A review of joint attention and social-cognitive brain systems in typical development and autism spectrum disorder

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Abstract

This article provides a review of the increasingly detailed imaging literature on the neurodevelopment of joint attention. Many findings from this literature support and inform the hypothesis that the neurodevelopment of joint attention contributes to the functional development of neural systems for human social cognition. Joint attention begins to develop by 5 months of age and is tantamount to the ability to adopt a common perspective with another person. It involves a whole-brain system with nodes in the: (a) dorsal and medial frontal cortex, (b) orbital frontal/insula cortex, (c) anterior/posterior cingulate cortex, (d) superior temporal cortex, (e) precuneus/parietal cortex, and (f) amygdala and striatum. This system integrates triadic information processing about (a) self-attention/action, (b) information about others' attention/action during social interactions that involve, (c) coordinated attention as well as processing a common referent in space. The results of this new imaging literature have the potential to advance current models of social cognition and the social brain, which rarely consider the contribution of the cognitive neurodevelopment of joint attention. The new neuroscience of joint attention is also extremely valuable for clinical research on social-cognitive neurodevelopmental disorders. This is most clearly the case for autism spectrum disorder (ASD) because it is consistent with the hypothesis of substantial functional neurodevelopmental continuity between the preschool impairments of joint attention, and childhood theory of mind ability that characterizes the development of ASD.

Introduction

Social cognition is a complex dimension of human mental development that is vital to social communication, social-relatedness, collaboration and competition, culture, and mental health. Social-cognitive processes have been described in many ways including but not limited to the following; (a) the ability to share the perspective or point view with another person, (b) mentally representing someone else's intentions, beliefs or emotions in order to draw causal inferences about their behavior, and (c) perceiving and interpreting social cues emanating from eyes, faces, body posture, and the voicing of speech to interpret the meaning of others behavior or language (e.g., Adolphs, 1999; Baron-Cohen, 1995; Brothers, 1990; Scaife & Bruner, 1975; Tomasello *et al.*, 2005; Wimmer & Perner, 1983).

Neurocognitive models of this mental dimension converge on the conceptualization of social cognition as a synthesis of multiple mental processes supported by a distributed and presumably interactive network of cortical and subcortical components (Corbetta *et al.*, 2008; Wolf *et al.*, 2010; Kennedy & Adolphs, 2012; Mahy *et al.*, 2014). Illustrative of these models Kennedy & Adolphs (2012) suggested that social cognition involves an amygdala–orbitofrontal stimulus salience system; a medial prefrontal and superior temporal mental state representational or 'mentalizing' system; and an insula–amygdala self-other emotion (empathy) system, and a parietal-prefrontal self-other action representation (mirror neuron) system.

Contemporary neurocognitive studies of social cognition are instructive; however, they are rarely *fully* informed by the developmental science of social cognition, especially research on the infant neurodevelopmental foundations of social cognition (Happé & Frith, 2014). This is not to say that current neurocognitive models have ignored this literature. Several highly relevant dimensions of infant development research have been explicitly included in models of the social brain. Foremost among these are face processing especially emotional face processing associated with ventral cortical social brain processes (e.g., Adolphs & Spezio, 2006), as well as self-other action representation and imitation associated with the mirror neuron system (Meltzoff, 1999; Iacoboni, 2005). However, joint attention is

another highly pertinent dimension of infant social cognition that is less frequently recognized in current models of the social brain development.

Joint attention behaviors involve the social coordination of one's own attention with that of another person to better adopt a common point of reference and share information (Mundy, 2016). These behaviors begin to emerge in the first 6 months of life. Their early development is manifest in two types of behaviors. One is responding to joint attention (RJA) or infants' ability to follow the direction of attention of other people (Fig. 1). This has also been referred to as 'gaze following' in the literature. The other is initiating joint attention (IJA) or infants' ability to spontaneously seek to direct the attention of others to share their experience of an object or event (Fig. 1).

Responding to joint attention is the most well-known form of joint attention and has been conceptualized as a perceptual component of face processing (Dawson *et al.*, 2005; Adolphs & Spezio,

2006) or a form of imitation (e.g., Williams *et al.*, 2005). However, others have argued that joint attention reflects the development of a codified mental dimension distinct from face processing and imitation, although it likely interacts with both during early development. The mental dimension of joint attention involves goal-directed spatial and declarative information processing about one's own perspective, and another person's perspective relative to a third object or event in space, or mental representation (Butterworth & Jarrett, 1991; Mundy, 2003; Tomasello *et al.*, 2005; Mundy & Newell, 2007). The triadic nature of social-spatial-referential information processing distinguishes joint attention from both face processing and imitation (Mundy, 2016).

Joint attention is a goal-oriented behavior the primary of aim of which is to share experience with other people (Mundy *et al.*, 2009). The capacity for sharing experience is a major mental function (Tomasello *et al.*, 2005) associated with specifiable neural systems that do not necessarily overlap with those for face processing
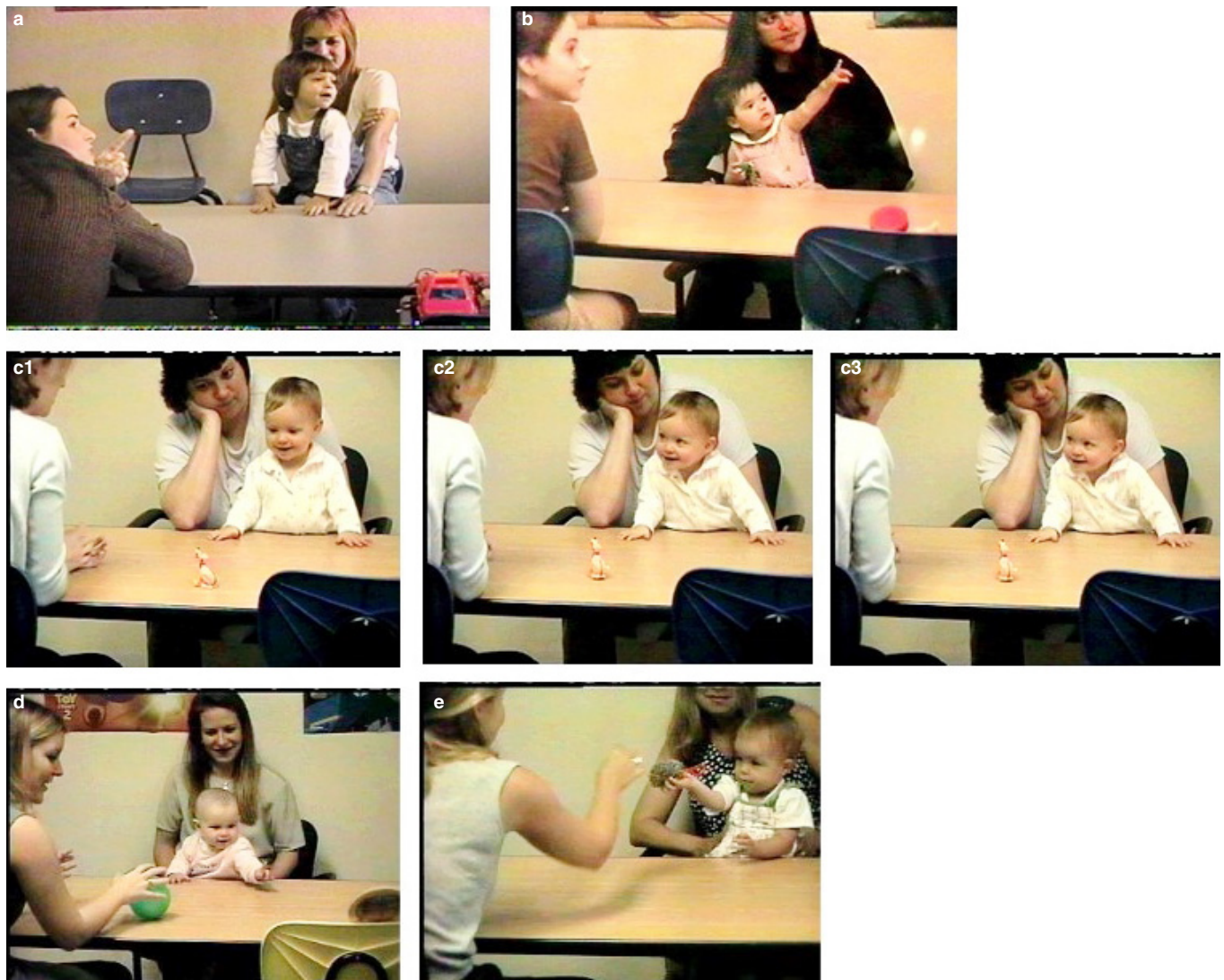

FIG. 1. Illustrations of different types of infant social attention coordination behaviors: (a) responding to joint attention (RJA) involving following and other persons gaze and pointing gesture; (b) initiating joint attention (IJA) involving a conventional gesture 'pointing' to share attention regarding a room poster, c1, 2, 3) IJA involving alternating eye contact to share attention with respect to a toy, (d) initiating behavior request—IBR involving pointing to elicit aid in obtaining an out of reach object, and (e) responding to behavior requests—RBR involving following an adult's open-palm 'give it to me' gesture. Figure reprinted with permission from John Wiley and Sons, Child Development, Mundy *et al.*, 2007).

or imitation (Baek *et al.*, 2017). The dynamic practice of social attention coordination and experience sharing in joint attention in the first years of life is postulated to provide specific types of brain–behavior experience that are fundamental to the life-span neurodevelopment of social-cognitive neurodevelopment (Mundy & Neal, 2000; Mundy, 2003, 2016; Mundy & Newell, 2007; Mundy & Jarrold, 2010).

Ironically, research groups have begun to recognize that the neurocognitive processes involved in the development of attention, and especially, the type of spatial social coordination of attention that is inherent to joint attention, may play a substantial role in adult social cognition (e.g., Corbetta *et al.*, 2008; Spreng *et al.*, 2009; Krall *et al.*, 2015). However, consideration of the ontological role that infant joint attention, per se, plays in the neurodevelopment of social cognition is not yet common to contemporary discussions of the social brain. Hence, one goal of this review is to facilitate the recognition that contemporary developmental and imaging studies have begun to provide compelling evidence consistent with the hypothesis that joint attention is fundamentally important to the neurocognitive development of human social cognition.

A second goal of this review is to emphasize the applied value of research on the neurodevelopment of joint attention and social cognition for research on autism spectrum disorder (ASD). The course of ASD is characterized by significant early impairments of joint attention development followed by equally significant disruptions of childhood social-cognitive mentalizing or theory of mind (Baron-Cohen, 1989; Mundy & Sigman, 1989; Pellicano, 2010; Lord & Jones, 2012). As ASD is a neurodevelopmental disorder this observation was one of the first to raise the hypothesis of a common neurological basis for joint attention and social-cognitive development (Mundy & Neal, 2000). Fortunately, the very considerable ingenuity of many research groups now makes it possible to begin to empirically examine this hypothesis (e.g., Grossmann *et al.*, 2007; Lachat *et al.*, 2012; Elison *et al.*, 2013; Hopkins *et al.*, 2014a,b; Caruana *et al.*, 2015; Committeri *et al.*, 2015; Oberwelland *et al.*, 2016).

A brief introduction to the dimension of joint attention

How does social cognition develop? A neuroconstructivist perspective (Quartz & Sejnowski, 1997; Mareschal *et al.*, 2007) suggests that the neural systems for social cognition develop incrementally through the interaction between information processing and problem-solving in social interactions and experience-expectant neurodevelopmental processes (Mundy *et al.*, 2009). There are certain social behaviors and problem-solving routines that are engaged in infancy that have specific affordances for the constructivist neurocognitive process of social-cognitive development. The practice of joint attention is primary in this regard. Much of human social interaction and communication pivots around the ability to: (1) first adopt a common frame of reference, and then (2) share information related to the object (s) or event (s) within that common frame of reference (Scaife & Bruner, 1975; Butterworth & Jarrett, 1991; Tomasello *et al.*, 2005; Mundy, 2016). The capacity to adopt a common perspective or point of reference is necessary, though not sufficient for language development, intersubjectivity, and our human ability to learn from instruction (Kasari *et al.*, 1990, 2008; Mundy *et al.*, 1992; Charman, 2004; Dawson *et al.*, 2004; Mundy, 2016). We must also learn to mentally appreciate the commonality or disparity of our perspectives with others in order to estimate their intentions, knowledge, beliefs or emotional responses (Buckner & Carroll, 2007). Theory has long held that this critical component of perspective sharing in social cognition begins with the infant development

of joint attention (Scaife & Bruner, 1975; Mundy & Sigman, 1989; Tomasello, 1995; Tomasello *et al.*, 2005; Mundy & Newell, 2007).

The ability to adopt a common point of view or frame of reference is not present at birth and caregivers, for the most part, do not explicitly teach infants to socially coordinate their attention. Rather, infants gradually become able to consider and adopt the viewpoint of others as they process information in episodes of RJA and IJA. Research now indicates that the development of RJA begins early and is characterized by increasing consistency of accurate attention coordination responses between 2 and 12 months (Scaife & Bruner, 1975; Mundy *et al.*, 2007; Gredebäck *et al.*, 2010). The development of greater spatial orienting precision to objects in view, and then to objects behind or completely out of view to children (i.e., mentally represented objects) also occurs (e.g., Butterworth & Jarrett, 1991; Delgado *et al.*, 2002). RJA development is also characterized by an increase in response efficiency. RJA response latency decreases from about 2.5 s at 4 months, to 1.5 s at 9 months, 0.8 s at 18 months, and 0.67 in adolescence (Gredebäck *et al.*, 2010; Van Hecke *et al.*, 2012; Oberwelland *et al.*, 2016).

By 8 to 9 months of age infants also develop the ability to use pointing, showing and shifts of their own gaze to spontaneously share their interest in and experience of a referent with another person (Fig. 1). The spontaneity of these types of IJA suggests that they involve choice and internal motivation systems to a greater extent than the more responsive even obligatory behaviors of RJA (Mundy, 1995, 2003). One indication of this spontaneous experience sharing function of IJA is provide by data that indicate that the sharing of positive affective responses to a referent with another person increasingly becomes of feature of IJA by 8–10 months of age, but not for RJA (Kasari *et al.*, 1990; Mundy *et al.*, 1992; Venezia *et al.*, 2004).

Task analysis of joint attention suggests that it involves a complex form of social information processing (Mundy & Newell, 2007; Mundy *et al.*, 2009; Mundy, 2016). Three sources of information are processed. The first is s*elf-referenced* processing (e.g., interoception and proprioception) of one's own position in space, information about one's own actions, affective responses and intentions, and memory for related episodic information (Mundy *et al.*, 2010). The second is o*ther referenced* information including the exteroceptive processing of other people's actions, direction of gaze, affect, and vocalizations. Finally, information processing about the common referent may involve, but is not limited to, spatial processing, sensory information processing (visual, auditory, tactile), emotional or affective information related to reactions to the referent, as well as processing of non-sensory information about the object or event (e.g., novelty or familiarity of the object).

The interaction of infants' experience as referential perspective *signal receivers* in RJA and referential *signal sender* in IJA is also part of the unique affordance of joint attention for social-cognitive development. The experience of the duality of the first and second person roles of joint attentions provide singular comparative information processing opportunities for infants. The practice of *both* RJA and IJA provides unique comparative information about self and other perspectives, as well as about the nature of the shifting viewpoints of people in social interactions. In theory, this type of experience plays a pivotal role in social-cognitive development (Fig. 2: Mundy & Newell, 2007; Mundy & Jarrold, 2010). Replicated longitudinal observations of continuity between individual differences in infants' joint attention and their subsequent childhood mentalizing performance now provides a significant body of evidence consistent with this hypothesis (see Table 1). These data, though, do not speak directly to the details of how or why joint
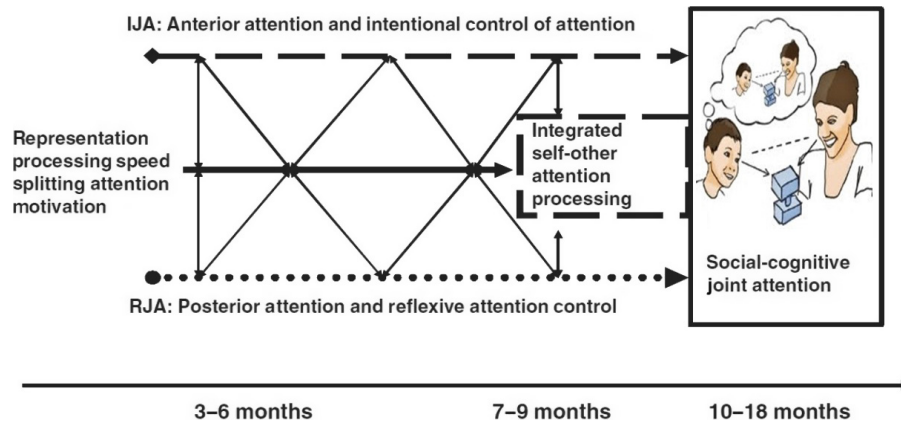
FIG. 2. An illustration of the interaction between initiating joint attention (IJA) and responding to joint attention (RJA) information processing in the development of joint attention and social cognition adapted from Mundy & Newell (2007). The different types of lines depict information processing associated with RJA development and information processing associated with IJA development. The central solid line in the figure depicts other factors that influence joint attention development during infancy, such as representational ability, speed of processing, motivation, and the executive attention control, as well as each other during infancy. The diagonal arrows reflect the dynamic and coactive nature of joint attention development whereby the maturation of attention, cognitive, and affective systems interacts in reciprocal cause and effect relations with experience. Finally, the development of integrated self and other attention processing is depicted as a social attention executive function of the anterior system that emerges in the 4- to 9-month period. The capacity to integrate and share attention to external common referents provides a foundation for the ability to share covert aspects of attention to internal mental representations and social cognition. Joint attention image from Gillespie-Lynch et al. (2013). Response to and initiation of joint attention: Overlapping but distinct roots of development in autism? OA Autism 13, http://www.oapublishinglondon.com/article/596.

TABLE 1. Longitudinal Evidence of the Link between Joint Attention and Social Cognition

Lee et al. (1998)	2- to 3-year-olds use triadic gaze for 'mind reading'
Charman et al. (2000)	20-month initiating joint attention (IJA) (alternating gaze) predicts 44-month ToM
Nelson et al. (2008)	18- to 20-month joint attention predicts ToM at 43–54 months
Kristen et al. (2011)	9-month responding to joint attention (RJA) predicts mental state words at 36 months
Schietecatte et al. (2012)	RJA in children with Autism related to intention understanding
Abreu et al., 2014)	9-month RJA predicts 48-month ToM
Brooks & Meltzoff (2015)	10-month RJA predicts 3-year mental state word which predicts 4-ToM
Sodian & Kristen-Antonow (2015)	12-month IJA predicts False Belief understanding at 50 months
Kühn-Popp et al. (2015)	15-month IJA, and associated frontal-central EEG coherence, predicts 48-month mental state word use

ToM refers to theory of mind assessment task performance. Mental State Words refer to the children's spontaneous use of terms such as 'think,' 'believe,' 'understand' in paradigms in language samples, social interactions, and explanations or descriptions of other people's actions. Predicts indicates a longitudinal study design.

attention and social cognition may come to be supported by common neural systems. For that, we need to consider the mentalizing hypotheses of joint attention (Mundy, 2016).

Mentalizing and connecting the neural systems of joint attention and social cognition

Mentalizing involves the ability to make inferences about the beliefs or intentions of other people (Frith & Frith, 2006). Making social-cognitive inferences is believed to require several processes, including but not limited to; (a) perspective taking, (b) simulation or the use of self-referenced experience (current or past) to estimate the information another person would have in a specific situation, and

(c) long-term episodic memories of information relevant to a given simulation (Frith & Frith, 2006; Buckner & Carroll, 2007; Spreng et al., 2009).

Current social-cognitive theory does not specify how mentalizing develops. In this regard, though, joint attention theory raises two hypotheses (Mundy, 2016). One is that social-cognitive mentalizing arises from constructive cognitive processes (Quartz & Sejnowski, 1997) that involve extensive preschool practice with joint attention. A reciprocal hypothesis is that practice with joint attention provides unique types of brain–behavior experiences that are necessary to the neuroconstructive processes (Greenough et al., 1987; Mareschal et al., 2007) that sculpt significant components of the neural systems for mentalizing (Mundy et al., 2009; Mundy, 2016).

Accordingly, children engage in the iterative practice of countless episodes of joint attention from 3 to 4 months of age through the preschool years. During joint attention episodes, children build social knowledge by processing and storing embodied information about their own experience of a referent (object or event) and simultaneously perceive and store information about other people's processing and reactions to the common referent (Mundy et al., 2009). This is essentially practice with perspective taking and simulation (see Meltzoff & Brooks, 2008 for an example of infant simulation). Thus, the iterative practice with joint attention, across a wide variety of situations and wide variety of people, is thought to build the capacity and experience with perspective taking and simulation necessary to support the development of social-cognitive inferential capacity for mentalizing (Mundy, 2016).

In addition, a cognitive neuroconstructivist perspective (Quartz & Sejnowski, 1997; Karmiloff, 2009) also suggests that months and years of behavioral practice with joint attention contributes to the dynamic development of the neural systems for joint attention. As cognition becomes more representational the neural systems for joint attention behaviors become the active neural systems for mental-representational joint attention processes. This internalized joint attention is the capacity to; (1) imagine or mentalize the perspectives of other people in a variety of situations, and (2) mentalize the effect that processing information about the corresponding referent

or situation is likely to have on the other people's behavior, beliefs or intentions (Mundy & Newell, 2007). Hence, the neural systems for joint attention become part of the neural systems for social-cognitive mentalizing. This model is related to previous data and theory that suggests that social-cognitive neurodevelopment emerges from the social behaviors (Klin *et al.*, 2003; Meltzoff & Decety, 2003; Sommerville *et al.*, 2005; Sebanz *et al.*, 2006).

To better illustrate this point consider the following. Mentalizing is central to theory of mind measures, which have often been a primary tool in the study of typical social cognition, and its atypical presentation in ASD (Baron-Cohen, 1989). The Sallie–Ann task is illustrative of these types of tasks (Fig. 3). In this storyboard task, a child research participant can see Sallie and Ann, a marble, a box and a basket. In the second panel, the child can see Sallie place the marble in the basket and the sees Sallie 'leave for a walk'. In the fourth panel, the child witnesses Ann move the marble into the box. In the final panel, Sallie has returned and a child research participant is asked, 'Where will Sallie look for the marble?'. The child has to 'mentalize' Sallie's false belief that marble is in the box in order to correctly answer this question. What are the steps involved in this mentalizing processes? According to joint attention theory, the child has to represent (recall) what he or she 'experienced' with Sallie and distinguish that from what she or he saw with Ann, *but not with Sallie*. That is the child has to internally represent, compare and distinguish episodes of the joint visual information experienced with Sallie and Ann in order to 'mentalizing' the false belief or visual information that Sallie has experience that that will lead to her choice behavior. I would argue that much the same process is invoked when theory of mind or social cognition is measured with video stories or verbally presented vignettes instead of a storyboard.

The 'mentalizing process' hypothesis of joint attention theory predicts that the neural systems involved in joint attention should be isomorphic, to some significant extent, with the neural systems of human social-cognitive mentalizing and their atypical development in ASD. The neural regions most often observed to correlate with mentalizing include systems of the dorsal, ventral and orbital frontal cortex, the cingulate cortex, the temporal poles, superior temporal cortex and the parietal cortex including the precuneus (Frith & Frith, 2006; Kennedy & Adolphs, 2012; Mundy, 2003; Overwalle, 2009; Schurz *et al.*, 2014). The best test of this hypothesis would be provided by imaging studies that examine joint attention and mentalizing performance in the same samples. Regrettably, combined joint attention and mentalizing imaging studies are not yet available. Therefore, to take a first step, this review will appraise the extent that the current imaging research is consistent with the hypothesis of that the neural systems of joint attention may overlap with those indicated in the imaging literature of social-cognitive mentalizing. To begin addressing this goal, the next section provides a brief overview of the initial studies of joint attention brain–behavior relations, before delving into the more contemporary imaging literature of joint attention.
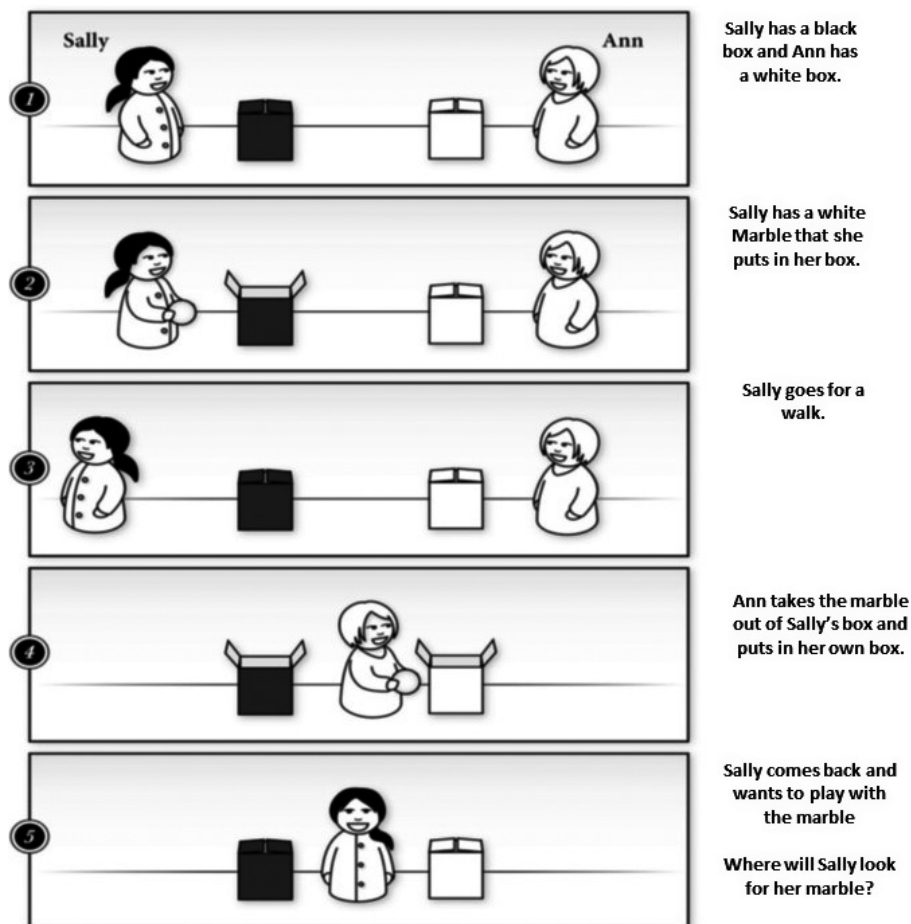

FIG. 3. Schematic illustration of the Sally–Ann false belief theory of mind task. (Figure reprinted with permission from Frontiers.org, Frontiers in Human Neuroscience, Byom & Mutlu (2013), in accord with the open access guidelines of the journal).

Autism and the initial model of the neurodevelopment of joint attention

Interest in research on the neurodevelopment of joint attention was initially motivated by observations of the significant early impairment of joint attention development in ASD (Mundy, 1995; Mundy *et al.*, 2000). ASD is a neurodevelopmental disorder characterized by the early infant onset of developmental differences in social-communication development (Jones & Klin, 2013). Joint attention impairments are a fundamental symptom of the early social communication of impairments of ASD (Mundy *et al.*, 1986). These can be observed by the sixth to eighth month of infancy (Ibañez *et al.*, 2013). In the second year of life, RJA and IJA impairments become central to the diagnosis of ASD (Charman, 2004; Gotham *et al.*, 2007). As alluded to earlier, though, IJA and RJA reflect somewhat different processes and IJA impairment appears to be more chronic and significant for the diagnosis and treatment of ASD (Mundy *et al.*, 1994; Gotham *et al.*, 2007; Kasari *et al.*, 2008). After the preschool period, impairments in task performance on measures of mentalizing and social cognition become a prominent and chronic characteristic of ASD (e.g., Baron-Cohen, 1995; Pellicano, 2010). This pattern of observations of preschool impairments in joint attention followed by childhood impairment in mentalizing in ASD was among the first to suggest a significant connection between joint attention and social-cognitive development (Baron-Cohen, 1989; Mundy & Sigman, 1989). Given the neurodevelopment basis of ASD this pattern also raised the hypothesis that joint attention and mentalizing share common neural supports (Mundy, 2003).

Early studies used EEG and PET to reveal that IJA was associated with a pattern of activation and coherence across the dorsal medial frontal, temporal, and posterior cortical regions (Caplan *et al.*, 1993; Henderson *et al.*, 2002). Alternatively, the data suggested that RJA was associated with a less cortically distributed pattern of temporal–parietal activation (Mundy *et al.*, 2000). Kühn-Popp *et al.* (2015) subsequently replicated the observation that EEG coherence between frontal medial and central dorsal electrode sites was specifically associated with joint attention. Kühn-Popp *et al.* (2015) also observed that individual differences in the frontal-central EEG associated with joint attention in 15-month-olds predicted

children's use of mental state terms (e.g., think, know, guess, believe) at 48 months of age.

Interpretation of the early data led to a view of the neurodevelopment of joint attention that was based on Posner's model of attention systems of the brain (Posner & Petersen, 1990; Posner & Rothbart, 2007). Mundy (2003) hypothesized that IJA recruited regions of dorsal medial frontal that play a role in the integration of proprioceptive information about one's own attention with posterior processing of exteroceptive information about the visual attention behavior of other people (Mundy, 2003). This type of integration of information was believed to be a necessary first step toward perspective taking. In addition, the integrated self-other information processing of IJA was thought to be influenced by the anterior cingulate and dopaminergic systems involved in volitional and internally motivated goal-related attention regulation (Fig. 4a). Mundy (2003) also proposed that a disturbance in these DMFC/AC functions contribute to the atypical development of intersubjectivity, joint attention and social cognition in people with autism. RJA was assumed to involve a less volitional system regulated by posterior cortex systems for the spatial orienting and processing of referents that were tagged as salient by external social cues (e.g., Mundy *et al.*, 2000; Fig. 4a).

Subsequent data reframed this model (e.g., Lombardo *et al.*, 2007; Northoff *et al.* 2006; Schilbach *et al.*, 2010). Joint attention and social cognition (mentalizing) were both proposed to involve a type of cognitive control that allowed for the simultaneous upregulation and integration of default system involvement in self-referenced processing, and the dorsal attention system roles in exteroceptive social information processing (Mundy & Jarrold, 2010; Fig. 4b). These preliminary models are now informed and supplanted by a much more comprehensive literature on the neural systems of joint attention that has begun emerge over the last decade (see Table 2).

Infant imaging and EEG studies of the neurodevelopment of joint attention

When do the neural systems for joint attention begin to develop? RJA behaviors at 4-to-5 months have been observed to be associated with frontal cortical (dorsal/ventral) and parietal cortical activation using optical imaging and gamma oscillation paradigms (Grossmann
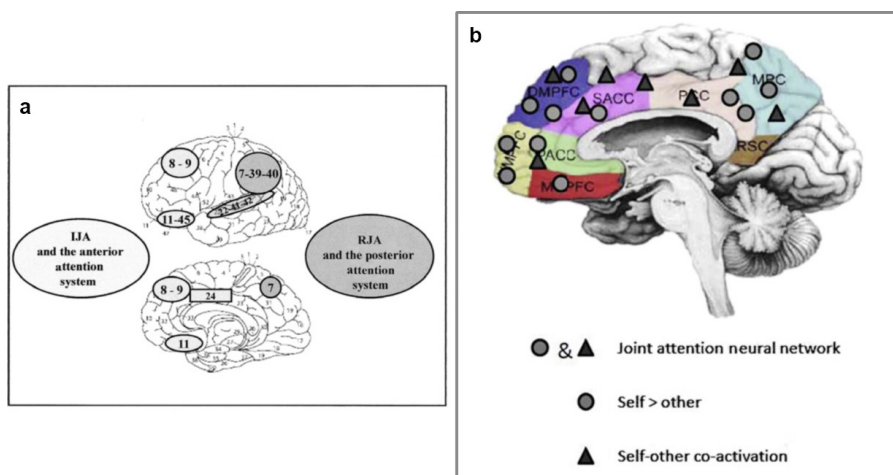
FIG. 4. Illustrations of two early models of the neural system of joint attention. The first model was based on Posner's model of anterior and posterior attention system functions (Mundy, 2003; Panel a). The second model was based on theory suggesting that a fundamental function of joint attention, and social cognition, was the neurocognitive capacity for the simultaneous or contiguous processing of self-referenced and other referenced information about attention and a common referent (Mundy & Jarrold, 2010, Panel b).

TABLE 2. Joint attention neural networks identified in studies from infancy through adulthood

Study	Developmental period	Type of JA	Neural system	Control network[a]
Infant studies				
Grossmann & Johnson (2010)*	5 months	RJA	Medial Dorsal Frontal	Default or FPC
Elison *et al.* (2013)*	6 months	RJA	Temporal, amygdala, insula, orbital, ventral, medial frontal, connectivity	Default & FPC
Grossmann *et al.*, 2007*	4 months	RJA	MPFC, Parietal	Default & FPC
Grossmann *et al.*, 2013*	5 months	IJA	Left Dorsal Frontal	Network Unspecified
Caplan *et al.* (1993)*	13+ months	IJA	dMPFC	Default
Mundy *et al.* (2000, 2003)	14 months	IJA & RJA	dMPFC (BA 8), Parietal Cortex & EEG Coherence	Default & FPC or Dorsal Attn.
Henderson *et al.* (2002)	14 months	IJA pointing	dMPFC, orbital & dorsolateral frontal temporal cortex	Default, FPC & Dorsal Attention
Kühn-Popp *et al.*, 2015	15 months	IJA pointing	Medial frontal & dorsal central EEG coherence	Default, Dorsal Attn
Mosconi *et al.* (2009)*	18 + months TD vs. ASD	IJA & RJA	Amygdala size	Default
Eggebrecht *et al.* (2017)*	12 & 24 months TD and ASD Risk	IJA	Frontal Dorsal Attention, Posterior Cingulate, Somatomotor, Frontal–Parietal, Salience Network	Default, Dorsal Attn FPC
Childhood studies				
Oberwelland *et al.*, 2016*	Children & Adolescents	IJA & RJA	Ventral striatum, medial frontal cortex, dorsal media frontal cortex. amygdala, precuneus, and temporal–parietal juncture	Default, Dorsal Attn. & FPC
Greene *et al.* (2011)*	Children TD vs. ASD	RJA	Inferior frontal gyrus; middle frontal gyrus; middle temporal gyrus; occipital gyrus; supramarginal gyrus; superior temp gyrus	Default & FPC
Vaidya *et al.* (2011)*	Children TD vs. ASD	RJA	Superior temp sulcus, anterior cingulate, Striatal/caudate, dorsolateral frontal	Default, FPC, Dorsal Attn.
Oberwelland *et al.* (2017)*	Adolescents TD & ASD	IJA & RJA	Diagnostic Group Differences: Temporal Pole, STS, Precuneus, TPJ: IJA, Medial Prefrontal Cortex. Fusiform Gyrus with familiar partner in ASD.	Default, FPC
Adult studies				
Brunetti *et al.* (2014)*	Adults	IJA pointing	dMPFC (anterior cingulate, temporal–parietal cortex)	Dorsal Attn., Default, FPC
Williams *et al.* (2005)*	Adults	RJA	dMPFC (BA 9,10) Cingulate cortex, Precuneous (parietal), Caudate nucleus	Default, Dorsal Attn., FPC
Schilbach *et al.* (2010)*	Adults	IJA & RJA	dMPFC, Anterior/posterior cingulate medial orbital PFC, temporal and occipital cortex, striatum/caudate	Default, Dorsal attn., FPC
Pfeiffer *et al.* (2014)*	Adults	IJA	Striatal	Motivation & Spatial Processing of Motor Movement
Gordon *et al.* (2013)*	Adults	IJA	Anterior cingulate, right fusiform gyrus, parietal cortex, amygdala, striatum, hippocampus	Dorsal attention, Default, FPC
Caruana *et al.* (2014)*	Adults	IJA & RJA	Both IJA & RJA Temporal–Parietal Juncture, Precuneus, Inferior Frontal Gyrus, Middle Frontal Gyrus, Middle Temporal Gyrus. IJA not RJA Supplementary Motor Cortex, Superior Frontal Gyrus, Left Temporal Pole, Thalamus, & Cerebellum	Default, FPC, Dorsal Attention.
Redcay *et al.* (2012)*	Adults	IJA & RJA	Medial prefrontal, Inferior frontal, Parietal, ventral Orbital frontal, Temporal	Dorsal attention, Default, FPC
Pelphrey *et al.* (2005)*	Adults ASD vs. TD	RJA	TD: Middle frontal gyrus, Anterior Cingulate, Middle & Superior Temporal Gyrus ASD: Less Superior Temporal, More Insula Inferior frontal gyrus	Default & FPC
Redcay *et al.* (2013)*	Adults ASD vs. TD	IJA & RJA	TD > ASD on RJA: dMPFC, Superior Temporal Cortex ASD > TD on RJA: Fusiform gyrus, middle occipital gyrus, putamen IJA > RJA: Right Anterior Insula, Left Inferior Parietal Cortex	Default, FPC Face processing Spatial Processing
Mizuno *et al.* (2011)*	Adults RJA-IJA ASD vs. TD	TD > ASD: Deictic Shift	Precuneous & Insula Connectivity	Default & FPC

FPC = frontoparietal control network; dMPFC = dorsal medial prefrontal cortex; TD = typical development group; ASD = autism spectrum development group; IJA = initiating joint attention; RJA = responding to joint attention. *Indicates an imaging study. [a]Control network designations from Spreng *et al.* (2013)

et al., 2007; Grossmann & Johnson, 2010). A diffusion tensor imaging study indicates that individual differences at 6 months in fractional anisotropy (FA) in the uncinate fasciculus predicts RJA development at 9 months (Elison *et al.*, 2013). The uncinate fasciculus connects the medial and anterior temporal lobe, as well as nuclei

of the amygdala, with the orbital and medial frontal cortex (Von Der Heide *et al.*, 2013). The system interconnected by the uncinate is likely involved in social-cognitive development, as the anterior temporal lobe is critical to storage of episodic and declarative knowledge and its integration frontal generation of self-referenced goal-related

behaviors (Olson *et al.*, 2013). Elison *et al.* (2013) also noted that their observations suggested that RJA may involve the amygdala and what has been described as valence processing of the biological relevance and/or the intentional nature of salient social cues (Menon & Uddin, 2010; Kennedy & Adolphs, 2012).

Grossmann *et al.* (2013) have also reported observations related to the study of early IJA development. They observed optical imaging activation of the left frontal pole in 5-month-olds when the gaze of a tester followed the activity of the infants. Awareness of attention to self is hypothesized to be a major component of IJA (e.g., Bates *et al.*, 1975; Reddy, 2003; Kim & Mundy, 2012; Edwards *et al.*, 2015) as well as subsequent social-cognitive development (Schilbach *et al.*, 2013). Evidence of the role of attention to self in IJA development comes from studies of interventions that improves IJA in young children with ASD (Kasari *et al.*, 2008; Murza *et al.*, 2016). An active ingredient in these interventions appears to involve increasing the child's awareness that they are the object of attention of other people which occurs when mirroring or imitating the child's behavior (Ingersoll, 2012; Gulsrud *et al.*, 2014).

Research on the infant neurodevelopment of IJA has also been advanced by the observation that IJA at 12 and 24 months was associated with resting connectivity between networks of frontal dorsal attention and posterior cingulate default systems (Eggebrecht *et al.*, 2017). This study also reported evidence of greater somatomotor and more differentiated involvement of the dorsal attention network and posterior cingulate aspects of the default network in IJA at 24 months than at 12 months. Interestingly, a dorsal attention and frontal posterior cingulate network have been hypothesized to pay a role in monitoring attention to self (Leech & Sharp, 2014; Herold *et al.*, 2016).

Understanding the change in the 12- to 24-month IJA may be especially important to understanding the neurodevelopmental links between joint attention and mentalizing. This period has been referred to as the 'learning from' phase period of infant joint attention development (Mundy *et al.*, 2009; p. 12), where in social cognition is thought to expand in the context of joint attention (Tomasello *et al.*, 2005) through the comparative experience of self and other referential perception and information processing (Meltzoff & Brooks, 2008).

Implications of joint attention imaging research in infancy

One important observation of the infant imaging data is that the neural nodes and systems associated with joint attention in the first 2 years display a significant degree of overlap with cortical regions associated with social-cognitive mentalizing. This overlap is illustrated in the top panel of Fig. 5. The current imaging data also suggest that the neural systems observed for joint attention in infancy display continuity with the systems observed for joint attention in samples of children and adults (Fig. 5). In infancy, RJA is associated with activity in the superior temporal cortex, intraparietal cortex, temporal pole, orbitofrontal cortex, and insular cortex. The observed systems for infant IJA involve activity within the frontal pole, dorsal frontal cortex, superior temporal and intraparietal cortex, posterior cingulate, and somatomotor cortex.

Age of onset of joint attention development

Observations of the early (4–6 month) cortical correlates of IJA and RJA are consistent with behavioral data that indicate that joint
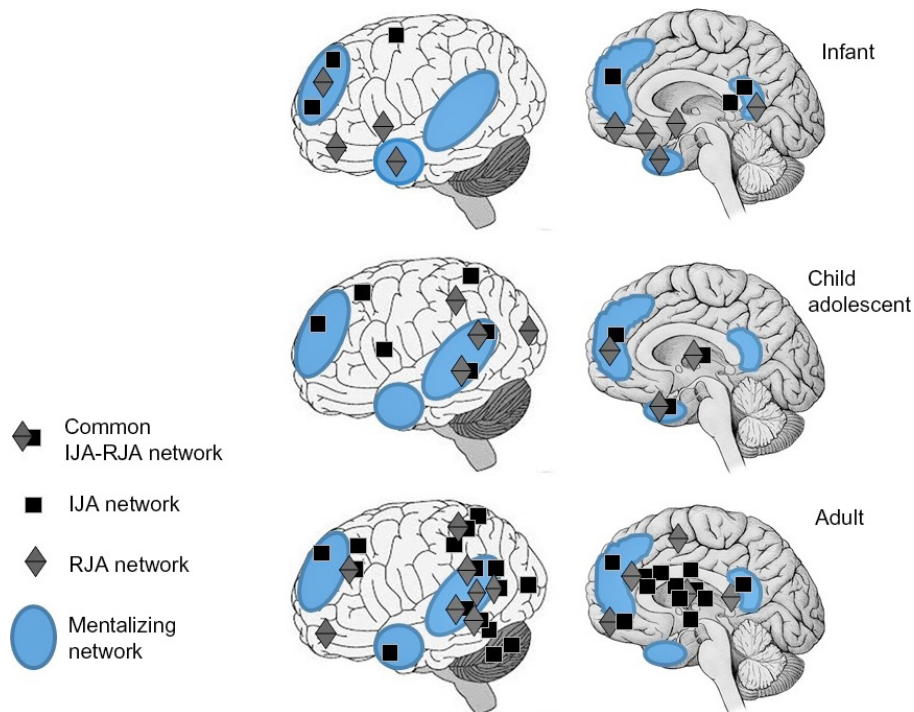

Fig. 5. An illustration of observations of the neural systems involved in initiating joint attention (IJA) and responding to joint attention (RJA) development in infancy, childhood, and adulthood. These illustrations do not reflect specific findings with regard to hemisphere localization of neural systems. The infant illustration was based on data from Elison *et al.* (2013), Eggebrecht *et al.* (2017), Grossmann & Johnson (2010), Grossmann *et al.* (2007, 2013), and Mosconi *et al.* (2009). The childhood illustration was based on data from Greene *et al.* (2011), Oberwelland *et al.* (2016, 2017), and Vaidya *et al.* (2011). The adult illustration was based on data from Brunetti *et al.* (2014), Caruana *et al.* (2014), Gordon *et al.* (2013), Mizuno *et al.* (2011), Pelphrey *et al.* (2005), Pfeiffer *et al.* (2014), Redcay *et al.* (2012, 2013), Schilbach *et al.* (2010), and Williams *et al.* (2005). The regions associated with mentalizing were based on a review by Kennedy & Adolphs (2012) and meta-analyses by Overwalle (2009) and Schurz *et al.* (2014).

attention begins to develop early in the first year of life (Gredebäck *et al.*, 2010). This is important because joint attention development has been characterized as a second-year phenomenon (Tomasello *et al.*, 2005). This invites speculation that aspects of social attention that emerge in the first 6 months of life, such as face processing, may be a primary precursor of joint attention. This has been an especially important idea in research on ASD. It gave rise to the hypothesis that joint attention impairments in ASD are the sequelae of neonatal face orienting and processing disturbance (e.g., Dawson *et al.*, 2005). Alternatively, we have argued that joint attention reflects a unique mental dimension that is prioritized early in neurocognitive development and cannot be fully explained as an outgrowth of the development of face processing or social orienting (Mundy, 1995, 2016; Mundy *et al.*, 2009).

Face processing

The imaging studies of joint attention speak directly to the face processing hypothesis of joint attention. Elison *et al.* (2013) observed evidence of a temporal pole and orbital frontal cortical system in infant RJA development. However, these authors also reported that fractional anisotropy of longitudinal fasciculus connecting the fusiform gyrus, associated with face processing with the anterior cortical system was not associated with joint attention. Indeed, only four of the 24 studies listed in Table 2 have reported fusiform activation in association with joint attention in studies of infants, children, and adults (Gordon *et al.*, 2013; Redcay *et al.*, 2013; Oberwelland *et al.*, 2016, 2017). Moreover, three of those studies suggest that recruitment of fusiform activity in the joint attention tasks used in these studies was limited to familiar partners, but not present with unfamiliar partners (e.g., Oberwelland *et al.*, 2016). However, joint attention is as easily observed in infants interacting with unfamiliar as familiar partners, if not more so (Gredebäck *et al.*, 2010). In two other studies, activation of the fusiform system was limited to individuals with ASD and interpreted as part of the atypical neurodevelopment of joint attention in ASD (Gordon *et al.*, 2013; Redcay *et al.*, 2013).

Face processing is important to social competence and social communication in typical development and in children with ASD. Nevertheless, joint attention is mental process that goes well beyond face processing. The development of this metal function is neither specific to visual processing of the face nor to information from in a particular sensory modality. Vision, hearing, and shared somatosensory information can all support joint attention development (Werner & Kaplan, 1963; Nuku & Bekkering, 2010; Tasker *et al.*, 2010; Rossano *et al.*, 2012). In blind infants, visual face processing is not possible, yet joint attention develops, albeit more slowly (e.g., Bigelow, 2003). Joint attention also develops in young deaf children (e.g., Lieberman *et al.*, 2014) but with a different developmental pattern of behaviors. Any of several types of sensory-perceptual information that can convey shared experience with respect to a common referent can be used in joint attention development. The spatial breadth and precision of vision afford the optimal input for human joint attention development. However, in other specifies such as dolphin auditory echo-location may provide the primary source of spatial social attention coordination necessary to support the development of joint attention (Pack & Herman, 2006). This is not to say that face processing is not involved in joint attention, only that joint attention is unlikely to be a simple linear outgrowth of face processing. Moreover, future iterations of precursor of models may need to assessed for their consistency with evidence of the early neural development of joint attention at 4–6 months (Grossmann *et al.*, 2007; Grossmann & Johnson, 2010; Elison *et al.*, 2013).

Joint attention, precursors, and early biomarkers of ASD

One precursor model of joint attention may be consistent with neurodevelopmental evidence. Recall that Reddy (2003) and others have proposed that the early development of joint attention is initially organized or motivated by the infant's perception of being the object of others' attention. The mechanism for this may involve the neural systems and functions that Senju & Johnson (2009) have described for the *eye-contact effect* (Mundy, 2016). The eye-contact effect refers to the changes in arousal and cognitive processing that occur when a child or adult perceives that they are the object of the direct gaze and attention of another person (e.g., Conty *et al.*, 2010; Edwards *et al.*, 2015; Mundy *et al.*, 2016). Senju & Johnson (2009) proposed that a *fast track modulator* network composed of the superior colliculus, pulvinar, and amygdala mediates the eye-contact effect. This fast track processing of eyes occurs earlier and is distinct from subsequent cortical processing of face structure and expression. This system is believed to process eye-gaze on self and relays it for ventral and medial frontal cortical processing (possibly of communicative intent) within 150–170 msec after stimulus onset in adults (Conty *et al.*, 2007). Notably, something like the fast track modulator was described by Baron-Cohen (1995) as the *eye direction detector* component of theory of mind processes.

Accordingly, the problem in the motivation to orient to and attend to faces that hypothetically leads to problems in joint attention development (e.g., Dawson *et al.*, 2005) may alternatively be described in terms of a diminution of the eye-contact effect, or a lack of cognitive arousal to being the object of others' attention (Mundy *et al.*, 2016). Optical imaging and EEG methods allow for tests of this hypothesis. Observations of frontal cortical response to being the object of attention of others in 5-month-olds (Grossmann *et al.*, 2013) have opened up the possibility of examining the eye-contact effect and its role as an early biomarker of ASD, as well as an index of response to IJA intervention. In addition to the methods described by Grossmann *et al.* (2013), other measurements may also be considered. Grossmann *et al.* (2007) reported that gamma activity in the frontal cortex may be sensitive to gaze on self in 4-month-olds.

The neural system of the eye-contact effect may also overlap with the neural network connected by the uncinate fasciculus that was observed to predict joint attention development from 6 to 9 months of age (Elison *et al.*, 2013). Elison *et al.*'s data suggested early RJA development. DTI methods for the appraisal of the early functional integrity of the uncinate fascicular network may also be worth examining in the search for biomarkers of ASD. This idea is underscored by two related observations. Shen *et al.* (2016) reported that that altered functional connectivity, between the amygdala, prefrontal cortex, temporal lobes and striatum, distinguished 3-year-old children with ASD from comparison peers. Second, Mosconi *et al.* (2009) observed longitudinal MRI indications of the atypical development of the amygdala in 2- to 4-year-old children with ASD that were related to differences in their joint attention development.

The resting frontal connectivity MRI methods used to study individual differences in IJA development from 12 to 24 months (Eggebrecht *et al.*, 2017) may also be useful in early ASD biomarker research. Eggebrecht *et al.* (2017) observed evidence of developmental changes in the neural systems that were correlated with IJA from 12 to 24 months of age. Sensitivity to neural system developmental change in this period may be significant because the 2- to 24-month period is an especially in important in terms of the onset of overt symptoms and symptom change in children with ASD (Ozonoff *et al.*, 2010). Methods with sensitivity to developmental change, such as those described by Eggebrecht *et al.* (2017) may

also prove useful for intervention outcome research. They could deepen the current understanding of the effectiveness and differences in response to interventions that effectively target joint attention development in ASD (Kasari *et al.*, 2008; Murza *et al.*, 2016). In addition, because IJA intervention may cause an increase of children's awareness of attention to self (Gulsrud *et al.*, 2014), cortical response measures to being the object of other's awareness (Saby *et al.*, 2012; Grossmann *et al.*, 2013) warrants consideration in future research on IJA intervention biomarkers.

Childhood imaging studies of the neurodevelopment of joint attention

Recall that Eggebrecht *et al.* (2017) reported evidence of increased activation of the frontal–parietal control (FPc) network and amygdala salience network in joint attention from 12 to 24 months of age. Oberwelland *et al.* (2016) have reported seminal observations with children that suggest that change in the pattern of contributions of FPc and the salience network may also be key elements of childhood joint attention development.

Oberwelland *et al.* (2016) examined the RJA and IJA development of 8- to 12-year-olds compared to 13- to 18-year-olds using virtual reality joint attention tasks. The IJA and RJA tasks activated a common system involving the ventral striatum, medial frontal cortex, amygdala, posterior superior temporal sulcus, and temporal–parietal juncture (Fig. 5). The amygdala displayed the strongest activation specific to joint attention. This observation is consistent with the previously noted research and theory on the involvement of the salience network in joint attention in infancy (Mundy, 1995; Elison *et al.*, 2013; Eggebrecht *et al.*, 2017). IJA was distinguished from RJA by activation of components of the FPc system including the dorsal medial prefrontal cortex, the middle and inferior frontal gyrus, and the medial occipital frontal cortex (frontal eye fields), along with posterior cortical activation along the inferior parietal gyrus and across the precuneus. There was also a trend toward greater precuneus activation in self-initiated joint attention (IJA) among adolescents. RJA was less a characterized by relatively robust activation of the left parietal lobe, precuneus, and middle and inferior occipital cortex, but less frontal mediation.

Finally, Oberwelland *et al.* (2016) also reported that latency to follow the gaze of the avatar on RJA trials decreased from a mean of 0.83 in the childhood sample to about 0.67 s in adolescents. Ultimately, it may be useful to consider the utility of measurements of behavioral latency as well as the neural time course of behaviors in the neuroscience of joint attention. For example, Caruana *et al.* (2015) reported that the cortical processing of the significance of gaze shifts in adults began, on average, no later than 350 msec after the onset of a gaze shift in an adult sample. This, though, may be much later than any role the eye-contact effect may play in the time course of joint attention given its estimated 150–170 msec range (Conty *et al.*, 2007; as cited in Senju & Johnson, 2009). Understanding the time course of events is an important goal for future studies of the typical and atypical neurodevelopment of joint attention.

Imaging joint attention in children with ASD

Oberwelland *et al.* (2017) went on to employ their virtual joint attention imaging paradigm to examine the joint attention system of adolescents with ASD. They found that adolescents with ASD displayed behavioral evidence of IJA and RJA that was comparable to typical controls, but they did not display the same level of neural system specialization for joint attention as did the controls. The

ASD adolescents displayed less evidence of superior temporal sulcus and temporal pole activation across IJA and RJA trials. They also displayed abnormal or non-specific activation of the temporal–parietal junction and precuneus across joint attention and control trials. Because their previous work had indicated that increases in the functional role of the precuneus may be part of the adolescent development of IJA, Oberwelland *et al.* (2017) suggested that underspecified functional contributions of precuneus may be part of atypical childhood IJA development in ASD. In what may be a related finding, Jaime *et al.* (2016) reported less evidence of temporal-central EEG coherence in a joint attention task in adolescents with ASD than in controls.

Oberwelland *et al.* (2017) also observed evidence of less medial frontal activation on the IJA task in ASD children. Moreover, individual differences in frontal IJA joint attention system activation were inversely related to social-communication symptom severity in the ASD sample. The latter observation emphasizes the previously discussed possibility that measures of frontal cortical correlates of joint attention may contribute to the search for diagnostic, prognostic, and intervention response biomarkers in ASD research. Noteworthy related findings have been reported studies of RJA using gaze following paradigms. These studies report evidence of greater recruitment of frontal, as well as striatal, parietal, and temporal systems in gaze following in typical children and adolescents than in children and adolescents affected by ASD (Greene *et al.*, 2011; Vaidya *et al.*, 2011).

Adults and the neural systems of IJA and RJA

Several different virtual reality paradigms have been designed and used to study the common and distinct cognitive processes and neural systems involved in IJA and RJA in adults (Schilbach *et al.*, 2010; Kim & Mundy, 2012; Redcay *et al.*, 2012; Gordon *et al.*, 2013; Caruana *et al.*, 2014). In general, the studies of adult IJA and RJA revealed activation of cortical systems that overlap with systems observed research with infants, children, and adolescents (e.g., Elison *et al.*, 2013; Oberwelland *et al.*, 2016; Eggebrecht *et al.*, 2017; Fig. 5). However, one distinctive feature of the adult research is that studies provide greater evidence of striatal, cingulate, and hippocampal contributions, especially to IJA (e.g., Schilbach *et al.*, 2010).

Schilbach *et al.* (2010) observed that RJA and IJA were associated with a distributed cortical system that involved nodes in the medial prefrontal cortex (including the rostral anterior cingulate), the medial orbital prefrontal cortex, the ventral striatum, the posterior cingulate cortex (PCC), and areas of the temporal and occipital cortex. However, IJA is distinguished from RJA by greater evidence of striatal activation. This is a fundamental observation. Early developmental studies noted that expression of positive affect often accompanied IJA, but not from other forms of joint attention behaviors (Kasari *et al.*, 1990; Mundy *et al.*, 1992). This suggested that social motivation may play a greater role in IJA, and that the atypical development of social motivation may contribute to an explanation of why IJA impairment was more chronic in people with ASD than RJA impairment (Mundy, 1995, 2003). Similarly, others have suggested that a system involving the striatum, amygdala, anterior cingulate, and possibly the insula is integral to processing the predicted reward value of *shifts of attention* (e.g., Gottfried *et al.*, 2003; Niznikiewicz & Delgado, 2011; Krebs *et al.*, 2012). Schilbach *et al.*'s (2010) observations provided initial evidence in support of the putative contribution of this system to IJA development, which is predicted by motivation theory on joint attention (Mundy, 1995;

Tomasello *et al.*, 2005) and the specific hypothesis that that IJA involves self-referenced processing of the predicted social reward value of attention shifts (e.g., Mundy, 2003; Mundy *et al.*, 2009).

Other studies have replicated the observation of striatal contributions to IJA and delineated the parameters under which this striatal contribution may be observed. Striatal activation was more prominent in tasks where participants believed they were engaged in IJA interactions with a real person rather than by a computer program, consistent with conceptualization of the socially specific nature of motivation in IJA (Pfeiffer *et al.*, 2014). Gordon *et al.* (2013) also reported that having one's own gaze followed by an avatar during IJA is associated with bilateral activations in the dorsal anterior cingulate gyrus, bilateral posterior parietal cortex, right amygdala, right fusiform gyrus (rFG), the bilateral striatum, and parahippocampal regions. Gordon *et al.* also hypothesized that the striatal cortex and amygdala likely play functional roles in the motivational component of IJA.

Not all studies, however, have revealed evidence of striatal contributions to IJA. Redcay *et al.* (2012) found evidence that RJA was associated with ventral–orbital prefrontal and posterior temporal cortical activation to a greater degree than was IJA. Meanwhile, IJA was associated with dorsal and medial prefrontal cortex, inferior frontal and parietal cortical activation to a greater extent than RJA. However, no evidence of striatal activation in IJA was observed.

Two other sets of observations are noteworthy. Gordon *et al.* (2013) noted that systems within the temporal–parietal cortical junction and cerebellum were especially active on incongruent IJA trials. Williams *et al.* (2005) also observed significant temporal–parietal activation in RJA trials that required inhibition of gaze following. Whereas most studies report data the cortical correlates of processing cues to engage in joint attention, these data illustrate the potential value of paradigms that enable the study of the role of the inhibition of neural systems in joint attention. Gordon *et al.*'s observations that the cerebellum may be involved in processing incongruent IJA trials may also be significant. Research and theory have long suggested that differences in the cerebellar influence on spatial encoding of a location for attentional and subsequent gaze shifts may play a role in the pathogenesis of ASD (Townsend *et al.*, 1996).

Lastly, Gordon *et al.* (2013) also noted that the pattern of activation observed for the rFG was different from the pattern of activation observed for other nodes of the IJA system. The rFG gyrus activated to both congruent (true) IJA trials and incongruent trials (false) trials, albeit at different intensities. The other nodes of the system activated only on true IJA trials. Thus, the rFG displayed a pattern of activation that was less specific to IJA. The explanation for this difference was not clear, but the pattern in the data was consistent with the need for caution in explaining joint attention principally in terms of neurocognitive functions of the structural face processing system.

Caruana *et al.* (2014) have developed and exemplary virtual reality cooperative joint attention game paradigm for their imaging research. They tested the parallel and distributed system model of joint attention (Mundy *et al.*, 2009) and observed that the common effects of IJA and RJA performance in terms of a common pattern of activation of the temporal–parietal junction, precuneus, posterior superior temporal sulcus, middle frontal gyrus, and middle temporal gyrus. Alternatively, activation of the superior frontal gyrus, anterior and middle cingulate cortex, thalamus, and cerebellum was specific to IJA.

In general, the widely distributed pattern of cortical activation in joint attention observed by Caruana overlapped with the patterns observed in other studies that used somewhat different virtual reality methods (Gordon *et al.*, 2013; Schilbach *et al.*, 2010; Redcay *et al.*, 2012; Fig. 5). Thus, the adult studies provided some evidence of the reliability of observations across imaging tasks. The Caruana *et al.*'s observations were also consistent with Gordon *et al.*'s (2013) regarding the involvement of anterior and middle cingulate, thalamic region, and cerebellum neural system activation specifically in conjunction with IJA performance. The observation of thalamic activation was also consistent with previous suggestions of the likelihood of the basal ganglia reward process in IJA (Schilbach *et al.*, 2010; Gordon *et al.*, 2013).

Several of the foregoing studies provided evidence that both the ACC and PCC play a role in IJA. In addition, Hopkins & Taglialatela (2013) reported that neural organization within the ACC to be significantly related to individual differences among chimpanzees in initiating triadic social attention with a human tester. Moreover, studies of pointing for joint attention (Committeri *et al.*, 2015) and related research on sharing attention in cooperative joint action (Schilbach *et al.*, 2013) also provided evidence of the involvement of the ACC as part of the joint attention system. However, the observations of PCC involvement in IJA in infants and adults (Schilbach *et al.*, 2010; Eggebrecht *et al.*, 2017) suggest that a singular emphasis on the ACC as the only region of interest in the cingulate cortex in IJA research (Mundy, 2003) may be inexact.

The PCC lies along the ventral surface of the precuneus. Thus, the repeated observations of precuneus activation in joint attention (Table 2) may indicate PCC contributions as well. A PCC/precuneus network is considered to be a central node of the default system associated with the processing of internal self-referenced information (Khalsa *et al.*, 2014). Recent data and theory suggest that the functions of the PCC/precuneus network, in connection with systems of the medial prefrontal cortex, may be integral to regulating the balance and integration of internal attention to self and external attention to others (Leech & Sharp, 2014; Herold *et al.*, 2016). Spreng *et al.* (2013) have also noted that some nodes of the frontal–parietal control system have unexpected connections to both the default and dorsal attention systems, whereas most nodes display the expected unilateral connection to one or the other. Leech & Sharp (2014) also suggest that PCC may influence how narrowly or broadly focused attention is on self and other referenced information and that variation in this and other PCC functions may play a role in ASD and other conditions.

These observations are consistent with the idea that joint attention, and many aspects of social cognition, involves a type of *cognitive control* that enables the neural upregulation of the simultaneous, or contiguous processing of information about self and other during referential interactions (Mundy & Jarrold, 2010; Fig. 4b). Observations of the role of the PCC in joint attention may be especially important for future clinical imaging work on ASD. Metabolic and functional abnormalities of the PCC have been repeatedly observed in ASD research (Leech & Sharp, 2014). For example, Chiu *et al.* (2008) have observed atypical self-referenced information processing associated with systems of both the ACC and PCC in individuals affected by ASD.

Gordon *et al.*'s (2013) observation of hippocampal activation in joint attention reminds us that joint attention, like the eye-contact effect (Senju & Johnson, 2009), influences memory and encoding (Kim & Mundy, 2012). Joint attention does not simply coordinate orienting with a social partner. Attention is a different construct from orienting. Attention involves the enhancement of information processing of a circumscribed part of the physical and mental environment, while decreasing processing of other information, much like a zoom lens or spotlight (Eriksen & James, 1986). Hence, joint

attention is a socially coordinated spotlight that results in enhanced information processing of a common point of references for social partners in ways that solo attention does not. Enhanced information processing during joint attention has been observed in infants (e.g., Striano *et al.*, 2006; Hirotani *et al.*, 2009; Kopp & Lindenberger, 2011) and adults (e.g., Conty *et al.*, 2010; Böckler *et al.*, 2011; Linderman *et al.*, 2011; Bayliss *et al.*, 2013; Boothby *et al.*, 2014). Interestingly, IJA may be more strongly associated with enhanced stimulus encoding and memory than RJA in children and adults (Kim & Mundy, 2012; Mundy *et al.*, 2016). This IJA enhancement of encoding and memory, however, is less apparent in children with ASD (Mundy *et al.*, 2016).

Imaging studies of joint attention in adults with ASD

There are surprisingly few imaging studies of joint attention in adults with ASD. Nevertheless, three important sets of adult observations have been reported. Pelphrey *et al.* (2005) examined neural systems responses to correct (congruent) and incorrect (incongruent) avatar-directed RJA trials. Both the congruent and incongruent trials activated regions along the superior temporal sulcus (STS). However, activation was stronger for inhibition to incongruent RJA trials in typical adults and involved regions of the superior temporal sulcus, middle temporal gyrus, parietal lobe, middle frontal gyrus, and anterior cingulate. In adults with ASD, a more limited pattern of activation to incongruent trials was observed in the middle temporal, occipital, inferior frontal, and insula cortexes. The groups were also significantly different in terms of activation in the superior temporal cortex, insula, and inferior frontal gyrus. Interestingly, behavioral and superior temporal sulcus imaging data suggested that individuals with ASD perceived and reacted at about the same speed to all avatar shifts of gaze. Thus, the ASD adults displayed aspects of correct RJA behavior, but the neural systems that supported recognition of an incorrect RJA bid by the avatar were different from those in adults with typical development. A similar pattern of typical behavior but atypical neural correlates was observed by Oberwelland *et al.* (2017) in their study of ASD adolescents.

Redcay *et al.* (2013) reported that adults with typical development displayed significantly stronger activity in the dorsal medial prefrontal cortex and left posterior superior temporal cortex on both IJA and RJA tasks than did individuals with ASD. Alternatively, both groups displayed activity in the right anterior insula, and left inferior parietal cortex in conjunction with IJA, rather than RJA. Again, these neural systems differences emerged even when there was little evidence of group differences in latency or accuracy on the joint attention tasks.

Redcay *et al.* (2013) also observed specific diagnostic group differences on RJA, but not IJA tasks. Similar to the findings of Pelphrey *et al.* (2005), the typical group displayed greater anterior dorsal medial frontal and posterior superior temporal activation to RJA than did the group with ASD. Alternatively, in RJA trials the ASD group displayed greater evidence of recruitment of the putamen, fusiform gyrus, and middle occipital gyrus than did the typical controls. Thus, the ASD group displayed less activation of key components of the social-cognitive mentalizing system (dMPFC and pSTS) during joint attention task performance, but greater activation of the cortical visual-spatial processing, face processing systems, and possibly the motor learning systems (putamen) as well.

The lack of observed differences in IJA by Redcay *et al.* (2013) was somewhat surprising because the atypical development of IJA is thought to be a more robust symptom of ASD than atypical RJA (e.g., Mundy *et al.*, 2016). However, the self-initiated and self-motivated nature of IJA likely makes it more difficult to emulate in a VR imaging paradigm than the more obligatory RJA responses. Hence, VR joint attention paradigms (e.g., Schilbach *et al.*, 2010; Redcay *et al.*, 2013; Caruana *et al.*, 2014) may be expected to display more variable sensitivity to typical and atypical IJA, than for RJA development. This is an important psychometric issue for future research.

Mizuno *et al.* (2011) provided a third study of adults, which may not be recognized as pertinent to the study of joint attention. Mizno *et al.* examined the neural basis of *deictic shifting* in a linguistic perspective-taking task in adults with ASD. *Deixis* refers to behaviors used to indicate a personal perspective or point of view in communication. Joint attention enables preverbal children to indicate their first-person perspective or to follow the second person perspective of a social partner. Hence, joint attention has long been considered to involve deictic communication and the capacity for deictic shifts (Scaife & Bruner, 1975; Tomasello *et al.*, 2005). Words such as pronouns are also used to denote deixis and deictic shifts. Mizno *et al.* examined the cortical network activation of ASD adults in a task that required them to respond to 'I' and 'you' to shift between the first and second person perspective while viewing a common referent (pictures) with a tester. The ability to use pronouns to correctly refer to personal perspectives (self or other) has long been recognized as problematic for many individuals with ASD (e.g., O'Connor & Klein, 2004; Mizuno *et al.*, 2011).

Mizuno *et al.* (2011) observed that individuals with ASD displayed slower responses to pronominal cues to shift between the self-or-other referenced visual perspectives than did typical controls. There was also evidence of attenuated functional connectivity between the precuneus and Insula cortex in response to pronoun-cued shifts in the ASD group compared to typical controls. Moreover, individual differences in this aspect of functional connectivity were correlated with differences in latency of task response in the adults with ASD, and this association was significantly stronger in the ASD than the comparison group.

Mizuno *et al.* (2011) noted evidence for the role of the parietal–precuneus in representing information about the spatial relation between self and others. They cited an observation that narrative shifts in oral story comprehension have been observed to elicit evidence of activation in the precuneus and posterior/middle cingulate cortex bilaterally (Whitney *et al.*, 2009). They also noted the role of the posterior parietal cortex in processing egocentric (body-dependent) and allocentric (body-independent) spatial information. They hypothesized that decreased functional connectivity between the parietal/precuneus and insular brain systems may result in a disturbance in rapid shifting between self and other referenced visual perspective in adults with ASD. This is similar to the notion that functions of the precuneus/PCC network may be integral to regulating the balance between internal (self) and external (other) attention (Leech & Sharp, 2014). Also, recall that Oberwelland *et al.* (2016, 2017) observed that changes in the involvement of the precuneus may be characteristic of the neural network development of joint attention from childhood to adolescence, and a focal point of the differences in the joint attention development in adolescents with ASD. Thus, the dimension of development and pattern of results reported by Mizuno *et al.* (2011) are aligned with imaging data in joint attention.

Summary and conclusions

A small but growing imaging literature indicates that joint attention is supported by neural systems that are widely distributed across the brain, and likely serve several functions (Fig. 5). The primary nodes

of the mature joint attention systems include (a) the dorsal and medial frontal cortex, (b) the orbitofrontal cortex and insula, (c) the anterior and PCC, (d) the superior temporal cortex, (e) the precuneus/parietal cortex, and (f) the amygdala as well as nodes of the basal ganglia including the striatum (e.g., Caruana *et al.* 2014; Elison *et al.*, 2013; Eggebrecht *et al.*, 2017; Mundy, 2003; Schilbach *et al.*, 2010; Oberwelland *et al.*, 2016). The functional development of this distributed brain system is evident in measures of the frontal node(s) by no later than 5 months for both RJA and IJA (e.g., Grossmann *et al.*, 2007, 2013; Grossmann & Johnson, 2010). The available data also suggest that the neural systems of joint attention continue to differentiate from infancy through adolescence and adulthood. In particular, more differentiated activation of medial frontal, the basal ganglia, and along the superior temporal and parietal cortices has been observed in adolescents and adults (Fig. 5; Eggebrecht *et al.*, 2017; Oberwelland *et al.*, 2016, 2017). However, these developmental observations are largely based on cross-sectional age data, rather than true longitudinal comparisons.

Nevertheless, the current imaging data deepen our understanding of joint attention as a fundamental dimension of human cognitive neurodevelopment, and its possible relation to social-cognitive mentalizing. For example, consider the processing functions of nodes A, E, and F itemized in the previous paragraph. Among the many functions of node A, the dorsal medial frontal cortex (dMPC) appears to play a role in adopting another person's perspective and comparing self-other perspectives (D'Argembeau *et al.*, 2007; Denny *et al.*, 2012). These are critical functions for engaging in joint attention (Mundy & Newell, 2007) and the perspective-taking thought to be necessary for mentalizing (Frith & Frith, 2006). Denny *et al.* have also proposed more details with regard to the function of this node. The dMPC may be more involved in other reference processing and ventral MPC (vMPC) is associated with self-referenced processing. However, Denny *et al.* also specify that there is a broad overlap of the regions recruited for each type of information processing and that the frontal processing of perspective occurs in conjunction with the left temporal–parietal junction and posterior cingulate activation. Denny *et al.* concluded that a 'whole-brain' process was involved in attending to one's own perspective (or mental state) and another's perspective or mental state (p. 7, Denny *et al.*, 2012).

One significant function served by the ability to appreciate self and other perspectives is the human predilection for sharing information. Joint attention serves a communicative or information sharing function that develops before the onset of language (Bates *et al.*, 1975). As previously noted, IJA can be described as spontaneously seeking to share experiences with other people through eye-contact, pointing, showing, and other behaviors (Mundy, 2016).

With this in mind, it is noteworthy that in a recent study of sharing information Baek *et al.* (2017) observed functional differentiation of dMPC and vMPC that is related to the observations of Denny *et al.* (2012). Baek *et al.* (2017) presented adults with newspaper headlines and asked them to decide if they (a) were not interested in the headline, (b) wanted to read more information related to the headline, or (c) would share the headline on social media such as Facebook. They observed vMPC activation when participants decided a headline was interesting to themselves (self-referenced processing), but a distributed system of dMPC and temporal–parietal junction activation when they decide to share a headline (self and other referenced processing). Thus, the functions of node A of the joint attention system may involve the abiding human motivation to share our own interests with other people (Mundy, 1995), and the cognitive process of coordinating self-other perspectives necessary to information sharing.

Exercising joint attention, attending to self and others' perspectives, and sharing information appear to also involve the precuneus and posterior cingulate (node E). Presumably, this node plays a role in first-person perspective taking and agency, as well as visual-spatial processing and imagery, and episodic memory (Cavanna & Trimble, 2006). Research has suggested that node E is also involved in integrating self-attention with attention to others attention and actions (Leech & Sharp, 2014), which occurs during the processing of information about some common referent in space in joint attention (Mundy, 2016). Moreover, integrating representations of stored knowledge about self-attention and action, with perceptions others attention and actions also likely contributes to mentalizing what others believe or intend.

Finally, the amygdala, striatum, hippocampus, and connections with the anterior cingulate cortex of node F are purportedly involved several functions of joint attention and mentalizing. These include processing information related to eye movements, the assignment of valence (positive or negative) to stimuli, goal relate motivations, episodic and working memory, and decision making (Hikosaka *et al.*, 2000; Olson *et al.*, 2013; Schroll & Hamker, 2013; Ikemoto *et al.*, 2015; Maia & Frank, 2017). This node may be involved in three aspects of the development of joint attention. First, it may be involved in the eye-contact effect (Senju & Johnson, 2009) an intrinsic motivation system important to the neonatal development of joint attention (Mundy, 2016). Second, it may continue to play a role in the mediating the positive valence of the sense of intersubjectivity and relatedness to others that accompanies sharing an experience via joint attention (Mundy *et al.*, 1992; Mason *et al.*, 2005; Bayliss *et al.*, 2013; Boothby *et al.*, 2014; Shteynberg *et al.*, 2014). Hypothetically, the valence system involvement in joint attention also may play a role in enhancing the impact of social attention coordination on encoding and information processing that has been in numerous studies (e.g., Striano *et al.*, 2006; Becchio *et al.* 2008; Kopp & Lindenberger, 2011; Wu *et al.*, 2011; Kim & Mundy, 2012; Gregory & Jackson, 2017).

This description of the functional nodes of the neural system for joint attention is consistent with the idea that a central function of the joint attention and social cognition is the capacity to appreciate the viewpoint of others (Buckner & Carroll, 2007). The incipient developmental of this function is likely guided by metabolic processes (Liu *et al.*, 2011; Stavropoulos & Carver, 2013; Hopkins *et al.*, 2014a,b; Nakako *et al.*, 2014; Wade *et al.*, 2014; Gangi *et al.*, 2016), although far too few studies have been conducted on this vital issue (see Mundy, 2016 for review). What imaging studies now make clear, though, is that by 4 to 5 months that both the behavior and neural substrates of joint attention can be measured. Theoretically, from that point on the early practice of joint attention plays a dynamic role in social-cognitive development. The practice or joint attention provides repeated but varied experiences with perspective sharing, in conjunction with cognitive maturation (e.g., enhancement of working memory and proprioceptive information processing), leads to more efficient neural systems for integrative processing the perspectives of self and other. That is, joint attention plays a significant experience-expectant role (Greenough *et al.*, 1987; Gordon *et al.*, 2003) in the neurodevelopmental of neurocognitive functions that support subsequent elaborations, such as the development of social-cognitive mentalizing (Mundy & Neal, 2000; Mundy & Newell, 2007).

Given the foregoing discussion, the observation that the functions of several of the nodes in the joint attention system overlap with the cortical regions involved in mentalizing or theory of mind (Fig. 5) should come as no surprise. Discussions of imaging data on joint attention often comment on the significant overlap regarding nodes

of the joint attention system and nodes of the social-cognitive mentalizing system (e.g., Schilbach *et al.*, 2010; Redcay *et al.*, 2013; Oberwelland *et al.*, 2016). However, recall though that studies have yet to collect imaging data on joint attention and mentalizing tasks from the same sample(s) in order to more precisely examine the nature of this system overlap. So this review is based on what must be recognized as circumstantial, albeit compelling evidence that joint attention and social-cognitive mentalizing employ common neural systems. The evidence is compelling, in part, because it comports with a-prior hypotheses that are explicit or implicit in long-standing theory about the relations between joint attention and social-cognitive development (Baron-Cohen, 1989; Mundy, 1995; Tomasello, 1995; Mundy, 2003; Tomasello *et al.*, 2005; Mundy & Newell, 2007). Furthermore, the circumstantial evidence of the shared neural systems accords with the numerous reports of significant longitudinal continuity between infant joint attention behaviors and childhood mentalizing task (Table 1).

The recognition that the neurodevelopment of joint attention and mentalizing may be fundamental related supports new ideas about social cognition. For example, Schilbach *et al.* (2013) argued that social cognition is often and perhaps incorrectly conceptualized in too limited a fashion as merely a spectator process. That is, social cognition is often viewed and measured as an isolated, first-person process involving the construal by one individual of the ideation of another person. Alternatively, Schilbach *et al.* argue that social cognition most often occurs embedded in real-time social interactions and involves embodied perceptual processing that is not precisely measured in non-interactive paradigms. Joint attention theory converges with this perspective. It suggests that social cognition is a complex form of hybrid neurocognition, the full appreciation of which demands that we understand how it develops *from* many real-time interactions. The observations of Baek *et al.* (2017) also encourage the field to think beyond the limits of our experimental paradigms. We must recognize that social cognition is more than an isolated first-person process involving the construal by one individual of the ideation of another person (Schilbach *et al.*, 2013). Rather, the real value of research on the commonality of the neural systems of joint attention and mentalizing is that it contributes to the study of the neuro-architecture of the culture-enabling, fundamental human capacity for sharing experiences with each other (Tomasello *et al.*, 2005).

Autism and the neuroscience of joint attention

Another goal of the paper was to point out the relevance of the emerging neuroscience of joint attention for the study of the neurodevelopment of ASD. From infancy through adulthood, the capacity or tendency to spontaneously share experience with others is fundamentally different in people with ASD, almost irrespective of their language development (Mundy, 2016). Yet it has been difficult to measure and perceive the developmental course and continuity in symptoms of this social dimension across age in research on ASD. Lord & Jones (2012) recently stated this problem in the following way.

> Many of the most theoretically important constructs proposed as social deficits [in ASD], such as theory of mind ... joint attention ... and social motivation ... are striking in their presence at some ages and in some individuals, but not observable in very young children or no longer present in significant numbers of older children or adults (p. 7).

There is now substantial behavioral and imaging evidence (Tables 1 and 2), however, that make a compelling case for the argument that joint attention and social-cognitive mentalizing represent a developmentally continuous axis of the cognitive phenotype of ASD (Baron-Cohen, 1989; Mundy & Sigman, 1989). Moreover, the imaging studies of joint attention reviewed here provide a methodological armamentarium that begins to enable an infant to adult life-span approach to investigating the atypical neurodevelopment of this axis ASD.

One major domain of useful application for the new joint attention imaging toolbox may be its potential to contribute to the search for biomarkers of ASD (Walsh *et al.*, 2011). In this regard, three questions come to mind. If the eye-contact effect (Senju & Johnson, 2009) is involved in the neonatal development of joint attention, then measures of the eye-contact effect could provide bio-behavioral markers related to the neonatal identification of ASD (Jones & Klin, 2013). Joint attention imaging methods may also contribute to the development of useful outcome measures for the new generation of early joint attention intervention methods for children with ASD (e.g., Kasari *et al.*, 2008, 2012, 2015; Murza *et al.*, 2016). If intervention leads to an increase in joint attention, does it also lead to changes in one or several nodes of the joint attention system? Attempts to answer this and related questions could enrich the understanding of the neurodevelopment of joint attention, the causal effects of intervention methods, and the factors that influence individual differences in response to such interventions.

Joint attention imaging could also inform research on how the amygdala plays a pivotal role in the atypical neurodevelopment in ASD that directly connects to the social phenotype (e.g., Schumann & Amaral, 2006; Schumann *et al.*, 2009; Gotts *et al.*, 2012; Nordahl *et al.*, 2012). Recall, that several studies suggest the amygdala play a role in joint attention disturbance in ASD. These include Elison *et al.*'s (2013) observations on 6-month neural connectivity and joint attention, Shen *et al.*' (2016) data on the atypical functional connectivity of the amygdala in preschool ASD children. Mosconi *et al.*'s (2009) study on amygdala volume predictions of joint attention in 2- to 40-year-olds with ASD is also important in this regard. Finally, the finding of a link between the amygdala volume and mentalizing in typical children is significant (Rice *et al.*, 2014). This set of observations points to the potential of a more concerted program of research on joint attention, the amygdala, and social-cognitive development in ASD.

Finally, a phenomenon observed in studies of older individuals suggests a fourth target for future research. Individuals with ASD may not display clear evidence of behavioral differences in joint attention task performance in imaging studies, yet they may exhibit atypical neural system activation associated with their task performance (e.g., Redcay *et al.*, 2013; Oberwelland *et al.*, 2016, 2017). Does this mean that individuals with ASD learn to engage in joint attention via alternate neurodevelopmental systems? If so, does this mean that although the behavioral topography of their joint attention appears typical, the cognitive phenomenology of joint attention is different for people with ASD? Finally, what happens when children with ASD respond to joint attention interventions? Does a corresponding change in the neural systems for joint attention occur, and/or is there a pattern of atypical neural development that predicts attenuated intervention responsiveness? We are approaching a point of convergence in the developmental, behavioral and neuroscience of ASD where such questions can be asked, and answered. However, we have barely scratched the surface of understanding the neurodevelopment and impact of joint attention in ASD. Another decade of studies or perhaps more will be needed to understand if the apparent promise of the neuroscience of joint attention for informing ASD research is substantive or ephemeral.

Methodological issues and current limitations

Schilbach et al.'s (2013) admonition about the limited perspective provided by social-cognitive paradigms, especially Non-interactive paradigms, alludes to a major methodological issue and limit for current imaging studies of joint attention and social cognition. It is possible, if not likely, that system activation patterns may vary across subtle (or not so subtle) across the task demands of different joint attention and social-cognitive paradigms. Schurz et al. (2014) have illustrated this 'paradigm task-demand reliability' issue in a meta-analysis of brain imaging studies of theory of mind using false belief, trait judgment, strategic game, social animation, mind in the eyes, and rational action paradigms. They observed some overlap in activation patterns across paradigms, but also noteworthy differences. For example, although they observed activation of a dMPC for the false belief, trait judgments, and strategic game paradigms, activation of this node was less clear for the other three paradigms.

A degree of commonality of observations reported across joint attention imaging studies in adults was noted above, as were differences in observations of system activations. For example, studies differed regarding the observation of striatal contribution to IJA. The spontaneity and social motivation characteristics of IJA (Parlade et al., 2009) may make it difficult to measure. Therefore, it may be important to provide parametric studies that directly compare results using the different available IJA paradigms (e.g., Redcay et al., 2012; Caruana et al., 2014; Oberwelland et al., 2016). Comparative parametric studies of the different methods used across development such as optical imaging, resting state system activity with behavioral observations, and virtual joint attention emulation tasks using fMRI may also ultimately be necessary. Nevertheless, even in the context of these and other methodological issues, a remarkably information picture of the neurodevelopment of joint attention has begun to emerge that will only increase in clarity and impact with additional studies. The basic and clinical sciences of the causes and effects of human social-cognitive neurodevelopment will no doubt benefit from the new neuroscience of joint attention.

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Conflict of interest

P. Mundy declares that he has no conflicts of interest regarding the content of this paper.

Data accessibility

No original data were presented in this review. For data accessibility see the specifics provided in the citation(s) of interest.

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