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The Development of Social Brain Functions in Infancy

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One fundamental question in psychology is what makes humans such intensely social beings. Probing the developmental and neural origins of our social capacities is a way of addressing this question. In the last 10 years the field of social–cognitive development has witnessed a surge in studies using neuroscience methods to elucidate the development of social information processing during infancy. While the use of electroencephalography (EEG)/event-related brain potentials (ERPs) and functional near-infrared spectroscopy (fNIRS) has revealed a great deal about the timing and localization of the cortical processes involved in early social cognition, the principles underpinning the early development of social brain functioning remain largely unexplored. Here I provide a framework that delineates the essential processes implicated in the early development of the social brain. In particular, I argue that the development of social brain functions in infancy is characterized by the following key principles: (a) self-relevance, (b) joint engagement, (c) predictability, (d) categorization, (e) discrimination, and (f) integration. For all of the proposed principles, I provide empirical examples to illustrate when in infancy they emerge. Moreover, I discuss to what extent they are in fact specifically social in nature or share properties with more domain-general developmental principles. Taken together, this article provides a conceptual integration of the existing EEG/ERPs and fNIRS work on infant social brain function and thereby offers the basis for a principle-based approach to studying the neural correlates of early social cognition.

Keywords: social cognition, social neuroscience, development, infancy

One major function of the human brain is to recognize and interpret social information. The field of social cognition attempts to understand and explain how thoughts, feelings, and behavior of individuals are influenced by the presence of others and through interaction with others (Allport, 1985; Fiske, 1995). Critically, humans are such intensely social creatures that already as young children they outperform their closest living primate relatives (the great apes) in terms of their social–cognitive skills, while showing very similar skills as great apes when dealing with the physical world (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007).

There is more evidence for this relative independence of social cognition from other aspects of cognition. For example, individuals with either frontal or prefrontal cortex (PFC) damage show impaired social behavior and functioning, despite the retention of some intact cognitive skills such as memory and language (Anderson, Bechara, Damasio, Tranel, & Damasio, 1999; Anderson, Wisnowski, Barrash, Damasio, & Tranel, 2009; Blair & Cipolotti, 2000). The fact that social cognition can be relatively impaired after such an injury while sparing aspects of nonsocial cognition raises the possibility that unique neural circuits may contribute to social cognition. Furthermore, it has been shown that while social

and nonsocial behaviors are both heritable, they show a degree of partial independence, with some of the genetic variation dissociating social and nonsocial behaviors (Ronald, Happe, & Plomin, 2005). More evidence for the partial independence of social cognition is gleaned from studies of persons with Williams' syndrome or autism. Individuals with Williams' syndrome appear to have relatively preserved basic social–cognitive skills (i.e., facial processing and abilities in understanding mental states), despite having deficits in physical cognition (Bellugi, Lichtenberger, Jones, Lai, & St. George, 2000; Karmiloff-Smith, Klima, Bellugi, Grant, & Baron-Cohen, 1995). This partial preservation of social cognition is in direct contrast to persons with high-functioning autism and Asperger's syndrome, who show impairments in social cognition and social behavior that some suggest may not be related to general cognitive abilities (Heavey, Phillips, Baron-Cohen, & Rutter, 2000; Klin, 2000). While the opposing cognitive profiles observed in Williams' syndrome and autism provide some evidence for the partial independence of social and physical cognition, it is important to acknowledge that in neither of the two neurodevelopmental disorders can the less affected (partially preserved) domain of cognition be considered typical (Karmiloff-Smith, 1998, 2007).

Together, these findings lend support to the hypothesis that there is a network of specific brain areas preferentially involved in the processing of social information. This network has been referred to as the social brain (see Adolphs, 1999, 2001, 2003). This hypothesis has also been maintained and influenced by the thinking in the area of evolutionary anthropology (Brothers, 1990; Brothers & Ring, 1992). To explain primates' and particularly humans' unusually large brains, it has even been claimed that the computational demands of living in complex social groups selected for increases in neocortex—a view put forward as the social brain

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hypothesis (Dunbar, 2003) or the Machiavellian Intelligence hypothesis (Whiten & Byrne, 1997).

A discipline called social–cognitive neuroscience has emerged that investigates the neural underpinnings of human social behavior. Its agenda has been described in terms of seeking “to understand phenomena in terms of interactions between three levels of analysis: the social level, which is concerned with the motivational and social factors that influence behavior and experience; the cognitive level, which is concerned with the information-processing mechanisms that give rise to social-level phenomena; and the neural level, which is concerned with the brain mechanisms that instantiate cognitive-level processes” (Ochsner & Lieberman, 2001, p. 717). The majority of the research activities in this area have been focused on how adults’ brains make sense of the social world (for reviews, see Adolphs, 1999, 2001, 2003; Beer & Ochsner, 2006; Blakemore, 2008; Blakemore & Frith, 2004; Frith & Frith, 1999, 2006). This provides us with important insights into the full-fledged, fully developed neural machinery that deals with complex social problems. However, from an ontogenetic perspective, the question arises, how do these capacities of the brain in interacting with others and making sense of their social behavior develop? And what are the critical developmental precursors of these adult abilities? The answers to these questions are important for a variety of reasons. For example, it has been argued that a better understanding of the early emergence of the social brain will be of relevance for social, educational, and clinical policies (Blakemore & Frith, 2005). Furthermore, a developmental perspective may shed light on debates within adult social–cognitive neuroscience such as that concerning the domain-specificity of certain brain processes (see Cohen Kadosh & Johnson, 2007) and help inform evolutionary accounts of human social cognition by providing insights into the neurodevelopment of uniquely human forms of social cognition (Saxe, 2006; Tomasello, Carpenter, Call, Behne, & Moll, 2005).

The first year of postnatal development, infancy, is the time of life during which enormous changes take place—the “helpless” newborn seems almost a different creature from the active, inquisitive 1-year-old. During this period, human infants develop in a world filled with other people. Relating socially to others has not only profound effects on what they feel, think, and do, but is also essential for their healthy development and for optimal functioning throughout life (Nelson, Furtado, Fox, & Zeanah, 2009). Therefore, developing an understanding of other people and their actions is one of the most fundamental tasks infants face in learning about the world. The current review aims to provide a framework that conceptualizes the processes involved in the emergence of the neural underpinnings of social information processing in infancy.

Before I begin with the presentation of the proposed framework it needs to be emphasized that any account of the emergence of social information processing needs to acknowledge and incorporate the fact that, contrary to what was often assumed in the past (James, 1890/2007; Piaget, 1952), human infants enter the world tuned to their social environment and readily prepared for social interaction. At birth, infants exhibit a number of biases that preferentially orient them to socially relevant stimuli. In particular, it has been shown that newborns prefer faces over other kinds of visual stimuli (Johnson, Dziurawiec, Ellis, & Morton, 1991; Johnson & Morton, 1991), voices over other kinds of auditory stimuli (DeCasper & Fifer, 1980; Vouloumanos, Hauser, Werker, & Mar-

tin, 2010), and biological motion over other kinds of motion (Simion, Regolin, & Bulf, 2008). While these biases may provide an important foundation for the emergence of social–cognitive abilities, biases observed in newborns are thought to be only broadly tuned to social stimuli and are assumed to mainly be mediated by subcortical mechanisms (Johnson, 2005a, 2005b). It is thus critical to understand how the cortical systems develop, allowing the human infant to make sense of the social world. These are the processes that this review is most concerned with and aims to conceptualize.

In the last 10 years the field of social–cognitive development has witnessed a surge in studies using neuroscience methods to elucidate the development of social information processing during infancy. While the use of electroencephalography (EEG)/event-related brain potentials (ERPs) and functional near-infrared spectroscopy (fNIRS) has revealed a great deal about the timing and localization of the cortical processes involved in early social cognition (Grossmann & Johnson, 2007; Lloyd-Fox, Blasi, & Elwell, 2010), the principles underpinning the early development of social brain functioning remain largely unexplored. Here I will provide a framework that delineates the essential processes implicated in the development of the social brain during infancy. In particular, based on a review and synthesis of the literature, I will argue that the development of social brain functions in infancy is characterized by the following key principles: (a) self-relevance, (b) joint engagement, (c) predictability, (d) categorization, (e) discrimination, and (f) integration (see Table 1 and individual sections for details regarding the definition and properties of the proposed principles). For all of the principles, I will provide a conceptual characterization followed by empirical examples to illustrate when in infancy the principle emerges. Critically, the review is centered on the question of when in infancy the proposed principles emerge. Moreover, I will discuss how these principles interrelate and to what extent they are in fact specifically social in nature or share properties with more domain-general developmental principles. The order of the presentation of these principles follows their developmental emergence (early vs. later in infancy) and domain-specificity (specifically social vs. domain-general), with early developing principles and domain-specific principles discussed first and later-developing principles and domain-general principles discussed later. Note that while the current review attempts to be broad and far-reaching in its scope, it is not a meta-analysis based on an exhaustive literature review but rather represents a focused research review that conceptually integrates existing bodies of work.

Before delving into the characterization of the various principles, it is critical to further clarify the focus of the current review and acknowledge limitations that may result from this focus. First, it is beyond the scope of this review to cover speech and language development in infancy and how this relates to the development of the social brain (see Kuhl, 2007, for a discussion of this question). Second, because infant social brain function has predominantly been studied by using EEG/ERP and fNIRS methods, the focus here is on the cortical systems involved in the early development of social information processing. This focus on cortical processing therefore reflects the current state of the literature and represents a methodological limitation. It is, however, important to acknowledge and recognize, at the beginning of this review, that subcortical systems have been shown to play a vital role in the functional

Table 1

Overview of the Proposed Principles of Developing Social Brain Functions and Their Characteristics

Principle	Definition	Brain basis	Developmental emergence	Domain-specificity
Self-relevance	Sensitivity to any sign of or change in an agent's action that indicates that the interaction or communication is directed at the infant	Prefrontal cortex (PFC), particularly medial PFC	Early in infancy (before 6 months)	Domain-specific (social)
Joint engagement	Sensitivity to any signs of an agent's action that indicates the interaction or communication about an external object/event is shared with the infant	Prefrontal cortex, particularly medial PFC	Early in infancy (before 6 months)	Domain-specific (social)
Predictability	Sensitivity to any features of an agent's action that helps anticipate the next step or goal of that action	Inferior frontal and premotor cortex	Early in infancy (before 6 months)	Domain-general (social and physical)
Categorization	Sensitivity to any features of an agent that helps categorize the agent (find out what kind of agent it is and what "group" it belongs to)	(Inferior) temporal cortex	Late in infancy (after 6 months)	Domain-general (social and physical)
Discrimination	Sensitivity to any (overt) changeable features of an agent's action that help to detect certain states that index likely future behavior	Temporal cortex, particularly the right superior temporal cortex	Late in infancy (after 6 months)	Domain-general (social and physical)
Integration	Sensitivity to any information about an agent or an agent's action that helps matching across processing channels and modalities	Temporal cortex, particularly multisensory regions in the superior temporal cortex	Late in infancy (after 6 months)	Domain-general (social and physical)

development of cortical brain circuits (Innocenti & Price, 2005). Relatedly, given the focus on studying infant brain function using EEG/ERP and fNIRS, another limitation concerns the lack of information regarding structural brain development during infancy and how it relates to brain function (see Payne & Bachevalier, 2009, for an extensive review of the neuroanatomy of the developing social brain). These are limitations that will be returned to in the discussion, as they provide critical considerations in guiding future work in this area of research.

Self-Relevance

Characterization

Self-relevance can be defined as the sensitivity to any sign of or change in an agent's action that indicates that the interaction or communication is directed at the infant. The primary cues that infants use to detect self-relevance are eye contact, infant-directed-speech, and contingency (see also Csibra & Gergely, 2009, for a proposed theoretical framework that emphasizes an innate sensitivity to these cues). For the current context, it is important to stress that the form of self-relevance invoked here does not require any explicit (conceptual) understanding of the self and the action being intentionally directed at the self but rather refers to an implicit and cue-based detection of self-relevant signals. The detection of self-relevance is thought to result in a privileged processing of what follows the self-relevant signal. The key brain region involved in assessing and representing information with reference to the self in adults is the medial prefrontal cortex (mPFC), a region that has also been more generally implicated in theory of mind (for a review, see Amodio & Frith, 2006).

Empirical Support

There is behavioral evidence that already newborns are sensitive to eye contact and infant-directed speech as potential cues to

self-relevance (Cooper & Aslin, 1990; Grossmann & Farroni, 2009). Critically, there is also neuroscience work using fNIRS, showing that newborns' sensitivity to infant-directed speech is reflected in their mPFC responses. Specifically, newborns have been shown to show significantly increased responses in mPFC to their own mother's voice reading a story in infant-directed speech (IDS) compared with their mothers reading the same story in adult-directed speech (ADS; Saito, Aoyama et al., 2007). This indicates that newborn infants discriminate between these two forms of speech and dedicate increased mPFC processing resources to IDS, which is of high socioaffective relevance to the infant. In another study, Saito, Kondo et al. (2007) showed that mPFC activation can be obtained in response to nonmaternal emotional speech. This finding suggests that the emotional tone of voice that characterizes infant-directed speech, as one potential cue to self-relevance detection, correlates with mPFC responses in newborn infants. However, one critical limitation of these studies is that cortical responses were only measured from two locations in infant prefrontal cortex, which prevents us from assessing whether the prefrontal response was selective to mPFC or present in other parts of PFC as well.

Furthermore, eye contact, as a visual self-relevant signal during social interactions, has also been shown to activate mPFC in 4-month-old infants (youngest age group tested with fNIRS in visual social perception study, no newborn fNIRS data available; Grossmann et al., 2008). In this study, infants watched two kinds of dynamic scenarios in which a social partner either established eye contact or averted its gaze followed by a smile (Grossmann et al., 2008). The results revealed that, similar to what is known from adults (Kampe, Frith, & Frith, 2003; Pelphrey, Viola, & McCarthy, 2004), processing eye contact activates not only superior temporal cortex implicated in processing information from biological motion cues but also the mPFC important for detecting self-relevant social information. Moreover, in the same study, measuring electrical brain responses (gamma band oscillations, which are high-

frequency bursts of electrical cortical activity that occur around 40 Hz and are highly correlated with the hemodynamic response measured by fNIRS) over PFC in another group of 4-month-old infants showed that only a smile that was preceded by eye contact evoked increased PFC responses in 4-month-old infants (Grossmann et al., 2008; see Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008, for evidence that microsaccades may account for scalp-recorded gamma band activity in some instances, note that this explanation is unlikely because fNIRS and EEG gamma methods yielded similar results in this infant study). Similarly, in an ERP study with infants of the same age, smiles paired with eye contact resulted in greater electrophysiological responses measured over frontal cortex (Rigato, Farroni, & Johnson, 2010). These EEG findings corroborate and extend the results relying on fNIRS and further support the notion that from early in infancy mPFC plays a role in interpreting social and affective information directed at the self.

That smiling at an infant while making eye contact is a powerful interactive cue triggering mPFC activation has also been demonstrated in another fNIRS study (Minagawa-Kawai et al., 2009), in which 9- to 12-month-old infants were presented with videos of either their own mother or a female stranger smiling at them or looking neutrally at them. Smiling at the infants evoked greater activity in mPFC regardless of the familiarity with the face, suggesting that mPFC is flexibly employed during positive social interactions. Nevertheless, mPFC activity was significantly greater in response to the own mother smiling when compared with the female stranger smiling, suggesting that infants' mPFC responses are particularly sensitive to self-relevant affective cues from the primary caregiver. Interestingly, this study showed that mothers exhibited a very similar mPFC response when looking at their own infants' smiling, thus pointing to a shared neural mechanism engaged during social interaction between caregivers and infants.

In adults, initiating a social interaction by eye contact and calling a person's name results in overlapping activity in the mPFC (Kampe et al., 2003), suggesting that, regardless of modality, self-relevant signals are detected by the same brain region. In a recent fNIRS study (Grossmann, Parise, & Friederici, 2010), 5-month-old infants watched faces that either signaled eye contact or directed their gaze away from the infant, and they also listened to voices that addressed them with their own name or another name, in order to examine the neural basis of detecting self-relevant signals. The results of this study revealed that infants recruit adjacent regions in the mPFC when they process eye contact and their own name. Moreover, 5-month-old infants that responded sensitively to eye contact in the one mPFC region were also more likely to respond sensitively to their own name in the adjacent mPFC region as revealed in a correlation analysis. This indicates that responding to self-relevant signals in these two regions is functionally related. The findings of this study suggest that infants at the age of 5 months selectively process and flexibly attend to self-relevant signals across modalities. Further evidence that infants at this age flexibly respond to visual and auditory signals that indicate self-relevance comes from a recent study that examined infants' brain responses using EEG (Parise & Csibra, 2013). Specifically, in line with prior work (Grossmann, Johnson, Farroni, & Csibra, 2007; Grossmann et al., 2008) this study shows that eye contact and infant-directed speech result in overlapping

electrophysiological activity (gamma band oscillations) over anterior frontal electrode sites.

This review of the available evidence suggests that mPFC involvement in infancy is likely to be important for the detection of self-relevant information. Given that there is an extensive body of evidence from prior work with adults that implicates mPFC in assessing and representing information with reference to the self (Amodio & Frith, 2006), this proposal can be seen as a developmental extension of prior accounts of adult mPFC function into infancy. This increased sensitivity to self-relevant information might serve critical learning functions because it highlights potentially useful information that others present to the infant (Csibra & Gergely, 2009; Sperber & Wilson, 1995). In support of this view, it has been shown that infants' learning is influenced and improved when they are addressed by infant-directed speech and eye contact (Senju & Csibra, 2008; Singh, Morgan, & White, 2004; Yoon, Johnson, & Csibra, 2008). The mPFC might thus be involved in learning from others by detecting the relevance of others' communication and actions to the self. Obviously, this sensitivity to self-relevant information in infancy does not imply that infants have an explicit (conceptual) understanding of the self. But it may rather reflect an emerging implicit form of self awareness that developmentally precedes higher levels of self awareness found in older children and adults (Rochat, 2003, 2011). Nonetheless, it has been proposed that this implicit form of self-awareness, which emerges during infancy, still exists and plays an important role in adulthood and operates in addition to more explicit forms of self-awareness in adults (Rochat, 2003). Moreover, one may argue that the sensitivity to self-relevant information serves as a powerful foundation for developing a sense of self because it provides infants with the opportunity to experience when the self is addressed in an interaction. In fact, it has been argued that early social interactions during infancy and the experiences gained therein can be considered the cradle of self development (Reddy, 2003).

One intriguing implication of this proposal is that by measuring mPFC involvement in a given context, one might be able to examine the extent to which an infant responds to self-relevant information by predicting subsequent cognitive and behavioral effects on the basis of prior neural markers. For example, on a trial-by-trial basis one could look at infants' mPFC response to eye contact and then see whether or not infants are more likely to show gaze following in response to an eye gaze shift of a social partner. The prediction based on the proposal presented above is that on trials during which infants show mPFC involvement when seeing eye contact they should be more likely to gaze follow. In behavioral work, it has already been shown that infants are more likely to gaze-follow when they have previously been presented with eye contact or heard infant-directed speech (Senju & Csibra, 2008); however, it is unclear what the underlying neural processes are that correlate with this behavioral phenomenon. Moreover, the proposed approach might also be useful in assessing very early interindividual differences in the perception of relevance to the self in response to identical stimuli. We might thus also be able to identify infants that tend to show little sensitivity to perceptual social signals indicating self-relevance but also infants that are overly sensitive to social information even if it is not directed at them. Extreme biases in either direction in early development could potentially have serious detrimental effects on social devel-

opment in the long term. For example, a strongly reduced sensitivity to self-relevant information might be linked to neurodevelopmental disorders such as autism, where it has been shown that lacking behavioral sensitivity to self-relevant signals such as eye contact and name cues are some of the earliest detectable warning signs for the later development of autism (Elsabbagh & Johnson, 2007; Elsabbagh et al., 2012; Zwaigenbaum et al., 2005). The development of biomarkers such as brain-based measures to guide an early identification of developmental disorders is still in its infancy but has been shown to be of great promise, especially when relying on measures that assess infants' responses to eye contact (Elsabbagh et al., 2012).

Joint Engagement

Characterization

Joint engagement can be defined as the sensitivity to any signs of an agent's action that indicates that the interaction or communication about an external object/event is shared with the infant. The primary cues that infants use to detect joint engagement are referential visual, auditory, or body cues (gaze, voice, and body direction/orientation). This sensitivity is closely related to self-relevance as self-relevance can be seen as a precondition for establishing joint engagement. The detection of joint engagement is thought to be critical for the coordination of actions and thus an integral part of human cooperative activities (Tomasello et al., 2005; Tomasello, Melis, Tennie, Wyman, & Herrmann, 2012). Attending and responding to eye gaze is crucial for establishing joint engagement during human social interactions. Specifically, eye gaze plays an important role in directing and coordinating attention during triadic interactions between self, other, and the environment. During a typical triadic interaction, a person may establish eye contact with another person and then direct that person's gaze to an object or event. The psychological process by which two people share attention toward the same object or event is referred to as joint attention. The ability to engage in triadic social interactions is thought to be critical for a wide range of human activities, supporting teaching, cooperation, and language learning (Csibra & Gergely, 2009; Tomasello, 1995; Tomasello et al., 2005). Moreover, impairments in joint attention are one of the earliest warning signs of neurodevelopmental disorders such as autism spectrum disorder (Charman, 2003). At the neural level, joint attention mainly relies on the recruitment of the mPFC in adults (Schilbach et al., 2010; Williams, Waiter, Perra, Perrett, & Whiten, 2005), a brain structure that has been more generally implicated in social interaction, social cognition, and theory of mind (Amodio & Frith, 2006; Schilbach et al., 2013), but also involves other brain regions such as the ventral striatum related to reward processing (Schilbach et al., 2010).

Empirical Support

In behavioral work it has been shown that the ability for joint engagement emerges during the first year of life (Striano & Reid, 2006; Tomasello et al., 2005). However, the exact time of its emergence during infancy is still debated and depends on what is considered to be truly joint attention (see Carpenter & Call, 2013). There is behavioral evidence suggesting that already newborns

show a rudimentary sensitivity to eye gaze cueing of object locations important for the detection of joint engagement (Farroni, Pividori, Simion, Massaccesi, & Johnson, 2004) and that 3-month-old infants distinguish between dyadic and triadic interactions (Striano & Stahl, 2005). Furthermore, in agreement with findings implicating mPFC in both joint engagement and theory of mind (Schilbach et al., 2013), differences in the display of joint attention behaviors observed during infancy predict later differences in the more explicit understanding of others' mental states assessed during childhood (Charman et al., 2001). Even though much progress has been made in understanding the behavioral emergence of joint attention during infancy (Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Rossano, Carpenter, & Tomasello, 2012; Striano & Stahl, 2005), we have only recently begun to examine the neural correlates of joint engagement in the developing infant.

First insights into this question came from a line of ERP studies. Namely, Striano, Reid, and Hoehl (2006) examined the ERP correlates of joint engagement in 9-month-old infants in paradigm in which an adult interacted live with the infant in two contexts. In the joint-attention context, the adult looked at the infant and then at the computer screen displaying a novel object. In the nonjoint-attention context, the adult only looked at the chest of the infant and then at the novel object presented on the screen. Objects presented in the joint-attention context, compared with objects in the nonjoint-attention context, were found to elicit a greater negative component (Nc) over frontal and central electrodes around 500 ms. The Nc is thought to be generated within the PFC and indicates the allocation of attention to a visual stimulus (Reynolds & Richards, 2005). It was therefore suggested that infants benefit from the joint-attention interaction and thus devote more attentional resources to those objects presented in this context. This ERP paradigm has also been used to examine joint attention in younger infants (Parise, Reid, Stets, & Striano, 2008). This study found that even by the age of 5 months, infants show an increased allocation of attention to the object in a joint-attention condition, as indexed by an increased Nc. Similar to what has been reported in these studies using live interactions, in another ERP study (Senju, Johnson, & Csibra, 2006), 9-month-infants watching a person on a screen make eye contact and then look at an object also showed similar ERP responses over frontal cortex. Despite these insights from using ERP methods, the exact localization of cortical activation during joint engagement has only recently been studied.

Specifically, Grossmann and Johnson (2010) examined brain responses in 5-month-old infants' PFC during triadic social interactions using fNIRS. In order to investigate whether young infants engage specialized prefrontal brain processes when engaged in joint attention, in this study infants were presented with scenarios in which a social partner (virtual agent presented on a screen) (a) engaged in joint attention by gaze cueing the infant's attention to an object after establishing eye contact (joint-attention condition); (b) gaze cued the infant's attention to an empty location (no referent condition); or (c) looked at an object without prior eye contact with the infant (no eye contact condition). Only in the joint attention condition, infants recruited a specific brain region within the PFC, demonstrating that 5-month-old infants are sensitive to triadic interactions. Moreover, 5-month-old infants recruited a prefrontal region localized in left dorsal PFC when engaged in joint attention with another person, suggesting that young infants

engage similar brain processes as adults when sharing attention with others (Schilbach et al., 2010).

While Grossmann and Johnson's (2010) study provided first insights into the brain regions implicated in joint attention in infancy, an important outstanding question was whether infants are also sensitive to when a social partner follows *their* gaze. This is a particularly critical question because it can inform theories that posit that brain processes are shared and flexibly engaged by self- and other-initiated actions and interactions (Meltzoff, 2007; Schilbach et al., 2013). Recently, Schilbach et al. (2010) showed that in adults there are key brain regions, such as the left medial dorsal PFC, involved in both responding to joint attention and to initiating joint attention. This suggests that adults flexibly engage specific brain processes that are shared between self- and other-initiated gaze interactions.

Grossmann, Lloyd-Fox, et al. (2013) examined 5-month-olds' sensitivity to when a social partner follows their gaze by measuring infant brain responses using fNIRS during scenarios in which a social partner either followed the infants' gaze an object that they had previously looked at (congruent condition) or a social partner shifted attention to look at a different object (incongruent condition). The fNIRS data revealed that a region in the left mPFC showed an increased response when compared with baseline during the congruent condition but not during the incongruent condition, suggesting that infants are sensitive to when someone follows their gaze. From a developmental perspective, this finding is in line with theories emphasizing the importance of the early emergence of social-cognitive abilities required to engage in joint action (Csibra & Gergely, 2009; Tomasello et al., 2005) and supports theories positing a link between brain processes implicated in actions performed by self and by others (Meltzoff, 2007). From a neuroscience perspective, this finding further strengthens accounts that—in contrast to the commonly held notion of a late maturation of PFC functions—assign a pivotal functional role to the PFC in infant cognition in general (Grossmann, 2013a) and mPFC in infant social cognition in particular (Grossmann, 2013b).

Grossmann, Lloyd-Fox, et al.'s (2013) findings further showed that the infant prefrontal brain response during the congruent condition was observed in the left hemisphere, which is not only in line with the adult functional MRI (fMRI) work (Schilbach et al., 2010) but also corresponds with findings showing that greater cortical activation in the left PFC is positively correlated with children's tendency to initiate joint attention (Caplan et al., 1993; Mundy, Card, & Fox, 2000). With respect to the lateralization of the prefrontal brain response, it is noteworthy that prior work with infants and adults has shown that left prefrontal cortical activation is indicative of a motivation to approach (Davidson & Fox, 1982; Fox, 1991; Harmon-Jones, 2003). This raises the possibility that infants responded with the motivation to approach the social partner that followed their gaze, whereas this motivation was absent when the social partner did not follow gaze (Grossmann, Lloyd-Fox, et al., 2013). Such an effect of joint engagement on motivational systems may serve a vital function in guiding infant social behavior by driving infants to interact with, learn from and share experiences with cooperative partners (Tomasello et al., 2012).

Predictability

Characterization

Predictability can be defined as sensitivity to any features of an agent's action that helps anticipate the next step or goal of that action. The primary cues that infants use in the context of prediction are likely to be related to the familiarity, probability and more specific kinematic information of an action. It has been suggested that this sensitivity is closely related to infants' own motor representations and motor repertoires (Gallese, Rochat, Cossu, & Sinigaglia, 2009). Predictive processes are vital for human social behavior as they allow for coordination and competition between humans (Tomasello et al., 2012; Whiten & Byrne, 1997). The key brain regions involved in prediction in adults are localized in the inferior frontal and premotor cortex (Kilner, Friston, & Frith, 2007a, 2007b; Rizzolatti & Sinigaglia, 2010). Indeed, it has been argued that "predictive coding" is a general (and overarching) organization principle of human brain function, such that most of what the brain does can be accounted for by computations that work out the predictability of events or actions on the basis of prior experience (Friston & Kiebel, 2009).

Empirical Support

A promising and novel way toward understanding the brain systems that are involved in the observation and prediction of actions is to investigate their roles in development (Gallese et al., 2009; Marshall & Meltzoff, 2011). It is of particular interest to investigate action observation and prediction during infancy because it allows for the possibility to elucidate these processes while new perceptual and motor skills are acquired. So far, the research on infants' perception of biological movement has primarily been based on methods examining their looking behavior. This line of research has revealed that infants are sensitive to biological as compared with nonbiological motion from very early in ontogeny. For example, newborn infants prefer to look at the display of a walking point-light chicken compared with a scrambled or inverted walking point-light chicken (Simion et al., 2008). Furthermore, at the age of 3 months, infants discriminate between biologically possible and impossible displays of human point-light walkers (Bertenthal, Proffitt, & Kramer, 1987). At the same age, infants distinguish between biologically possible and impossible moving point-light spiders and cats (Pinto, 1994). This behavioral work shows that infants develop the basic but important ability to discriminate between biological and nonbiological forms of movement very early in ontogeny. This early perceptual sensitivity to biological motion is also reflected in infants' preferential brain responses to biological motion as seen in regions within the superior temporal cortex (Farroni et al., 2013; Lloyd-Fox et al., 2013; Lloyd-Fox, Blasi, Everdell, Elwell, & Johnson, 2011; Lloyd-Fox et al., 2009). Interestingly, regions within the superior temporal cortex were observed to preferentially respond to visually familiar (facial) biological motion soon after birth (Farroni et al., 2013). This preferential response correlated with newborn infants' age in hours, suggesting that these cortical responses require relatively little experience to develop.

Furthermore, there is behavioral evidence showing that infants are sensitive to the goals behind a person's action (movement),

suggesting that they see others as intentional agents and use others' goals to make sense of their actions (see Woodward, 2009, for review). This behaviorally shown sensitivity appears to fundamentally rely on infants' own motor experience, as infants' goal understanding has been shown to be influenced by action experience. For example, Sommerville, Woodward, and Needham (2005) found that when 3-month-old infants, who are not yet skilled at grasping objects, are given experience in grasping objects with the help of sticky mittens, they then construe others' actions as goal-directed, while a control group of 3-month-olds that simply viewed reaching actions during training did not show such effects. In general, this behavioral finding is in agreement with theoretical accounts positing a link between the processes implicated in actions performed by self and in understanding others' actions (Meltzoff, 2007). However, the relationship between own motor experience and goal understanding and prediction might not be as elementary and strong as assumed, because there is work to suggest that even in the absence of such experiences infants respond sensitively to others' goals (Hernik & Southgate, 2012; Southgate, 2013).

From a neuroscience perspective, there is evidence that brain processes associated with the motor system play a role during action observation in infancy. For example, Southgate, Johnson, Osborne, and Csibra (2009) showed that 9-month-old infants display a reduction in EEG mu activity over sensorimotor cortex, indexing motor activation, during performing and observing grasping actions. However, contrary to the dominant view, which stipulates that brain regions like the premotor cortex respond preferentially to familiar and executable action (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010), infant fNIRS data (Grossmann, Cross, Ticini, & Daum, 2013) show that, similar to what has been described in a recent fMRI study with adults (Cross et al., 2012), 4-month-old infant premotor cortex preferentially responds to robotic rather than to human motion (when presenting infants with whole body movements). Importantly, this study demonstrates that increased premotor cortex involvement during the observation of robotic motion does not depend on whether it was presented in the context of a familiar human or an unfamiliar robot figure, indicating that it is solely the motion patterns (kinematic cues) that drive the response in the premotor cortex. This kind of robotic motion is neither visually familiar to, nor executable by the infant. Nonetheless, it resulted in increased activation of the premotor region, suggesting that activation of the premotor cortex cannot be taken as an indicator for spontaneous simulation of an action present in the observer's motor repertoire (see also Southgate & Begus, 2013). These findings might be best accounted for by a predictive coding framework based on Bayesian principles (further explicated below) in which the observation of highly novel actions imposes greater demands on the motor system to predict or learn from actions with which the observer lacks prior physical experience, thus resulting in more motor system activity when viewing highly unfamiliar compared with relatively familiar actions (Cross et al., 2012).

That prior experience and familiarity with an action can play a role in the recruitment of the motor system has been shown by Stapel, Hunnius, van Elk, and Bekkering (2010) using EEG, who found that 12-month-olds showed greater motor activation (larger reduction of mu activity) during the observation of unfamiliar actions (e.g., cup to ear) than familiar actions (e.g., cup to mouth).

However, it is important to note that, in another study, 14- to 16-month-olds exhibited greater motor activation during the observation of a familiar (crawling) actions when compared with less familiar (walking) actions (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). While these prior infant EEG studies seem to have yielded conflicting patterns of results, they are in line with recent adult fMRI work mentioned above (Cross et al., 2012). Specifically, Cross et al. (2012) adopt a predictive coding perspective based on Bayesian principles to explain such findings (see Kilner et al., 2007a; Kilner et al., 2007b), suggesting that when observation of highly familiar actions leads to strong activation of the motor system, this is due to small deviations from extremely precise motor priors (gained by extensive physical or visual experience). Conversely, observation of highly unusual or unfamiliar actions can also lead to robust motor system activity, but in this case, activity is driven by a lack of motor priors, and the fact that sensorimotor cortices are highly engaged when trying to process (or predict or learn from) actions with which the observer has no prior experience.

This notion is in line with recent empirical findings from 12-month-old infants (Stapel et al., 2010) and with theories that implicate the motor system more generally in action prediction (Kilner et al., 2007a, 2007b; Schubotz, 2007) rather than specifically in a process of action mirroring via direct mapping (Avananti, Sirigu, & Aglioti, 2010; Buccino et al., 2004; Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). Clearly, much more work is needed to investigate the developmental emergence and exact nature of the neural mechanisms underlying predictive processes involved in social information processes in early development. The reviewed evidence suggests that predictive brain processes play an important role in action observation from early in ontogeny and can be evoked by relatively simple motion (kinematic) cues but also be based on more complex information such as the goal of an action.

Categorization

Characterization

Categorization can be defined as the sensitivity to any features of an agent that helps classify the agent (find out what kind of agent it is and what "group" it belongs to). The primary cues (facial, vocal, and body) that infants use to categorize are species, race, and gender. This sensitivity is closely tied to infants' experience and social environment. Categorization processes are vital for human social behavior as they allow for rapid judgment and decision-making on the basis of generalizable information (Fiske, 1995). The key brain regions involved in categorization in adults are localized in the (inferior) temporal cortex (Gauthier & Nelson, 2001; Gauthier, Skudlarski, Gore, & Anderson, 2000; Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Kanwisher, McDermott, & Chun, 1997) and also reflected in the N170 of the event-related brain potential (sources of the N170 localized in ITC; de Haan, Pascalis, & Johnson, 2002; Johnson et al., 2005). There is behavioral evidence that categorization of species and race information emerges during the second half of the first year of life (Kelly et al., 2007; Kinzler, Dupoux, & Spelke, 2007; Pascalis, de Haan, & Nelson, 2002). A basic sensitivity to gender as another cue that infants might use to categorize an agent develops during

infancy, as a preference for faces of the same gender of their primary caregiver can be observed in 3-month-old infants, but not in newborns (Quinn et al., 2008; Quinn, Yahr, Kuhn, Slater, & Pascalis, 2002). However, it is not clear whether (and when) gender results in similar categorization effects reflected in particular recognition advantages as seen for the processing own-species or own-race faces.

Empirical Support

For human infants it is vital to learn to identify conspecifics and distinguish them from others species. It is thus not surprising that a basic behavioral preference for familiar human stimuli can already be seen at the age of 3.5 months (Heron-Delaney, Wirth, & Pascalis, 2011). From prior behavioral work we also know that only later, namely between 6 and 9 months of age, infant's ability to discriminate between faces of differing identities narrows to human faces (Pascalis et al., 2002). That is, when presented with monkey and human faces, only younger infants (6 months) were able to discriminate between identities for both species, while older infants' discrimination (9 months) was limited to their own species. This process is commonly referred to as perceptual narrowing and can also be observed in other domains of perceptual development during the same developmental stage (see Lewkowicz & Ghazanfar, 2009, for a review). At the neural level, it was also examined whether the processing of faces becomes more specialized to human faces during the first year of life (Grossmann, Missana, Friederici, & Ghazanfar, 2012). Indeed, in this study it was shown the infant N290, which is thought to be the precursor to the adult face-specific N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996; de Haan et al., 2002), is modulated by the factor species (monkey vs. human) at the age of 8 months but not at the age of 4 months. More specifically, in 8-month-olds monkey faces when compared with human faces elicited an N290 that was larger in its amplitude. This suggests that the N290 becomes sensitive to species-specific information between 4 and 8 months of age.

Furthermore, in adults the N170 is larger in amplitude to inverted than to upright faces (Bentin et al., 1996; de Haan et al., 2002). Critically, this ERP component is neither modulated by the inversion of monkey faces (de Haan et al., 2002), nor when responses to upright versus inverted objects are compared (Bentin et al., 1996) in adults. In the studies that measured ERPs to upright and inverted human and monkey faces (de Haan et al., 2002; Halit, de Haan, & Johnson, 2003) the amplitude of the infant N290 at 12 months of age, like the adult N170, enhanced to inverted human but not to inverted monkey faces when compared with upright faces. However, in line with perceptual narrowing accounts, the amplitude of the N290 was not affected by stimulus inversion at an earlier age (3 and 6 months). Taken together, the studies reviewed above suggest that during infancy perceptual narrowing to human faces occurs and this narrowing, observed toward the end of the first year of life, is most reliably associated with changes in the infant N290. This specialization to human faces likely forms a critical basis for categorizing agents in infancy.

When considering infants' face recognition abilities, it is also important to mention that if young human infants are trained by their caregivers to individuate monkey faces (by giving each monkey face a proper name), infants do not undergo the typical perceptual narrowing of cross-species face processing (Scott &

Monesson, 2009) and older infants with such training develop face-specific ERP responses to monkey faces that is lacking in younger infants; that is, a neural specialization is constructed (Scott & Monesson, 2010). This suggests that this neural process is plastic and a specific kind of experience, namely the individuation of faces through labeling during social interactions with infants, is required for the neural categorization processes to take place during infancy (for more information concerning the timing and plasticity of these processes, see Maurer & Werker, 2014).

A very similar developmental picture emerges from the work on the neural correlates of processing racial information in infancy. In particular, Vogel, Monesson, and Scott (2012) presented 5- and 9-month-old (Caucasian) infants with African and Caucasian faces while measuring ERPs. This study revealed that 9-month-old infants, but not 5-month-old infants, were sensitive to racial information conveyed in the face. Specifically, 9-month-olds' ERP responses differed between African and Caucasian faces. Interestingly, contrary to the species-specific ERP response that occurred for the N290, the race-specific ERP response occurred later (P400) during visual processing. This suggests that species and race affect distinct stages of neural processing and detecting race-relevant information takes longer than detecting species-relevant information. It further shows the strength of ERP research in uncovering and delineating the timing of cortical processes associated with different levels of social perception. These findings are in line with general accounts of object categorization (Quinn & Slater, 2003) that assume that the categorization of objects, including faces, occurs at different levels (global, basic, and subordinate levels). The distinction between humans (conspecifics) and other animals likely takes place at the global level or at the basic level (de Haan et al., 2002; Grossmann, Gliga, Johnson, & Mareschal, 2009; Grossmann, Missana et al., 2012), while the distinction among humans of different races likely reflects subordinate level processes (Vogel et al., 2012). Moreover, from a purely perceptual point of view, it is presumably harder to distinguish between human faces based on race than between human faces and other animal faces that are perceptually more dissimilar. In any case, the available neural evidence suggests that, similar to the categorization effects to species, the sensitivity to race emerges between 5 and 9 months of age. This suggests that categorizing species-specific and race-specific information emerges over the course of the first year of life. While there is neural evidence concerning species and race, to date there is no work available on the neural basis of categorizing on the basis of gender. Furthermore, there is presently no fNIRS work available that has examined the brain regions involved in any of these processes. This is probably to do with the fact that the brain region that underpins categorization processes (particularly in the visual domain) is the fusiform gyrus located on the ventral surface of the brain. Due to methodological constraints to do with the optical signal obtained from deep (ventrally located) brain sources, it is unlikely that this brain region can be imaged using fNIRS (for a more extensive discussion, see Grossmann, 2008). However, there is some evidence using fMRI (Tzourio-Mazoyer et al., 2002) showing that 2-month-old infants' fusiform gyrus responds more strongly to faces when compared with objects. This shows that it is in principle possible to image the fusiform gyrus, but we currently do not know whether and when this brain region specializes in processing species or race.

Apart from the cues used by infants to categorize agents discussed in this section, there might be other critical cues that infants may use to categorize agents, especially cues that provide information regarding certain character traits such as niceness/trustworthiness and dominance. There is an emerging body of behavioral work showing that infants are sensitive to actions that convey these traits (Hamlin, Wynn, & Bloom, 2007; Mascaro & Csibra, 2012) and that children, like adults, infer such traits on the basis of minimal information from faces (Cogsdill, Todorov, Spelke, & Banaji, 2014) and use such traits to inform their decision-making (Harris, 2007). Extending this line of work by studying the neural basis of the development of these important trait attributions would be important to advance our understanding of the principle of categorization discussed in this section.

Discrimination

Characterization

Discrimination can be defined as the sensitivity to any (overt) changeable features of an agent's action that help to detect certain states that index likely future behavior. This is in contrast to the sensitivity associated with categorization that relies more on detecting and extracting persistent (enduring) features such as species, race, and gender. The distinction drawn between categorization and discrimination is based on existing models of face recognition that show that there are distinct pathways in the brain that deal with invariant and changeable visual information (Haxby, Hoffman, & Gobbini, 2000; Haxby, Hoffman, & Gobbini, 2002). The primary cues that infants use to differentiate in this way are changes expressed in face, voice, and movement or posture. This sensitivity is again closely tied to infants' experience and social environment. Discrimination abilities are thought to be important for providing specific insights into the agent's mental states and allow for precise attuning and coordination during social interactions. One vital aspect of such discrimination processes is the detection of emotional expressions. Discriminating between others' emotional expressions is a vital skill that helps us predict others' actions and guide our own behavior during social interactions (Frith, 2009). Emotional communication is thought to play an even greater role in daily social interactions in preverbal infants that do not yet have language as a means to interact (Grossmann, 2012). Emotional communication is inherently multidimensional and multisensory in nature as emotional information can be gleaned from various sources such as the face, the voice, and the body posture and motion of a person (Heberlein & Atkinson, 2009). The bulk of research investigating emotion expression perception has focused on facial and vocal expressions (Belin, Campanella, & Ethofer, 2012). Much less work has been dedicated to understanding the perception of emotional body expressions, even though body expressions may be the most evolutionarily preserved and immediate means of conveying emotional information (de Gelder, 2006). The work on emotional expression processing has revealed that adults are readily able to detect and recognize various emotions from facial, vocal and bodily cues (Bänziger, Grandjean, & Scherer, 2009). The key brain regions involved in emotion discrimination processes in adults are principally localized in temporal cortex, particularly the right superior temporal cortex (Allison, Puce, & McCarthy, 2000; Grandjean et

al., 2005; Heberlein & Atkinson, 2009). Differentiation processes have also been investigated by using ERPs in adults and the main ERP components implicated in emotion differentiation are the early posterior negativity (EPN) and late parietal positivity (LPP; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). However, to date it is not clear what the infant precursors to these adult ERP components are (see Grossmann, Striano, & Friederici, 2007, for evidence on how at the end of the first year of life ERP components to emotional expressions appear more adult-like). In what follows, I will focus on the developmental evidence on infants' emotion detection because it constitutes a vital part of the discrimination processes alluded to above. Here the focus is on emotion discrimination because most of the infant work is focused on that aspect of discrimination. Note, however, that discrimination can also involve the detection of other changeable characteristics such as those required to reason about desires and beliefs (Baillargeon, Scott, & He, 2010; Bartsch & Wellman, 1989; Repacholi & Gopnik, 1997), but those are much less studied in the first year of life, especially as far as their neural correlates are concerned.

Empirical Support

There is behavioral evidence that during the second half of the first year of life infants' sensitivity to emotional expressions emerges and that by the end of the first year they begin to use emotional cues to guide their own behavior (Baldwin & Moses, 1996; Campos et al., 2000; Mumme, Fernald, & Herrera, 1996). In particular, there is behavioral and neural evidence to suggest that infants begin to discriminate between positive and negative emotional expressions during the first year of life (Vaish, Grossmann, & Woodward, 2008). For example, 7-month-old infants but not 5-month-old infants showed longer looking times to fearful faces when compared with happy faces and differences in their event-related brain potentials (ERPs) during the processing of these facial expressions, indicating that infants' ability to discriminate between emotions emerges during the first year of life (Nelson & de Haan, 1996; Peltola, Leppänen, Mäki, & Hietanen, 2009). Specifically, ERP results demonstrate that the discrimination between fearful and happy expressions affects a series of ERP components (early-latency: positivity before [Pb]; midlatency: negative component [Nc]; and late-latency: positive component [Pc]; Nelson & de Haan, 1996). These components are thought to be associated with attentional/novelty (early Pb and midlatency Nc) and recognition memory (late-latency Pc) processes engaged by infants during visual experiments (see Webb, Long, & Nelson, 2005). Critically, ERP differences similar to what has been shown using facial expressions have been described in 7-month-olds when angry voices were compared with happy and neutral voices (Grossmann, Oberecker, Koch, & Friederici, 2010; Grossmann, Striano, & Friederici, 2005), suggesting that the sensitivity to emotional information across face and voice emerges during the first year of life. Recently, Missana et al. (2015) examined the neural correlates of emotional body expression processing during infancy by measuring ERPs in 4- and 8-month-old infants in response to point-light displays (PLDs) of happy and fearful body expressions. The ERP results of this study revealed that 8-month-olds but not 4-month-olds discriminate between emotions conveyed through body expressions. Specifically, 8-month-olds showed emotion-sensitive positivity over temporal and parietal

electrodes in the right hemisphere. Interestingly, this observed ontogenetic emergence of the sensitivity to emotional body expressions occurs at a time in development when facial and vocal emotion processing capacities undergo similar change (Grossmann, Oberecker et al., 2010; Peltola et al., 2009). Together, these findings thus provide evidence for accounts that conceive of emotion perception as a unified ability that develops in concert across various processing channels (face, voice, and body; Heberlein & Atkinson, 2009). At the neural level, Missana et al. (in press) showed that emotion discrimination from body expressions elicits brain responses that are lateralized to the right hemisphere. In agreement with prior work (Grezes, Pichon, & de Gelder, 2007; Heberlein, Adolphs, Tranel, & Damasio, 2004; Heberlein & Saxe, 2005), this suggests that the right hemisphere begins to play an important role in emotional expression processing from early in ontogeny.

More precise information regarding the brain regions involved in the emotion differentiation process comes from work using fNIRS. Grossmann, Oberecker, et al. (2010) showed that voice sensitivity emerges in the superior temporal cortex between 4 and 7 months of age (see Lloyd-Fox, Blasi, Mercure, Elwell, & Johnson, 2012, for a similar finding). More important for the current context, Grossmann et al. (2010) also showed that at 7 months of age, a voice-sensitive superior temporal region in the right hemisphere differentiated between angry, happy, and neutral emotional speech, suggesting that, similar to adults, superior temporal brain regions play a vital role in emotion differentiation processes. Critically, in infants of the same age, the superior temporal cortex has also been shown to be involved in emotion differentiation from facial expressions and angry facial expressions were also found to evoke stronger response in the superior temporal cortex in the right hemisphere (Nakato, Otsuka, Kanazawa, Yamaguchi, & Kakigi, 2011). This suggests that differentiation between a social agent's emotional states on the basis of facial and vocal cues implicates processes in the superior temporal cortex, especially in the right hemisphere. As of now there is no fNIRS work available on infants' processing of emotional body expressions but a similar developmental pattern and neural organization is expected to underpin infants' differentiation in this domain as well.

Integration

Characterization

Integration can be defined as the sensitivity to any information about an agent or an agent's action that helps matching across processing channels and modalities. The primary cues that infants rely on to integrate are more basic amodal cues such as temporal co-occurrence or more complex knowledge-based cues (e.g., common affect across senses; Bahrick, Lickliter, & Flom, 2004; Walker-Andrews, 1997). This sensitivity is again closely tied to infants' experience and their social environment and presumably relies on the differentiation abilities discussed earlier. From a functional perspective, this sensitivity is thought to be important for being able to make associations between information provided from different sources and form predictions on the basis of such associations. The key brain regions involved in integration (particularly concerned with sensory integration) in adults are local-

ized in multisensory regions in the superior temporal cortex (Allison et al., 2000; Ghazanfar & Schroeder, 2006).

Empirical Support

There is behavioral evidence showing that basic forms of integration relying on amodal information are present from birth or very early in infancy, while more complex knowledge-based integration only develops later during the first year of life (Bahrick et al., 2004; Lewkowicz & Ghazanfar, 2009). Early and basic forms of integration are likely to be mediated by subcortical structures such as the superior colliculus (Stein, Meredith, & Wallace, 1994; Wallace & Stein, 1997, 2001). Specifically, multisensory integration in superior colliculus relies on basic principles, namely that stimuli across different modalities co-occur in time and space. Although there is no direct evidence for superior colliculus involvement in infants, the processes associated with superior colliculus are similar to what has been argued to underpin early existing forms of multisensory integration in infants (see Bahrick et al., 2004). Critically, there is also recent evidence using fNIRS and ERPs suggesting that more complex integration abilities relying on cortical processing are present in 4-month-old infants as far as integration within one sense (vision: form and motion integration) is concerned (Grossmann, Cross et al., 2013) and in 5-month-old infants as far as integration across the senses (vision and audition: audio-visual speech) is concerned (Kushnerenko, Teinonen, Volein, & Csibra, 2008).

Grossmann, Cross et al. (2013) used fNIRS to examine the role of form and motion information when infants observe an agent's action. In this study, 4-month-old infants watched human or robotic figures (form manipulation) moving either in a human manner or in a robotic manner (motion manipulation) in a 2×2 design. This infant fNIRS study was based on work by Cross et al. (2012) showing that there is one region in the adult left STS that integrates form and motion information. In that study, the left STS responded preferentially when the human figure moved like a human and when the robot figure moved like a robot. This suggests that this region is involved in the detection of congruence between the agents' form and motion, supporting the notion that this region plays a critical role in the integration of information processed by the ventral (form) and dorsal (motion) visual pathways (Kourtzi, Krekelberg, & van Wezel, 2008). It is important to note that this integration occurred despite the fact that the robot form and motion were both unfamiliar to the adult observers.

Consistent with these findings, Grossmann, Cross et al.'s (2013) infant fNIRS data revealed that 4-month-old infants are also sensitive to the relationship between the form and the motion of an agent. More specifically, they seem to be able to integrate information about form and motion during action observation, as indicated by their superior temporal cortex responses. Infants' superior temporal cortex responses were similar in terms of their overall pattern (preferential response when the human figure moved like a human and when the robot figure moved like a robot), localization and lateralization to what was previously shown in adults (Cross et al., 2012). This demonstrates that a region in the left superior temporal cortex was preferentially engaged during the processing of congruent form and motion information, that is, during trials when infants saw a human figure moving like a human and a robot figure moving like a robot. The ability to match human form to

human motion might be explained by the visual experience that infants have in observing human action. However, it is more challenging to explain the surprising finding that infants are able to detect the congruence between robot form and motion, based on the temporal cortex responses. One possible explanation might be that infants' temporal brain responses measured in this study are a result of an associative mechanism by which familiar form is associated with familiar motion (human case) whereas an unfamiliar form is likely to be associated with an unfamiliar motion (robot case). This explanation might also account for what has been observed in the adult work (Cross et al., 2012). Much more work is needed, however, to clarify the exact mechanism that underlies this phenomenon. Nonetheless, infants' temporal brain responses observed in Grossmann, Cross et al.'s (2013) study indicate that they are sensitive to the relation between the form and the motion of an agent, which is considered to be an important social perceptual skill.

Moreover, the observed lateralization of infants' temporal cortex response to the left hemisphere (Grossmann, Cross et al., 2013) is consistent with findings from adults demonstrating that this region in left hemisphere is part of a multimodal association area (Decety & Sommerville, 2003). Another complementary interpretation of this left-lateralized effect in infants might be derived from the postulated links between action observation and language processing in the human brain (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Pulvermueller, 2005). According to this framework, the left-lateralized effect seen in infants' action observation might be considered an early precursor to left-lateralized brain functions that are later shared by language and action processing. Again, this proposal remains to be tested in future studies.

Another line of work has looked at integration processes in the context of audio-visual speech processing. For example, Kushnerenko, Teinonen, Volein, and Csibra (2008) measured ERPs in 5-month-olds and demonstrated that brain responses at frontal and temporal electrodes differed (starting around 290 ms) depending on whether conflicting auditory and visual speech cues were integrated or not. This study provided electrophysiological evidence for the McGurk effect in infants' audio-visual speech perception. Furthermore, Hyde, Jones, Flom, and Porter (2011) were able to show that 5-month-olds are sensitive to temporal synchrony in audio-visual speech presentations. In particular, asynchronously compared with synchronously presented face-voice pairings elicited a greater (more negative) early visual ERP response (peak around 150 ms) and a greater negative component at fronto-central electrodes during later processing stages (peak around 600 ms). This has been taken to indicate greater demands during early sensory and later attentional stages of processing unfamiliar (asynchronous) information across face and voice. Moreover, temporally synchronous compared with asynchronous face-voice pairs elicited greater ERP responses during early (peak around 250 ms) and late stages (after movement offset) of face-voice processing at temporal electrodes. Interestingly, these synchrony effects were observed over the left hemisphere and might be correlates of (language-sensitive) brain processes related to processing familiar audio-visual speech information. Given that these findings are likely linked to the emergence of language-sensitive brain processes that follow their own developmental principles (Kuhl, 2004), from these data it is not possible to identify the emergence

of integration in the context of social information processing more specifically.

Grossmann, Missana, Friederici, and Ghazanfar (2012) extended these prior studies by (a) presenting cross-species non-speech stimuli (monkey vocalization and humans mimicking monkey vocalization); and (b) by testing infants at different ages (4 months and 8 months) that span the time over which perceptual narrowing occurs. Specifically, in this study, ERPs were measured while 4- and 8-month-old infants watched and listened to congruent and incongruent audiovisual presentations of monkey vocalizations and humans mimicking monkey sounds. The ERP results indicated that younger infants distinguished between the congruent and the incongruent faces and voices regardless of species, whereas in older infants, the sensitivity to multisensory congruency was limited to the human face and voice. Furthermore, this study revealed that with development, visual and frontal brain processes (and functional connectivity) become more sensitive to the congruence of human faces and voices relative to monkey faces and voices. Similar audio-visual perceptual narrowing effects over the course of the first year of life have also been observed for race (Vogel et al., 2012). Specifically, infants listened to emotional sounds (laughing or crying) prior to seeing an image of an African American or Caucasian face expressing either a matching or mismatching emotion (Vogel et al., 2012). This study revealed that race-specific matching of emotion across voice and face was only seen at 9 months but not 5 months of age. In another ERP study, infants at the age of 7 months were shown to match emotional expressions across face and voice (Grossmann, Striano, & Friederici, 2006). These findings show that the neural processes involved in multisensory integration (face-voice matching) emerge over the course of the first year of life and support the notion that postnatal experience with human faces and voices is associated with the neural changes in multisensory integration processes (Lewkowicz & Ghazanfar, 2009).

The empirical evidence reviewed here suggests that while some basic forms of integration such as those relying on basic subcortical mechanisms and intramodal matching develop early in infancy, the more complex and sophisticated forms of cross-modal integration of human-specific social cues only emerge later in infancy. This pattern points to a development sequence according to which integration processes emerge in a hierarchical order from basic to complex and are constrained by the perceptual and cognitive development of the infant. Moreover, the reviewed findings are in line with general accounts of perceptual and cognitive development in the first year of life (Lewkowicz & Ghazanfar, 2009; Mareschal et al., 2007), which stipulate that the infant brain uses environmental experiences to shape perceptual and cognitive abilities related to integration. In this context, it should also be noted that other sensory modalities, apart from the ones focused on here (vision and audition), such as touch should be included in the investigation of integration processes relevant to social cognition. This is not only because touch has been shown to be of critical importance during social interactions with infants (Fairhurst, Löken, & Grossmann, 2014; Field, 2001) but also because tactile perception and visuo-tactile integration might follow a different time course than audio-visual integration and develop earlier in infancy (Filippetti, Johnson, Lloyd-Fox, Dragovic, & Farroni, 2013).

Discussion

This review serves as a first stride in illuminating the principles that underlie the early development of the social brain during infancy. We have seen that there are several key principles that can be applied to describe infants' emerging social brain functions. This provides a novel framework that can account for most of the developmental patterns observed in prior work on social information processing in infancy and shall help inform future work in the area. While the current overview of principles attempts to be as general and broad as possible, the list of principles highlighted here might not be exhaustive, meaning that this framework is open and should indeed be expanded upon, if necessary. Note also that while the current review aims at being far-reaching in its scope, it is not a meta-analysis based on a complete literature review. Crucially, one insight from surveying the literature in this area is that there is a need for community-augmented databases of neuroscience research with infants, which can then serve as a basis for performing meta-analyses (such an online database already exists for fNIRS work with infants, see Cristia et al. (2013), but is currently not available for EEG/ERP work with infants). Furthermore, one limitation is that the findings presented in the current review are based on cross-sectional work with infants. Clearly, there is a great need for longitudinal studies in order to examine trajectories and identify predictors of developing social brain function. The following discussion will deal with a number of critical issues that arise from this conceptual integration of the empirical work presented here.

Social or Not?

One critical question that needs to be addressed with respect to the proposed account is whether (or to which extent) these principles are truly social in nature or may rely on domain-general principles. This is important because it can help us understand which developmental principles are shared between the social and the physical (object) domain and which can be exclusively applied to the social world. The strongest candidates for being exclusively social in nature are the self-relevance and the joint engagement principle, as they are by definition intrinsically linked to social interactions and demand for a social partner to be involved in the process. This view is supported by theoretical accounts that emphasize the importance of both self-related processing and joint engagement for the development of human social cognition in the first years of life (Rochat, 2003, 2011; Tomasello & Carpenter, 2007; Tomasello et al., 2005). However, it might be argued that between the two principles, self-relevance may also apply to the physical domain. This is because objects might be perceived as self-relevant by infants in certain contexts, particularly due to their affordances and functions (Gibson, 1984). Indeed, in future work this issue should be taken into account by devising object-based control conditions. Joint engagement, however, is likely to be truly social in nature and it has even been proposed that joint engagement and its psychological functions represent a uniquely human form of social engagement vital for human cooperation (Saxe, 2006; Tomasello et al., 2005). Given the assumed significance of joint engagement for human social cognition it seems all the more important to further examine the developmental emergence of joint engagement and its neural correlates in infancy.

On the other hand, the principles of categorization, differentiation, and integration presumably share much in common with processes employed in the physical domain and used for object cognition. In fact, all three principles have been suggested to be domain-general principles permeating various developmental phenomena (Johnson, 2001, 2005a; Johnson, Grossmann, & Cohen Kadosh, 2009)—a view with a long tradition in developmental theorizing (Werner, 1957). This suggests that much that has been learned about the developmental principles from the extensive work in the physical domain can also be used to describe and explain development in the social domain. Although such domain-generalness is likely, the processes required might still differ between the social and physical domain at closer examination. For example, infant face and body processing becomes specialized to the upright orientation and is disrupted by inversion (de Haan et al., 2002; Missana, Atkinson, & Grossmann, 2015), indicative of holistic processing that is specific to faces and bodies, not observed for other objects. Similar to what was stated above, it seems critical to employ nonsocial object control conditions to further elucidate the similarities and differences in social and object processing. More generally, such an extension of the current research by comparing between social and nonsocial cognition more directly would critically advance our understanding of early social brain development.

Predictability is also likely to be a principle that can be broadly applied to the physical and social domains (Friston & Kiebel, 2009). However, the work presented here suggests that the prediction involved in interpreting an agent's action may rest on specifically social mechanisms because they depend on the detection of certain characteristics that underlie the agent's behavior such as intentions and goals. This notion is in line with the view that one of the major functions of the social brain is to enable us to make online predictions during social interactions and thereby enhance adaptive social responding (Frith, 2007). More generally, it should also be acknowledged that even though some of the principles discussed here might not be specifically social (because they can be applied to other domains), this does not preclude the possibility that they have evolved and developed to even higher levels of sophistication by the complexities of human social living (Humphrey, 1976).

Along these lines, it has also been argued that domain-specificity of information processing might be the outcome of development and learning rather than innately specified (Karmiloff-Smith, 1998). According to this view, it is possible that the brain functions that appear as specifically social in young infants are driven by learning in the intensely social environment that infants are born into. One could imagine that the early and frequent experience of eye contact, infant-directed speech, own name, and triadic interactions results in the early emergence of the brain processes that deal with these kinds of events.

Finally, one critical factor that might play a role in the distinction between social and nonsocial aspects of brain functioning is that social functions tend to involve affective and motivational processes, whereas nonsocial functions do not involve such processes or do involve them but to a lesser degree. Therefore, social and nonsocial functional principles might alternatively be divided into what is sometimes referred to as "hot" and "cool" forms of brain function (Zelazo & Carlson, 2012; Zelazo & Müller, 2002). This distinction has been particularly useful in providing a model

of executive functions and how they relate to PFC activation in adults, according to which “hot” executive function is associated with the medial PFC and “cool” executive function is linked to lateral PFC (see Zelazo & Müller, 2002). The neuroimaging evidence available on infants’ prefrontal cortex functioning generally supports this functional and anatomical distinction (see Grossmann, 2013a for a review and discussion), suggesting that this distinction is important from early in development. Critically, the work reviewed herein shows that infant brain functions considered as specifically social (self-relevance and joint engagement) mainly involve medial PFC. This observation is in line with the notion that affective and motivational processes play a pivotal role in the early development of social cognition (e.g., Reddy, 2003) and is also consistent with the view that these early emerging affective processes serve as a vital basis for social–cognitive development (Chevallier, Kohls, Troiani, Brodtkin, & Schultz, 2012).

Early or Late Emergence in Infancy?

This review shows that there are some principles that emerge earlier in infancy than others. In particular, self-relevance, joint engagement, and predictability develop in the first months of life, while categorization, differentiation, and integration only develop later during the second half of the first year of life. This developmental pattern is noteworthy because it indicates that the later developing processes may to a greater degree be influenced by experience than the early developing ones (Greenough, Black, & Wallace, 1987; Markham & Greenough, 2004). Indeed, there is work showing that particularly categorization and differentiation processes heavily depend on experience and the environment the infant grows up in (de Haan et al., 2002; Grossmann, Missana et al., 2012; Grossmann, Oberecker et al., 2010; Scott & Monesson, 2009, 2010; Scott, Pascalis, & Nelson, 2007). This also suggests that the later developing principles might be more malleable, whereas the early developing principles might be more influenced by the infants’ biological predispositions and thus be under greater genetic control (McCall, 1981; Zwaigenbaum et al., 2005). This notion receives support from work on neurodevelopmental disorders that affect social behavior such as autism, showing that autism is associated with impaired self-relevance detection and joint engagement (Charman, 2003; Elsabbagh et al., 2012). In fact, these impairments have been argued to be some of the earliest warning signs for autism, detectable in infants’ behavior by the end of the first year of life (Zwaigenbaum et al., 2005). In order to understand the genetic basis of autism it might therefore be a useful strategy to identify genes that account for variation in self-relevance and joint engagement rather than looking for genes that are associated with diagnosed autism, a strategy that has yielded only limited insights into the genetics of autism (Elsabbagh & Johnson, 2010; Happe, Ronald, & Plomin, 2006).

Another critical aspect for discussion has to do with the brain regions shown to be involved in the early versus late emerging principles. Specifically, as seen in this review, the early emerging principles (self-relevance, joint engagement, and predictability) are associated with activity within regions in the frontal cortex (prefrontal cortex, premotor cortex), whereas the later developing principles (categorization, differentiation, and integration) are associated with activity in the temporal cortex. This pattern may seem to contradict accounts that (a) postulate that frontal cortex is

functionally silent during infancy and only matures much later during development (see Zelazo & Müller, 2002, for a review); and (b) assume that posterior cortex (including temporal cortex) matures earlier than frontal cortex (Chugani & Phelps, 1986). However, there is now considerable evidence from neuroimaging studies with infants suggesting that frontal cortex plays an important role in social and cognitive functioning from early in infancy (Grossmann, 2013a, 2013b). Moreover, this pattern of early involvement of frontal cortex might also suggest that infants are actively engaged in rather than passively (reflexively) responding to their social environments. This view of infant social functioning gained from the neuroscientific evidence concurs with extensive behavioral work showing rather sophisticated social abilities in infants (Baillargeon et al., 2010; Spelke & Kinzler, 2007; Woodward, 2009).

The aforementioned classification of principles into (a) early and later developing ones, and (b) domain-specific and domain-general ones may also provide a useful framework to theorize about the relation between the proposed principles. In particular, according to this classification the greatest similarity appears to exist between self-relevance and joint engagement on the one hand (early emerging and domain-specific) and categorization, differentiation, and integration (later emerging and domain-general) on the other hand. This suggests that there are two families of principles that develop during the first year of life.

The observation that self-relevance and joint engagement as domain-specific principles emerge early in infancy has important implications. First, it may suggest that these two principles pose what could be conceived of as core aspects of social information processing (Spelke & Kinzler, 2007) that require little or no experience to develop. That self-relevance and joint engagement can be considered core aspects of human social cognition is in line with major theoretical accounts of behavioral development (Csibra & Gergely, 2009; Tomasello & Carpenter, 2007; Tomasello et al., 2005). In fact, according to these accounts it has been argued that what has here been discussed in relation to self-relevance and joint engagement principles can be considered to be part of uniquely human social cognition. Second, as already alluded to in the individual sections, self-relevance and joint engagement might be part of a functionally integrated processing system in the sense that perceiving some action as self-relevant might be a prerequisite for construing the subsequent interaction as joint. Equally, based on the observation that categorization, differentiation and integration as domain-general principles emerge later in infancy, one may argue that by developing slowly there is greater potential for experiential influence on the development of these brain functions.

Importantly, predictability as supported by the brain’s motor system seems to be somewhat different from the other principles as it emerges early but is likely a domain-general principle, because at least in adults it has been observed to become involved even when adults anticipate sequences of perceptual events that they cannot themselves produce (see Schubotz, 2007, for evidence how adults use the motor system to predict nonsocial external events). One possibility therefore is that predictability represents an overarching principle that is an integral part of the other principles, as predictive processes seem to play a critical role in almost all of the principles discussed here. This possibility requires closer examination in future work with infants. In particular, further work should capitalize on the existing neural measures available for

identifying predictive brain processes and find out whether predictive processes are generally involved in social and physical contexts that necessitate predictions. Taken together, the proposed way of classifying developmental principles according to their emergence in infancy can inform future work as it provides a conceptual basis for formulating hypotheses and predictions for empirical investigations.

Brain Connectivity

One critical limitation of the studies presented in this review is that they are mainly focused on activation within specific regions of interest. However, in order to gain a better and more complete picture of developing social brain function in infancy, it is also vital to understand how connectivity between brain regions develops during the first year of life. A closer look at brain connectivity patterns may also help to better understand why, as discussed above, particular brain regions are preferentially involved in certain social brain functions as the connections may critically shape and constrain the function of a brain region (Sporns, 2011). More generally, one important aspect to consider is that while we have observed activation of individual brain regions during infancy, we do not know whether the activity of these regions is coordinated into functional networks as seen in adults. In other words, we still know very little about how cortical networks develop. Here, I briefly outline some emerging evidence that speaks to this important issue.

As seen in this review, specific brain regions, including prefrontal regions, are activated from early on in infancy but at that point may not be functionally connected with other regions of cortex due to a lack of myelination of the relevant connections (fibre tracts; Deoni et al., 2011). Specifically, there is work using resting-state fMRI with infants indicating that some of the functional connections between certain parts of PFC and posterior cortical regions known in adults are not yet developed in infants (Fransson et al., 2007). Furthermore, resting-state studies testing infants across various ages show that long-range integration of cortical activity between anterior and posterior brain regions emerges throughout the first few years of life (Fransson, Aden, Blennow, & Lagercrantz, 2011; Homae et al., 2010) and that so-called cortical hubs within the PFC, that is, PFC regions that are heavily connected to other cortical regions, can be first identified at the end of the first year of life and then become progressively more complex and adult-like during development (Gao et al., 2009). The relevance that these changes in resting-state activity during infancy have for infants' brain function while actively engaged with their social worlds is unclear, and requires attention in future work.

Nevertheless, based on the connectivity findings using resting-state fMRI in infants one may generate likely scenarios with respect to the developmental emergence of the social brain network in infancy (Grossmann & Johnson, 2013). For example, the PFC may be activated from early on in infancy but at that point may not be functionally connected with more posterior regions of cortex and thus play little role in selectively activating ("controlling") posterior regions due to a lack of myelination of relevant long-range connections (fiber tracts; Johnson et al., 2009). Only once these long-range connections are functionally established, which at least for some connections appears to occur around the end of the first year of life when considering the evidence from

resting-state fMRI described above (Gao et al., 2009), a more finely orchestrated and controlled interaction between brain regions involved in social-cognitive processes develops. This raises the possibility that changes in brain connectivity might be linked to social behavioral development. Indeed, there is recent evidence to show that individual differences in structural connectivity between amygdala, anterior temporal cortex, and medial prefrontal cortex at 6 months of age predict behavioral differences in joint engagement at 9 months of age (Elison et al., 2013). This study used diffusion tensor imaging (DTI) to examine white matter structure of the right uncinate fasciculus in infants. This highlights DTI as a powerful tool that can be used to study structural connectivity between social brain regions, including subcortical structures such as the amygdala that cannot be imaged with fNIRS and EEG/ERP methods. Importantly, with respect to language development during infancy, DTI has also been used in combination with ERPs, allowing for stronger inferences regarding the relation between developing brain structure and brain function (Dubois et al., 2008). These advances in integrating methods should also be applied to the study of social brain development during infancy. Taken together, the points raised in this section call for an integrated approach to study the emergence of the social brain *network* in infancy by using complimentary measures derived from EEG/ERP, fNIRS, fMRI, and DTI to assess functional and structural brain development (see Paterson, Heim, Friedman, Choudhury, & Benasich, 2006).

Brain and Behavior Relationship

A further issue that needs discussion is the question of how the stipulated principles of developing social brain function relate to actual social behavior. This is an issue that has received fairly little attention in prior work. One rare example of how infant social brain function relates to behavior is the study by Peltola, Lepänen, Mäki, and Hietanen (2009). In this study, 7-month-old infants' brain responses showed a greater allocation of attention to fearful when compared with happy faces as indexed by a negative component in the ERP. Critically, fearful faces were not only associated with an increased neural sensitivity but also associated with increased looking time to the fearful stimulus. This kind of work relating brain responses and behavioral sensitivity should be an important aspect of future work. In fact, in the individual sections on the principles, I put forward a number of testable ideas concerning the (behavioral) functions of the proposed principles. Nonetheless, it is important to add that while it is valuable to include behavioral variables in order to study brain-behavior relationships during infant development, such behavioral measures are not always available for very young infants. In fact, this might be precisely the reason why infancy researchers resort to neuroimaging, because these methods provide a unique window into the infant mind by bypassing infants' limited behavioral repertoire.

Methodological Considerations Concerning Stimulus Presentation

An additional point for discussion is the fact that the great majority of infant neuroimaging studies presented in this review used two-dimensional stimuli. There is considerable evidence showing that infants have difficulty learning and transferring in-

formation to the real world from two-dimensionally presented stimuli (see Barr, 2010, for a review). For example, between 9 and 10 months of age infants show learning from live foreign-language experience but not from prerecorded video stimuli (Kuhl, Tsao, & Liu, 2003). Similarly, at the brain level, observing live actions evoked greater activation of motor regions in frontal cortex in 6- to 7-month-old infants than video presentations of the same actions (Shimada & Hiraki, 2006). However, it is important to note that while brain activation was stronger in the live context when compared with the video context, motor cortex activation was not absent in the video context (Shimada & Hiraki, 2006). Relatedly, mPFC activation to mutual gaze when compared with averted gaze was observed during live interactions (Nishijo, in press) but also when using video presentations (Grossmann et al., 2008). This suggests that, while video presentations might in some respects be less effective in engaging the infant, for the infant brain the distinction between video and real life might only be a matter of degree but may not constitute a qualitative difference, at least not before the end of the first year of life. In support of this view, infants develop a dislike of computer-animated human agents presented in video—known as the “uncanny valley effect” in adults—only by 12 months of age (see Lewkowicz & Ghazanfar, 2012). It might thus be the case that it is only with age and increasing social experience that infants begin to distinguish between real life and video social events. The difference between using video and real-life stimuli is also a contentious but unresolved issue in the adult social neuroscience literature (Schilbach et al., 2013). This issue poses a great methodological challenge because, regardless of the age of the participant, neuroimaging studies need to be well controlled (video) but at the same time ecologically valid (live interaction). In order to get a more complete picture it might thus be important to include both kinds of stimuli (video and live presentation) in future studies. Furthermore, it should be mentioned that this issue might be specific to visual social stimuli and may not apply or at least not to the same degree to other modalities such as auditory stimuli.

Theoretical Considerations Derived From the Principle-Based Review

At the end of this discussion, I outline a tentative theoretical proposal that is based on the developing social brain principles reviewed herein. This proposal is concerned with providing a functional framework that allows for the interpretation of social brain development in the first year of life. The key idea of this proposal is that the principles discussed as specifically social, namely self-relevance and joint engagement, can be seen as *primary* in early social-cognitive development as they serve as a vital basis for learning from (and collaborating with) others, whereas the principles identified as more domain-general, namely categorization, differentiation, and integration, can be viewed as *secondary* in early social-cognitive development as they may be the result of learning (and collaborating with others) rather than a precondition of learning that, according to this proposal, is mainly instantiated by self-relevance and joint engagement. That self-relevance and joint engagement may serve such adaptive functions in human development is in line with prior theories based on behavioral evidence (Csibra & Gergely, 2009; Tomasello et al., 2005) and is also in agreement with infant neuroimaging work

indicating that self-relevance and joint engagement impact (improve) attention and learning during infancy (Parise et al., 2008; Striano et al., 2006).

The division into *primary* and *secondary* principles of emerging social brain function is also reflected in the developmental pattern observed across the reviewed studies, with *primary* principles emerging early and *secondary* principles emerging late. This is consistent with the argument that *primary* principles are a precondition, whereas *secondary* principles are an outcome for the infant’s brain preparedness to learn from and collaborate with others. Furthermore, the proposed view fits well with the broad functions assigned to the brain regions, prefrontal cortex and temporal cortex, respectively implicated in the *primary* and *secondary* principles. Specifically, prefrontal cortex is involved in learning and top-down modulation of posterior (including temporal) cortical regions, whereas temporal brain regions are implicated in representing (or retrieving) learned information (Gilbert & Sigman, 2007; Sigman et al., 2005; Zanto, Rubens, Thangavel, & Gazzaley, 2011). According to this view, it would be predicted that prefrontal cortical regions are more heavily involved when acquiring new social skills during development, while temporal cortex becomes more important once a social skill has been acquired. Indeed, this migration of activity from prefrontal to temporal regions with development is evident in fMRI work investigating theory of mind in children, adolescents and adults (see Johnson et al., 2009). In this context it is important to emphasize that, although the weighting of activity between these regions might change with development, both prefrontal and temporal cortices are critically involved in the acquisition of new skills (Blakemore, 2008; Johnson et al., 2009). In future work it will be essential to see whether this relationship between prefrontal and temporal brain regions also applies to the development of social brain functions in infancy (see also section on Brain Connectivity above). However, what has become clear from the neuroimaging work conducted with infants in the last 10 years is that, other than previously assumed, prefrontal cortex plays an important role in early social and cognitive development (Grossmann, 2013a, 2013b), supporting the notion that learning and top-down modulation of posterior brain regions is a primary process in early development.

Conclusion

In summary, this review examined the principles that underlie the early development of the social brain during infancy. The empirical evidence from neuroimaging studies with infants revealed that self-relevance, joint engagement, predictability, categorization, differentiation, and integration constitute key principles that account for infants’ emerging social brain functions. Critically, this review suggests that these principles differ with respect to their domain-specificity, developmental timing and brain localization. These insights have important implications for our understanding of developing brain function in general and the early development of social cognition in particular. The proposed principle-based account provides a novel framework that helps to conceptualize social information processing in infancy and to inform future work examining the neural and developmental origins of social cognition.

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