to investigate the relevant motivational mechanisms, which might be key to understanding why and when individuals actually use their social perceptual skills (e.g. Schilbach et al., 2010). Such studies should also include an investigation of the neurochemical basis of social reward (e.g. Dölen et al., 2013; Dölen 2015) and could address how differences and/or similarities across interacting individuals may impact whether individuals are motivated and able to interact with one another. Here, clinical intuition and anecdotal evidence suggests that individuals with autism might be more motivated and/or able to interact with other individuals with autism (Schilbach, 2016a). To investigate these questions systematically, we have generated an experimental platform, in which behavior and its underlying computational mechanisms can be assessed individually and collectively while two persons perform the same task. It is to the description of this setup that we now turn.

3. Two-person psychophysiology and computational modeling: a framework for studying the interrelation of sensory and social processes in social interaction

In this section, we present an experimental framework and analysis schemes for future research of multilevel mechanisms of social interaction, i.e. from (sub-)individual to interpersonal processes, and most importantly their interrelationships. The importance of considering the dialectics between individual and socio-cultural processes, with an emphasis on social interaction, in psychological and psychopathological research has been emphasized in the past (e.g. in cultural historical theories; Vygotsky, 1930–1935/1978; views of Vygotsky and colleagues in Dafermos, 1930–1935/2002). However, due to conceptual and methodological constraints, neuropsychiatric research has not until recently addressed these issues (for some recent attempts of the field to consider more interactive scenarios see Montague et al., 2002; Schilbach et al., 2006, 2010; Pfeiffer et al., 2011; Dumas et al., 2012; Müller et al., 2013; Konvalinka and Roepstorff, 2012; Froese et al., 2014; Dumas et al., 2014b; Bilek et al., 2015). Such studies have been successful in tapping into some intra-, as well as interpersonal aspects of social interactions, such as joint attention, imitation, interpersonal synchronization and joint decision-making. In this article, we have emphasized the importance of interplay between sensory and social processes for the development and manifestation of cardinal characteristics of autism. Consequently, we are now describing a two-person setup, which allows for a formal investigation of this interplay during gaze-based social interaction. In this setup, participants are sitting opposite to each other, trying to accomplish *perceptual tasks individually*, while *interacting via gaze behavior* in real time through a micro-camera communication system. This

dual functionality will be pivotal for relating multilevel processes, ranging from the level of the individual (e.g. observation and reaction to perceptual information; Fig. 1: **blue and green arrows**) to the level of the collective (e.g. social interaction loop; Fig. 1: **red arrows**).

Crucially, such a setup will enable the consideration of all possible types of dyads (i.e. dyads consisting of neurotypical persons, dyads of persons with autism, as well as neurotypical-autistic dyads). Furthermore, its design allows for using tasks that comprise both free viewing and strictly structured tasks that can be performed individually, cooperatively or competitively. This compromise will allow for formal interpretation of the data, while preserving adequate degrees of ecological validity. To this end, the two-person setup transparently obtains high-resolution empirical data via infrared eye-trackers, micro-cameras, biological motion sensors and (electro-)physiological recorders, thus, providing multiple behavioral and (electro-)physiological readouts, such as gaze position, facial expression, heart rate variability and brain activity. Collection of biological measurements will enable the specification of lower level biological mechanisms, such as genetic and epigenetic mechanisms, while consideration of cultural factors, e.g. through priming or targeted selection of participants, might allow for touching upon higher level processes at the level of interpersonal exchange. Such a multi-level approach could complement enactivist and multi-scale approaches (e.g. De Jaegher and Di Paolo, 2007; Froese et al., 2011; Dumas et al., 2014c), as well as facilitate an integration of seemingly disparate perspectives (e.g. Frith, 1996; Gordon, 2016; Harris, 2016).

Importantly, the acquisition of high dimensional two-person data sets will allow for multi-level analyses via advanced computational methods (e.g. Bayesian and cross-recurrence approaches; Montague et al., 2012; Stephan and Mathys, 2014; Marwan et al., 2007). Firstly, intra-individual processes (Fig. 1; **green arrows**) could be modelled on the basis of Bayesian integration (Fig. 2a). Here, studying mechanisms for combining non-social (Fig. 1; **blue arrows**) with social (Fig. 1; **red arrows**) information will be mostly relevant (see Sevgi et al., 2016). More specifically, non-social information could take the form of perceptual stimuli, while social information may be constituted by both individual social cues, such as other person's gaze, and collective parameters, such as interpersonal coupling. Secondly, inter-individual processes (Fig. 1; **red arrows**) could be modelled on top of intra-individual ones (Fig. 1; **blue and green arrows**) via an intersubjective Bayesian analysis (Fig. 2b; Bolis et al., under review). The latter scheme aims at modeling both individual mechanisms (**orange boxes**; e.g. from neurobiological to cognitive-behavior levels) and processes of collective behavior (**green box**; e.g. joint decision making and interpersonal synchronization). More concretely, in Fig. 2b, μ and π symbolize individual beliefs and confidence placed on these beliefs respectively. The latter are translated and interlinked on a collective level of description via transformative (e.g. q and ω) and coupling parameters (e.g. ρ), resulting in observable activity (for more details see Bolis et al., under review).

Everyday life scenarios could be linked and potentially be studied in relevance to such kind of mechanisms. To make this point more intuitive, let us imagine two simple examples. First, let us imagine a lady, Penelope, who is planning to go out for dinner, being still unsure about whether she needs to wear a coat or not. Thus, she is opening the window and is feeling a cool breeze, which makes her thinking that it might be cold out tonight. However, people in the city are all very lightly dressed this night. After a look down the street, Penelope is not sure that wearing a coat would be a good idea after all and decides to leave her coat at home. What might have happened in this case is that Penelope combined social (i.e. other people's behavior) with non-social (i.e. perceptual) information for deciding on her dilemma. Eventually, going out without

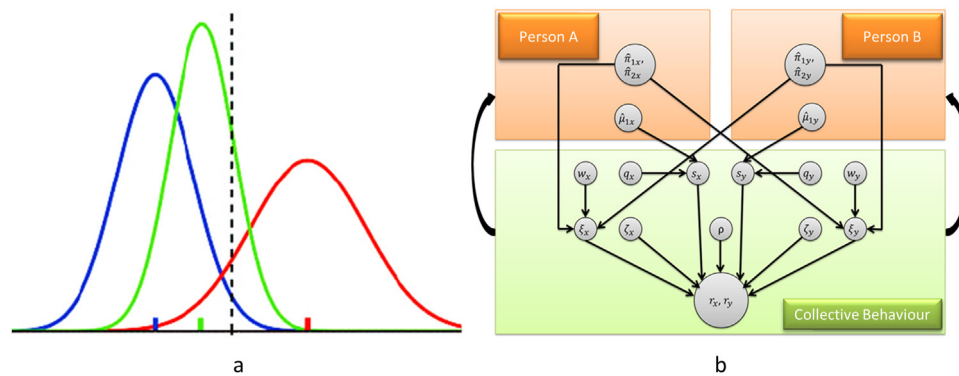


Fig. 2. (a) An example of statistically optimal Bayesian integration (green) between non-social (blue) and social information (red). (b) A schematic representation of inter-subjective Bayesian analysis for capturing both individual mechanisms (orange boxes) and processes of collective behavior (green box); adjusted from Bolis et al., 2015; under review). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

her coat might have come (not surprisingly from a Bayesian perspective) as a result of placing greater confidence on one (i.e. here social) versus the other (i.e. non-social) clue. Second, let us imagine two friends having a euphoric conversation over the phone on a pleasantly sunny day. Shortly before they finish the call, subtle perturbations of the telecommunication line are resulting in minor signal delays. However minor these delays are, the two friends, being unaware of this fact, are both left with a bitter feeling, at the end of the call. What might have happened here is that the strength of their interpersonal coupling during communication (a collective parameter) has been so negatively affected, that the initially positive impression of sunshine (perceptual information) was outweighed.

4. Conclusions

In this article, we have emphasized the importance of studying sensory-motor integration at the individual as well as at the dyadic level to more fully understand sensory and social aspects of autism. This line of research parts from more traditional theories, which have focused on specific cardinal aspects of autism that fall either into the social realm, such as social motivation, or a non-social domain, such as central coherence, while being restricted to the level of the individual. In order to extend those previous attempts of investigating the integration of sensory and social cues at the individual level, recent developments of predictive coding accounts appear most promising and allow for an investigation of the computational mechanisms of autistic trait-related differences in social cognition. Furthermore, we have reviewed empirical evidence, which indicates that autistic individuals might not face the greatest difficulties during passive observation of either social or non-social stimuli, but rather when it comes to real-time interaction, which make cue integration necessary and the generation of adequate behavioral responses in the context of ongoing and reciprocal social interactions. Taking social interaction seriously, however, we believe, also means that hypotheses and empirical studies to test them will have to go beyond the individual as the level of analysis. Here, an important objective will be to explain how processes of interpersonal coordination can emerge from and are reciprocally connected to the functioning of individual sensory-motor processes. In order to realize such truly social studies in autism (and other psychiatric disorders), we have developed a two-person setup, which allows for the study of mechanisms at both the individual and the collective level during real-time social interaction. This development opens up completely new avenues for autism research and might help to arrive at a more comprehensive

understanding of how exactly autism might be neither an exclusively sensory nor an exclusively social condition.

Conflict of interest

None.

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