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CHAPTER 10

The Developing Social Brain

ordPress Social Connections and Social Bonds, Social Loss, and Jealousy in Infancy

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On social connections:

Before language takes over as the instrument of interaction one cannot interact humanly with others without some proto-linguistic "theory of mind." –JEROME BRUNER (1990, p. 75)

On social rejections:

According to an old Russian proverb, "jealousy and love are sisters." This seems to suggest that both come from the same brain regions and because love exists early in life, so might jealousy.

Over the last century, the psychology of infancy has become a major subject of study and has answered many questions about infants' developing ability for social cognition. Social cognition is about understanding people. Although people are like objects in that they have various physical characteristics (e.g., size and shape), they are different because only people communicate and have feelings and intentions (Gelman & Spelke, 1981; Legerstee, Anderson, & Schaffer, 1998; Legerstee, Corter, & Kienapple, 1990: Legerstee & Markova, 2007; for reviews, see Legerstee, 1992, 2005). Thus, whereas physical events can be specified because they present stable and predictable reactions, social events are subtle as well as unpredictable. That is because, unlike objects, people have minds and experiences that are not easily accessible.

Developmental research on representing the minds of people has found that by 4 years of age, most children are aware that people have minds and that their beliefs may be different from their own (Wellman & Lui, 2004). However, the way preverbal children represent people's minds remains enigmatic (see Sabbagh et al., Chapter 13, this volume). Various scientists and philosophers have proposed that the infant is born with a tabula rasa, and as a consequence their impression of the world is a "great blooming, buzzing confusion" (James, 1890, p. 462; Piaget, 1954).

Accordingly, before infants develop a realistic view of the world and the people in it, they have to learn to distinguish between the mental and the physical through a lengthy domain-general process. Thus for the first 2 years, people are known behaviorally rather than psychologically. It is not until the end of the sensorimotor period (second year of life) that infants' actions turn into thoughts and that children become aware of other minds.

In contrast, others postulate that infants are born with a "social brain," containing domain-specific abilities that allow them to connect with the social world from the start. Theorists interested in domain specificity support either a neuroconstructivist view (Karmiloff-Smith, 1992, in press; Legerstee, 2005, 2009) or a nativist orientation. Nativists propose a kind of genetic predeterminism, arguing that infants are born with modules or neural mechanisms (Baron-Cohen, 1991) that mature at different developmental times as a function of neural maturation. According to Karmiloff-Smith (1992, p. 6), one should not confuse modules with domains. A domain consists of specific areas of knowledge (e.g., linguistics, physics), "but a module is an information processing unit that houses this knowledge as well as the computations on it."

Empirical evidence has shown that the mind and its intellectual processes have a large range of reaction to environmental input. This suggests that the ontogeny of the structure of the mind and its resulting products are much more variable than the modular position suggests. Modules are rigid and less plastic; as a consequence, modules provide the infants with more information at the onset but are less amenable to change. Thus, rather than proposing that infants are born with a module to perceive mental states in others, the neuroconstructivists propose that infants have domain-specific predispositions that direct them to the necessary social input. Subsequent development is a function of an interaction between this prespecification and plasticity for learning. Thus, for neuroconstructivists, nature (nativism) or nurture (domain-general development) is clearly a false dichotomy because "genes, brain, and environment play a dynamic, multidirectional role in shaping, not merely triggering, developmental outcomes" (Karmiloff-Smith, 2009, p. 60). For example, if one adopts a neuroconstructivist view rather than a domain-general or nativist position, then one should expect infants to be predisposed to perceive mental states of people and changes in the complexity of this awareness with development. Accordingly, neuroconstructivists propose that newborns are preadapted to the early structure of communication, and argue that initially intersubjective sharing can be observed during dvadic interactions between caregiver and infant (Bruner, 1999; Fogel, 1993; Legerstee, 2009; Stern, 1985; Trevarthen & Delafield-Butt, Chapter 8, this volume; Tronick, 1981) and subsequently during triadic interactions, which extends the communicative context to a third party or object (Legerstee, Markova, & Fisher, 2007). During the dyadic communication period (0-3 months), infants connect with the social world, share emotions, and bond with others. They also show anxiety about being separated from their loved ones. During the triadic communication period (3-5 months), infants begin to share interesting aspects of the environment with people, but also develop a fear of losing a loved one to a rival (jealousy). Because both dyadic and triadic abilities imply mentalist construals, there is a connection between prelinguistic dyadic communication during the first months of life and more complex triadic communication during the subsequent months. Bruner (1999) argues that the progression from primary to secondary intersubjectivity is facilitated through "narrative scaffolding" where caretakers treat infants as if "they have things in mind." Legerstee and colleagues (2007) supported this hypothesis by showing that mothers who were emotionally attuned to their infant's actions had infants who engaged in longer eye contact during dyadic communication and progressed sooner to triadic communication than infants of low-attuned mothers.

Until now, the investigation of infant core abilities as revealed during dyadic and triadic communication, their relation to later sociocognitive abilities, as well as the role the environment plays in this relation has relied on clever experimentation and the collection of behavioral data. As the result of methodological and technological advances and the merging with developmental social-cognitive neuroscience, new light has been shed on important aspects of the infant brain. As a consequence, the behavioral data of social-cognitive phenomena are being clarified by their neural foundations, thereby revealing the roles that various neural structures, genes, and neurotransmitter systems play in social cognition. For instance, cognitive neuroscience has shown that in adults "cortical regions in the temporal lobe participate in perceiving socially relevant stimuli, whereas the amygdala, right somatosensory cortices, orbitofrontal cortices, and cingulate cortices all participate in linking perception of such stimuli to motivation, emotion, and cognition, (Adolphs, 2001, p. 231). Developmental social neuroscience has similarly revealed a biological basis for the perception of social stimuli in infants, such as face and eye gaze processing, perception of emotion, biological motion, but also infant mental states such as attention and intention (for a review, see de Haan & Gunnar, 2009; Grossman & Johnson, 2007; Mundy, Chapter 14, this volume). In addition, factors that promote the perception and conception of social stimuli, such as temporally matched interactions between mothers and infants, are underpinned by biological rhythms (see Feldman, 2007, for a review). Thus, recent works support the idea that infants have a social brain that provides the biological basis for social interaction.

Methodological Considerations

Although there is increasing biological evidence for infants' sensitivity to social stimuli, as discussed earlier, questions remain about the domain specificity of social cognition (emotions and thought) and the role the environment plays in development. According to de Haan and Gunnar (2009, p. 5), "Although a reasonable amount is known about the function of this network in adults, very little is known about its *development* and how it supports the progressive emergence of complex social abilities." As a result, mature or complex social processes are best analyzed by focusing on their precursors or *subcomponents*. For example, Legerstee, Ellenbogen, Nienhuis, and Marsh (2010) recently examined the development of jealousy in infants during the first half year of life. Jealousy is defined as an aversive reaction that results from the fear of losing a loved one to a third party, a rival. In adults, jealousy is a complex emotion, and the way it is expressed varies depending the context. That is, jealousy may conjure up emotions such as sadness (loss), anger (betrayal), and fear/ anxiety (loneliness). In addition, the intensity of the feeling may be linked to subcortical emotional networks, and variations in human jealousy may further be a function of different cognitive capacities and environmental situations (see Markova, Stieben, & Legerstee, 2010). Consequently, the accompanying coherent infrastructures in the brain vary in adults, and thus mapping jealousy onto a specific region is difficult (Panksepp, 2010). As a result, speculations about the nature of jealousy in adults are primarily drawn from secondary sources. For instance, neurochemicals that reduce the impact of jealousy (because they reduce the painful feelings of being excluded) may be found among those that strengthen social bonds such as endogenous opioids (endorphins—substances in the brain that attach to the same cell receptors as morphine) and the pituitary hormone oxytocin, which regulates separation distress in animals, as well as those chemicals that reduce anxiety/fear (cf. Panksepp, 2010), an emotion commonly associated with the feelings of jealousy.

Given the complexity of the mature social emotion of jealousy, Legerstee and colleagues (2010) have focused on subcomponents of jealousy that people and infants have in common, such as the existence of a social bond and the fear of losing this bond to a rival (social exclusion). The most important relationship that develops soon after birth is with the caregiver (Ainsworth, Blehar, Waters, & Wall, 1978; Bowlby, 1980). Consequently, it is plausible that infants are born with an innate desire to develop a social bond, and jealousy could be seen as a reaction to the presence of one who threatens this social bond (Fivaz-Depeursinge, Favez, Scaiola, & Lopes, 2010; Hart & Legerstee, 2010; Legerstee et al., 2010; Panksepp, 2010). If so, then jealousy is not purely a creation of human culture, but goes back into deeper ancestral regions of brain and mind, and hence behavioral reactions of jealousy in infants should have neurological underpinnings (Panksepp, 2010). Thus, the ability to experience jealousy likely develops early in infancy and might even vary as a function of the quality of the social bond infants have with their caregivers. This social learning is unlikely to start from nothing.

Nevertheless, there are debates whether the social emotion of jealousy might present itself in infants (see Hart & Legerstee, 2010). Domain-general theorists argue that to experience jealousy the child must have attained a certain level of cognition, which is not present during the first year of life, such as the ability to differentiate self and other (consciousness) and the ability to perceive triadic relationships (Lewis, 2010; Piaget, 1954). In order to decide the issue, an examination of the development of the behavioral and biological core processes that enable infants to experience jealousy is necessary, since it would show how these subcomponents coalesce and relate to mature complex social processes later on.

Sociocognition and Jealousy

The aim of this chapter is to address the existence of a social brain in infants by examining the behavioral and neurophysiological correlates of jealousy in 3- and 6-month-old infants. If, as earlier defined, jealousy is the fear of losing a loved one to a third party—a rival—then we need to show that they have the sociocognitive prerequisites to apprehend such triadic situations. What might this be? First, infants would need to recognize social stimuli and differentiate them from nonsocial stimuli. In addition, because jealousy-evoking situations rely on the perceived separation from a loved one, infants need to have established a social bond. The social bond is the

primary relationship within the interpersonal system of jealousy. In order to experience jealousy, infants have to be aware of the secondary relationship (the one between their caregiver and the rival). Thus, infants need to have developed an understanding of triadic relationships (the self, the beloved, and the rival). Finally, infants need to understand why they are excluded (the goals underlying people's actions).

Through examining these intersubjective transactions, it should be possible to establish whether infants have a "social brain," in which case infants should be able to experience jealousy within the first months of life, or a tabula rasa, in which case the neonate would have to learn everything about people. In the next paragraphs, I document that infants have various sociocognitive abilities during the first months of life. "Such sophistications indicate that implicit social understandings exist long before children acquire language, and long before they are capable of theorizing that others might have different wants and false beliefs about the state of the world" (Rochat, 2010, p. 2). Before turning to the empirical evidence, it is important to examine the hypotheses about the social brain put forth by recent theoretical frameworks.

The Biological Basis of Social Interaction

Dunbar (Chapter 1, this volume) argues that the biological basis of social interaction is a result of the evolution of bondedness, which is the formation of a close emotional tie between primates, such as the establishment of a relationship between mother and child, but in particular between various members of a social group. That is because whereas the hardware of the brain might be better predicted by parental care and bonding, mental state awareness is better predicted by interactions with our complex and dynamic social world later in life, where interactions involve deceptions as well as perspective taking.

Thus, Dunbar does not believe that the specific abilities that make up the social brain are hard-wired or modular. Instead, he argues that maintaining social relationships demands flexible social-cognitive abilities because the social environment is complex and, in order to be successful in the social world, primates need to adjust and conform to others. To do that, they need to become competent in readings others' minds. As a result of this mentalizing, human primates have developed a social brain with a neocortex, which accounts for 50–80% of total brain volume. Interestingly, the important brain regions are the frontal lobe regions because they are primarily implicated in sociality and thus in the amount of people we regularly interact with (group size). Although individual differences in social cognition may have a genetic basis, social interaction plays an important role in species that have large neocortices.

In addition to having a large neocortex, Gallese and colleagues propose that the social brain has a mirror neuron system, which underpins intersubjectivity and social cognition (Gallese, 2009). These neurons, observed in regions corresponding to inferior frontal cortex and inferior parietal cortex in macaque monkeys (Gallese & Rochat, Chapter 2, this volume; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), fire when a specific action is executed (e.g., breaking a nut) but also perceived. Similar processes are hypothesized to take place when human infants reproduce facial gestures, such as proprioceptive behaviors (i.e., mouth openings and tongue protrusions) (Legerstee, 1991; Meltzoff & Moore, 1992). "Thus, it is proposed that a common underlying functional mechanism mediates our capacity to share the meaning of actions, intentions, feelings, and emotions with others, thus grounding our identification with and connectedness to others" (Gallese, 2009, p. 520). Although some argue that the existence of mirror neurons has not been fully empirically validated (e.g., Lieberman, 2007), there are strong suggestions that mirror neurons play an important role in intersubjectivity in infancy (Gallagher, Chapter 3, this volume) and nonverbal communication such as gestures, facial expressions, posture, and goals (DePaulo, 1992; Lieberman, 2007, p. 271). For instance, when we observe others crying, areas in the brain associated with these feelings become activated. Such empathic sharing can be elicited in very young infants (Hoffman, 1975). Thus, mirror neurons do more than automatically reproduce surface actions. That is because when two agents socially interact with one another, the activation of mirror networks creates shared representations (i.e., representations simultaneously activated in the brains of two agents; Gallese & Rochat, Chapter 2, this volume). These shared representations allow people to understand not only *what* others are doing but also *why*, thereby revealing an awareness of their intentional state.

In a functional magnetic resonance imaging (fMRI) study, Iacoboni and colleagues (2005) demonstrated that human mirror areas respond differentially to the observation of the same grasping actions, if the actions are embedded in different contexts, which suggests different motor intentions associated with the grasping actions such as drinking or cleaning up. This finding supports data of an imitation study in which infants between 5 and 8 weeks of age, when presented with mouth openings and tongue protrusions, imitated the gestures presented by a person but not when the same actions were presented by inanimate objects (Legerstee, 1991). Similarly, in another imitation study, 10-month-olds imitated the actions of people when they successfully put a ball in a bowl. If the adult was unsuccessful, the infants *completed* the intended goal of the adult (i.e., put the object in the bowl). However, infants did not complete the unsuccessful actions of inanimate objects (Legerstee & Markova, 2008). Thus, mirror neurons encode not only movements but also the meaning behind them.

In overview, theoretical accounts as well as empirical findings favor a biological basis for our social behaviors and their evolution. However, if indeed human infants have a biological basis for social behavior in general, and for jealousy in particular, then they should possess certain prerequisites that promote their recognition of and subsequent interaction with conspecifics.

Recognizing Conspecifics: Behavioral and Neurological Correlates

Research shows that neonates discriminate between faces of their mother and a stranger while potential olfactory cues are masked (Bushnell, Sai, & Mullin, et al., 1989). Infants also begin to recognize their own faces and voices as familiar social stimuli, discriminate them from inanimate objects and sounds, and become better at it between 5 and 8 months (Legerstee et al., 1998). In general, infants smiled and vocalized more to the social (faces and sounds) versus nonsocial stimuli (see Figure 10.1).



FIGURE 10.1. Video capture of five-month-olds discriminating between the moving and immobile face of self, peer, and dolls. Copyright by Maria Legerstee.

Event-related potential methods support the finding that infants are sensitive to faces early on. By 6 months, infant brains react differently to upright and inverted faces in a way that is similar to the way adults process this difference (de Haan & Carver, Chapter 6, this volume).

It is not surprising that infants recognize their own voice by 5 months (Legerstee et al., 1998) because at birth they prefer their mother's voice (which they have heard in utero) over that of a female stranger (DeCasper & Fifer, 1980). More surprisingly, infants pay attention to both the auditory and the visual identifier of a vowel, such as /a/ and /u/. Infants will imitate the vowel if the components match, but not if they are incongruent (i.e., seeing /a/ but hearing /u/) (Legerstee, 1991). Interestingly, at 6 months, infants' phonetic perception predicts language development at 24 months (Tsao, Liu, & Kuhl, 2004). According to Kuhl (2007), this link between natural speech and language learning depends on children's awareness of the communicative intentions of others. Relating human language learning to a broader set of neurobiological cases of communicative development, Kuhl argued that the earliest phases of language acquisition—the developmental transition from an initial universal state of language processing to one that is language specific-require social interaction (see also Trevarthen & Delafield-Butt, Chapter 8, this volume). Kuhl proposed that the social brain "gates" the computational mechanisms involved in human language learning.

Infants' ability to recognize faces and voices documents their capacity for storing and recalling information from *memory*; however, until recently they were assumed to lack this ability (Bauer, Chapter 7, this volume). Recognizing faces and voices indicates that infants are familiar with these stimuli; this familiarity provides the opportunity for establishing social bonds with the mother.

Not only does the ability to recall information improve rapidly during infancy, but *emotionally salient* events are better remembered. For instance, Bornstein, Arterberry, and Mash (2004) revealed long-term memory in 20-month-olds who had participated in a social interaction where an adult looked at them but refrained from communicating (the still-face procedure, during which infants respond with increased negativity and gaze aversions and reduced positive responses) at 5 months.

These infants (experience group) fixated the face of the person who had instigated the still face significantly less than the faces of two other novel persons. Control 20-month-olds (no-experience group) looked longer overall and fixated on the target person equally or more than on the two novel persons. That 2-year-olds were able to remember something that happened when they were 5 months of age reveals their early *intersubjective nature* and how communication is represented during the first months of life.

Overall, these findings suggest that infants have an early specialization of the cortical network involved in the recognition of social cues and signals. This sensitivity, so early in life, familiarizes infants with their caregivers, promotes bonding, and prepares infants to engage in communication with conspecifics and to learn from them.

Person-Object and Self-Other Differentiation

If infants have a social brain and a mirror neuron system that are activated by social signals, then we should find that infants' responses to people are different from their responses to nonsocial objects. It is clear that from birth infants smile, vocalize, and alternate their gazes more when facing people than objects (for reviews, see Gelman & Spelke, 1981; Legerstee, 1992). An important question is whether this differential responsiveness is based on infants' conceptual rather than perceptual abilities. Studies introducing proper controls (for reviews, see Legerstee, 2005, Ch. 4; Legerstee, 2009) with typically developing infants as well as with infants with Down syndrome at approximately the same mental age or level of perceptual-cognitive sophistication as the nondelayed infants revealed the same pattern of differential responsiveness during the first year of life. In particular, already at 5 weeks, infants communicate with people and act on interactive dolls (Legerstee, Pomerleau, Malcuit, & Feider, 1987). Between 2 and 3 months, infants imitate mouth opening and tongue protrusion in people but not of inanimate objects that simulate these gestures (Legerstee, 1991). Infant imitative responsiveness to people and not physical objects supports Gelman and Spelke's (1981, p. 54) contention that "the infant implicitly 'knows' that he and another person can act in kind." Moreover, at that age, infants expect people to share their affective states with them, but they do not have such expectations of inanimate objects (Legerstee et al., 1987; Legerstee & Markova, 2007). Affect is relational by its very nature, and it is the earliest emotional information that is being shared between two communicative partners (Barrett, 1995; Stern, 1985). According to Stern, "Affect, more than cognition, seems to determine whether one is engaged with an 'it' or another human being" (p. 214). Already by 6 months, infants expect people to communicate from a distance, but not inanimate objects (Legerstee, Barna, & DiAdamo, 2000).

There is also evidence from behavioral neuroscience to support the notion that a global animate-inanimate distinction is deeply rooted in our categorical thinking because different neural mechanisms have been found to underlie the processing of the two classes of stimuli. Apparently, brains of 7- to 8-month-old infants respond differently when presented with animates and inanimates (Jeschonek, Marinovich, Hoehl, Elsner, & Pauen, 2010, p. 863). Infants' brain responses to both categories differed systematically regarding the negative central (Nc) component (400–600 msec) at anterior channels. In particular, the Nc was more activated for living things then for nonliving things in two groups of infants. Different brain mechanisms also underlie the processing of the two classes of stimuli in adults. Results of fMRI showed ventrolateral activation for animates and ventromedial activation for inanimate objects, supporting the idea that this distinction is fundamental to human cognition (Wiggett, Pritchard, & Downing, 2009). Thus, it appears that the social brain has systems for recognizing and understanding people and to discriminate these from inanimates.

Mental States: Attention-Intentions

Although by discriminating between the attributes of people and objects infants show various aspects of social intelligence, the question is, are infants aware that only people mentalize? Mentalizing refers to the ability to read the mental states of others; consequently, differentiating as a function of mental state is the sine qua non of the difference between people and objects (Frith & Frith, 2010; Kampe, Frith, & Frith, 2003; Legerstee, 1992, 1994; Legerstee & Barillas, 2003). Frith and Frith (2007) argued that it is a unique ability of the brain to represent the mental states of the self and the other; their connection enables communication of ideas.

For instance, infants soon after birth react to eye gaze of people as an intention to communicate, but they do not have such expectations of inanimate objects that are matched on stimulus configurations (Legerstee et al., 1987). Similarly, by 5 months, infants use social signals such as eye contact to share attention about interesting toys with people, but not with inanimate objects (Legerstee, 2005, Ch. 6; Legerstee, Markova, & Fisher, 2007; see Figure 10.2), and by 12 months, infants may follow the direction of gaze of people and head turns of objects, but they will only direct people's gazes through pointing to interesting sights (Legerstee & Barillas, 2003; see Figure 10.3).



FIGURE 10.2. Video capture of five-month-old infant sharing attention over interesting toy with mother. Copyright by Maria Legerstee.



FIGURE 10.3. Twelve-month-old infants follow the direction of gaze of people and heads of objects, but only point to direct people's gazes to interesting sights. Copyright by Maria Legerstee.

Thus, infants are trying to "show" *people*, but never inanimate objects, something. That during the first year of life infants are expecting people to communicate with conspecifics, and their inclination to use declaratives with conspecifics of which the only reason is to share knowledge, suggests that neural mechanisms (Gallese & Rochat, Chapter 2, this volume) might underpin these deeply social interactions.

Grossman and Johnson (2010) examined 5-month-old infants' ability to follow the responses of the gazes of adults, and found that the prefrontal cortex was activated during triadic social interactions using near-infrared spectroscopy. It should be noted that infants in the Grossman and Johnson study responded only to the attention cues of the adult. Mundy (Chapter 14, this volume) reveals that responding to joint attention (RJA) and the actual initiation of joint attention (IJA) involves separate and distinguishable neural networks. Whereas frontal electroencephalographic (EEG) data are associated with IJA bids, RJA is associated with parietal EEG activation. It is not surprising that the two types of joint attention involve different neurological substrates. IJA is a more advanced ability than RJA because it involves an awareness that the play partner has some information about the object the infant initiates attention to, whereas RJA is simply a bid to follow the physical trajectory to the object (Camaioni, Perucchini, Bellagamba, & Colonnesi, 2004; Legerstee & Fisher, 2008).

In overview, infants are aware of the crucial distinctions between people and objects, which suggests that they develop a theory of mind differently from a theory of physical matters (Legerstee, 1992). These domain-specific predispositions serve as foundations on which infants further categorize and come to understand the distinctive properties of the social and nonsocial worlds (Legerstee, 1994; Legerstee, Anderson, & Schaffer, 1998).

Self-Other Differentiation: Consciousness

Although infants' differential responsiveness to people and objects lends credence to the idea that a concept of people has its roots in infancy, and hence is a result of early brain development, an important feature of a concept of a person is that it is distinguished from the concept of self. A sense of self is the result of the interactions infants have with other people during which representations are shared and the intersubjective nature of the self is formed. It is these interactions with other people that lead not only to subsequent changes in brain activity (Decety & Chaminade, 2003, p. 578) but to the development of a theory of mind (Dunbar, Chapter 1, this volume).

Evidence of dyadic social-emotional sharing (intersubjectivity) but also empathy (see Knafo & Uzefovsky, Chapter 5, this volume) is evidence of a concept of the self. Empathy involves an awareness of the other without necessarily involving a change in the self. To comprehend another person's mental state, it is important to be able to feel what they feel and to represent what they represent or feel. Lack of empathy is related to low theory of mind abilities in children with autism (Baron-Cohen, 1991).

Decety and Sommerville (2003) suggest that the right hemisphere, which is predominant early in life, is implicated in the ability for shared representations and thus may be responsible for the infant's feeling of empathy, namely that others are "with me" emotionally (Markova & Legerstee, 2006). Recent research suggests that empathy is largely biologically determined and is present in most mammals (Preston & deWaal, 2002), although the expression of empathy in human infants varies as a function of child rearing (Knafo & Uzefovsky, Chapter 5, this volume). Infants whose mothers empathize or are attuned to infants' emotions are infants who empathize with others (Ainsworth et al., 1978; Markova & Legerstee, 2006).

Gallese (2009) argues that our capacity to empathize with others is mediated by embodied simulation mechanisms—that is, by the activation of the same neural circuits underpinning our own emotional and sensory experiences. Thus, empathy is to be conceived as the outcome of our natural tendency to experience our interpersonal relations first and foremost at the implicit level of intercorporeity—"the mutual resonance of intentionally meaningful sensory-motor behaviors) as the main source of knowledge we directly gather about others" (Gallese, 2009, p. 523).

Connecting with the Social World

Thus far, the evidence suggests that newborns have predispositions that allow them to recognize conspecifics at birth: What are the mechanisms that allow them to connect with people? There are various theoretical opinions about this process. According to Piaget (1954), infants are born with reflexes that react to incoming stimulation. Others argue that infants connect with the social world because they are sensitive to movement, such as social contingencies. Specifically, these authors propose that from birth infants are only able to detect the effect their own actions have in the world, which is important for the development of an awareness of the self (e.g., "By kicking the sides of the crib I become aware of my feet"), but it is not until 3 months of age that infants begin to be sensitive to the type of contingent interactions provided by people (Gergely & Watson, 1999). Some suggest that infants establish intersubjective connections with people by detecting similarities between own and others' actions through imitation games. Imitation is an "attention-getter," and through it infants begin to perceive others to be "like me" (Meltzoff, 2007). Thus, according to these authors (Piaget included), infants for the first few months of life are not capable of connecting with their caregivers in a meaningful way.

According to Legerstee (2005, 2009), infants perceive others to be "like me" because they are born with an affect sharing device (AFS) that is made up of three

components that act together: the ability to (1) recognize people as similar to themselves, (2) be sensitive to their own and others' emotions, and (3) perceive whether adults are attuned to their emotions and needs. The interplay among these three predispositions results in affectively attuned relationships that are important mechanisms for infants' sociocognitive development (Legerstee & Varghese, 2001; Markova & Legerstee, 2006). Thus, according to AFS theories, infants have an innate sense of people, which is activated through sympathetic emotions. Infants learn about themselves and other people through ongoing relationships, during which infants progress toward an increased consensus about shared meaning. Thus, AFS does not characterize others as providers of certain levels of temporal contingencies or of structurally similar responses to their actions but as beings with whom they can exchange intersubjective experiences and establish social attunement. As a consequence, infants not only perceive people to be "like me" physically but more importantly "with me" emotionally.

Markova and Legerstee (2006) assessed the predictions of the independent roles of contingency, imitation, and affect sharing in the development of social awareness. Infants were observed during natural (Figure 10.4a), imitative (Figure 10.4b), and yoked (Figure 10.4c) conditions with their mothers at 5 and 13 weeks of age. The dyads were divided into high- and low-attunement groups. Attunement was defined as (1) shared focus of attention (mothers would follow infants' attention), (2) social responsiveness (temporal coordination and contingent responsiveness), and (3) sensitivity (warm and appropriate behaviors) (see also Isabella & Belsky, 1991; Legerstee & Varghese, 2001). To determine whether infants enjoyed their mothers' responsiveness, their smiles, vocalizations, gazes, and negative emotions were observed. Results showed that at both ages infants of highly attuned mothers gazed longer, smiled, and vocalized positively more during the natural than the imitative and yoked conditions, whereas they increased negative vocalizations during the yoked conditions. In contrast, infants of less attuned (LA) mothers did not differentiate between the conditions, except at 13 weeks when the LA infants increased their gazes during the imitative condition. Thus, whereas contingencies and imitation draw infant attention to conspecifics, affective communication appears to lay the foundation for infants' social awareness and subsequent social relationships.



FIGURE 10.4. Mother and infant in (a) natural, (b) imitative, and (c) yoked interactions. Copyright by Maria Legerstee.

According to Gallese and Rochat (Chapter 2, this volume), the human neural system, well before birth, is already instantiating functional properties enabling social interactions, and such social interactions are expressed obeying different motor potentialities. They argue in support of Legerstee (2005; Markova & Legerstee, 2006) that neonates are innately prepared to connect to their caregivers not only through imitation but also affective attunement.

Social Bonds and the Development of Jealousy

So far, evidence for the existence of a social brain has been provided by focusing on the existence of prerequisite sociocognitive abilities of infants that enable them to experience jealousy: the ability to discriminate between (1) people and objects and 2) self and other and (3) an innate tendency to connect with the social world through attunement. It is clear that if jealousy is the fear of losing a loved one to a rival, then in order to experience jealousy, infants need to have formed a social bond, the one they fear to lose.

Social bonds are fundamental for human beings because social connections with others ensure the availability of not only physiological needs (e.g., food, shelter) but also social needs, such as the formation of relationships (see Bornstein, Chapter 12, this volume). However, as discussed earlier, maintaining dynamic social relationships is cognitively demanding because it involves an awareness of other minds. According to Dunbar (Chapter 1, this volume), "The social brain is really about behavioural complexity and thus about individual relationships." One reason why social relationships might increase brain size and promote subsequent cognitive and emotional development is that for successful bonding to take place, one needs to engage in perspective taking, which for mothers and infants means the reciprocal tuning in of each other's emotions. Variations in social experiences (high- or low-attuned interactions) may produce variations in intersubjectivity, bonding, and subsequent mental state awareness (Dunbar, Chapter 1, and Gallagher, Chapter 3, this volume; Legerstee, 2005).

Neurological evidence shows that social bonds have great adaptive value and are regarded as innate human predispositions (MacDonald & Leary, 2005). Biological rhythms (e.g., heart rate), hormonal levels, and activation in specific brain regions (i.e., superior temporal gyrus, anterior cingulate cortex, thalamus, and midbrain) underlie temporally matched interactions between mothers and infants (see Feldman, 2007). Because, in general, emotion reaction systems generate a sense of well-being with regard to important physiological and social needs (Panksepp, 1998), emotions that arise within relationships are essential and thus appear early in life (Markova et al., 2010). As a result of their inherent need for social connections, a great deal of an infant's life is spent interacting with others (Baumeister & Leary, 1995). During these interactions, infants as young as 1 week monitor people's gazes and exchange facial expressions, vocalizations, and movements in a reciprocal fashion. Such multimodal interactions (Walker-Andrews et al., Chapter 9, this volume) have been labeled protoconversations (Bateson, 1979) because they have a turn-taking structure that very much resembles adult-like verbal communication (Legerstee & Varghese, 2001;

Markova & Legerstee, 2006). As early as 5 weeks of age, infants recognize whether they are in tune with caregivers, since they get upset when mothers are not responsive to their signals (Legerstee et al., 1987; Markova & Legerstee, 2006). Chronically depressed mothers do not respond reliably to their infants' emotional states. As a result, infants generally show depressive states, expressed with lack of positive and negative responsiveness, because they have not developed expectations for affect sharing (Field et al., 1998; Legerstee & Markova, 2007; Legerstee & Varghese, 2001). Thus, infant–adult interactions are reciprocal in that infants perceive adults' acts as meaningful and adults interpret infant behavior as meaningful and communicative.

It is through the caregivers' attuned and empathic interactions that infants develop an increasingly sophisticated understanding of the minds of others. Recent works have elucidated the significance of epigenetic mechanisms of transmission that focus on the developmental outcomes of variations in parental care (Knafo & Uzefovsky, Chapter 5, and Pluess et al., Chapter 4, this volume; Meaney, 2001). For instance, Meaney and colleagues (Francis, Diorio, Liu, & Meaney, 1999; Parent et al., 2005; Szyf, Weaver, Champagne, Diorio, & Meaney, 2005) showed that harsh environmental conditions can contribute to stressful parent-offspring interactions in rats. This stress may affect gene expression in brain regions that are responsible for the proper regulation of behavioral, endocrine, and autonomic responses to stress, which may result in an increased risk for stress-related illness (Parent et al., 2005; Szyf et al., 2005). The authors studied epigenetic changes in rat pups. When rat mothers give birth, they will lick and groom (LG) their pups. However, not all mothers groom their young similarly. As a result of this variation in maternal care, adult offspring of high-LG mothers showed reduced corticotropin-releasing factor (CRF) production in the hypothalamus as well as reduced plasma adrenocorticotropin and glucocorticoid responses to acute stress compared with adult offspring of low-LG mothers (Liu et al., 1997). Thus, offspring of high-LG mothers demonstrated less fear and attenuated hypothalamus-pituitary-adrenal responses to stress than offspring of low-LG mothers. Furthermore, when pups born to high-LG mothers were raised by low-LG mothers (and vice versa), the adult offspring of high-LG mothers showed a significantly increased expression of specific proteins within the receptor that increase its function of inhibiting CRF expression (thereby increasing the fear response). The results of these cross-fostering studies indicate that individual differences in stress reactivity or in the expression of relevant genes can be directly altered by maternal behavior. Apparently, this effect is "particular to the amygdala and is reversed with cross-fostering" (Parent et al., 2005, p. 230).

Swain, Lorberbaum, Kose, and Strathearn (2007) studied how effects of environmental adversity on the emotional well-being of parents affected subsequent behavior in their infants. The authors examined human mother–infant pairs and found that their behaviors were influenced by infant signals that activated particular interacting neurotransmitters, such as oxytocin, prolactin, vasopressin, and dopamine. For instance, oxytocin released during breast-feeding was associated with reduced anxiety and stress in infants, which elicited more attuned behaviors of the mothers. However, when mothers became less attentive to infant social signals as a result of drug abuse or depression, it affected social bonding. Overall, the authors suggested that "infant stimuli activate basal forebrain regions, which regulate brain circuits that handle specific nurturing and caregiving responses and activate the brain's more general circuitry for handling emotions, motivation, attention, and empathy—all of which are crucial for effective parenting and bonding" (Swain et al., 2007, p. 262).

Social Loss

One way to examine the meaning infants assign to their relationships with others is to observe their reactions when they are faced with a possible loss of these relationships. According to Bowlby (1980), the deepest emotions surface during changes to the social bond. Changes that leave the social bond unchallenged elicit joy and security, whereas those that endanger the social bond engender anxiety and fear. Pank-sepp (2003) argues that two key brain areas are implicated in psychological pain in humans. Whereas the anterior cingulate cortex has been implicated in physical pain, the prefrontal cortex showed an opposite pattern of activity, becoming more active when the distress was least. Thus, both brain areas regulate the pain of social loss, suggesting that feelings of social exclusion might come from the same brain regions. He concludes: "Given the dependence of the mammalian young on their caregivers, it is not hard to comprehend the strong survival value conferred by common neural pathways that elaborate both social attachment and the affective qualities of physical pain" (Panksepp, 2003, p. 238).

Revisiting Jealousy

Throughout this chapter, I have defined jealousy as a fearful emotion that is being felt when one loses a loved one to a rival. This definition presupposes certain sociocognitive prerequisites such as the ability to distinguish between people and objects and being self-aware. In addition, the individual needs to have a primary bond with another person, and finally perceive that a third party is somehow a threat to this bond, to which one usually reacts with negative emotions, withdrawal, but also approach (Legerstee et al., 2010).

Thus, in addition to implicating these sociocognitive abilities, jealousy involves a variety of emotions. Jealousy has often been called a blended or mixed emotion (Plutchik, 1970), and has been suggested to include "a bewildering" array of emotions (Parrot, 1991, p. 15). In fact, jealousy is not really a distinct emotion such as fear, anger, sadness, disgust, and happiness. Social or moral emotions such as jealousy, shame, guilt, and embarrassment only have meaning within a social context and may have their foundation in the infants' feel of being with the other (Trevarthen & Aitken, 2001). According to Panksepp (2010), jealousy stands out as being the most "prepared" among the social-moral emotions in terms of their likelihood of being exhibited by practically everyone, at some stage of life, if the correct precipitating circumstances are present. Although jealousy is not a basic emotion, it is certainly evolutionarily prepared to emerge developmentally from the types of mind-brain dynamics that can be defensibly deemed basic emotions (Panksepp, 2010). An interesting way to categorize emotions is to focus on their functions. Barrett and Campos (1987) refer to emotions that are connected to the realization of an end state as "concurrent-goal/desire" emotions. Jealousy fits this definition because the infants'

distress reactions during social exclusion from the loved one can be interpreted as aims to reinstate the social bond.

Onset of Jealousy

Research has revealed that infants as young as 5 months (Draghi-Lorenz, 2010) get upset when their mothers ignore them while paying attention to another child. This finding has since been replicated by others with 6-month-olds in paradigms where mothers pay exclusive attention to a doll (Hart, Carrington, Tronick, & Carroll, 2004; see Draghi-Lorenz, Reddy, & Costall, 2001, for a review). However, not all such reactions are the result of feelings of jealousy. To be certain that infants are not reacting to lack of attention, stimulation, and so on, when being excluded, infants need to be assessed in an experimental paradigm where their responses to the exclusion by a loved one are contrasted with their responses to someone with whom they do not have a social bond. Only if infants react with upset when excluded by the loved one in favor of a rival can one propose that their reactions are the result of jealousy.

To shed light on the development of jealousy in infants, Legerstee and colleagues (2010) recently studied 3- to 6-month-old infants under four triadic conditions during which a female experimenter and the mother were interacting with the infant, namely (1) natural, during which the female experimenter talked to the infants as one normally does when engaging babies; (2) still face, during which the experimenter looked at the baby but refrained from talking; and (3) two modified still faces, one during which the experimenter while looking at the infant drank from a water bottle and the other while the experimenter's looking and talking to the infant was interrupted by the mother, at which time the experimenter either began to talk to the mother about the experiment while the mother listened (monologue condition; Figure 10.5a) or engaged the mother in an active discussion about her baby (dialogue condition; Figure 10.5b and 10.5c). During the interrupted conditions both women excluded the infant.

It was expected that during the natural condition, infants would smile and vocalize. Based on evidence from the classic still-face research (Tronick, Als, Adamson, Wise, & Brazelton, 1978; Weinberg & Tronick, 1996), it was further expected that



FIGURE 10.5. (a) Infant reactions in the Monologue condition—quiet interest. (b) Infant reactions in the Dialogue condition—increased looking/approach. (c) Infant reactions in the Dialogue condition—covering face/withdrawal. Copyright by Maria Legerstee.

during the still face when no reason for a break in contact was given, infants would respond with more sadness and gaze aversions than during the bottle condition and also during the interrupted conditions, where the break in contact was more salient. That is, if infants experienced the modified still-face conditions as instances where people for some apparent reason were unable to communicate with them because they either had a refreshment or were interrupted by someone, then fewer smiles and vocalizations were expected compared with the natural interaction and also fewer negative emotions compared with the still-face condition. However, if mothers engaged with the experimenter in a joyful and exciting dialogue while excluding the infants, a jealousy evocation situation was created to which infants were expected to react with intense agitation.

The results confirmed the hypotheses. Infants between 3 and 6 months perceived the actions of people who engaged in exciting dialogues with their mothers as a threat to the social bond they have with their mothers because they behaved with approach (Figure 10.5b) and protest (Figure 10.5c). Infants did not display these behaviors when mothers simply listened to others (monologue condition; Figure 10.5a). These findings suggested that the more cognitive aspects of the nervous system rapidly became highly attuned to precipitate jealousy when one's social resources were compromised (Panksepp, 2010).

Although this study provided behavioral evidence for the existence of the affective precondition for the emergence of human jealousy in infants ages 3–6 months, apart from very informative and stimulating theoretical models (see the various chapters in Hart & Legerstee, 2010), there are no studies that have examined what was happening in the infant brain. What might infants' neurophysiological reactions be during the social exclusion situations?

Neural Correlates of Jealousy

To investigate simultaneously infants' behavioral and neurophysiological reactions during their experiences of jealousy in triadic interactions, we replicated the Legerstee and colleagues (2010) study. Infants were observed during various triadic contexts where infants interacted with mothers and strangers, such as during the dialogue, monologue, still-face, and natural interactions. Each condition lasted 60 seconds. Infants' behavioral responses (gazes, facial expressions, vocalizations, protest, and approach behaviors) were recorded. Infants' EEG data were also collected continuously during the experimental conditions from 128 EEG electrodes using the Geodesic Sensor Net. EEG data were segmented into 1,000-millisecond epochs, and a continuous wavelet= transform was conducted in the 4–9 Hz range. Power was expressed as mean square microvolts, such that the lower number indicated greater cortical activation. EEG data were Ln transformed.

On the basis of earlier findings (Legerstee et al., 2010), we expected infants to show greater maternal gazing and positivity during the natural interaction compared with all other conditions, and also greater maternal gazing, negative affect, and protest behaviors during the dialogue compared with the monologue condition. We further expected infants to show differences in frontal EEG activation among all four conditions. That is because when adults are excluded from interactions (i.e., during a virtual tossing game, the other players stopped throwing the ball to them), fMRI showed that they experienced emotional distress during social exclusion, as measured by substantial blood flow in the dorsal anterior cingulate cortex, which is located in the prefrontal cortex, an area associated with physical pain (Eisenberger, Lieberman, & Williams, 2003; see also Panksepp, 2003). Because EEG can only provide information about hemispheric activation, it is hypothesized that during the experience of jealousy in infants, frontal regions of the brain will show greater activation compared with parietal regions.

The findings revealed that infants showed greater maternal gazing and more protest behaviors during the dialogue compared with the monologue condition and less positive affect compared with the natural interaction condition. These behavioral findings were consistent with the predictions of the study and the findings of Legerstee and colleagues (2010).

With respect to the neurophysiological correlates of jealousy, EEG results revealed both greater left- and right-hemisphere activations during the dialogue compared to the natural interaction and still-face conditions, supporting the behavioral data that infants showed more distress (protest) as well as approach (gazes at mother). There was also a difference between the dialogue and monologue conditions. Infants had greater left-hemisphere activation in the dialogue (approach) compared with the monologue condition. The findings of this study did not reveal a specific brain location of activity during jealousy-evocative situations. However, when back- and front-channel activation comparisons were performed, there was greater hemispheric activation in the frontal regions of the brain during the jealousy condition. Furthermore, there were equally high left- and right-hemispheric activations during the jealousy condition, suggesting that both hemispheres may be involved during the experience of this emotion.

Overall, the jealousy-like emotions appeared to be processed in the prefrontal cortex. Thus, when faced with the fear of losing a loved one to a rival, infants were protesting at losing exclusivity with their mother and used activities in order to try to regain her attention to reestablish their primary relationship (Avci, Legerstee, Haley, & Polyanski, 2011; see also Campos, Walle, & Dahl, 2010). Interestingly, there was no difference between the negative expressions during the jealousy condition compared with the natural interaction condition. In Markova and Legerstee (2006), discussed earlier, maternal interaction style was measured as a function of maternal attunement (maintaining attention, warm sensitivity, and social responsiveness). The results showed that infants of mothers who ranked high on attunement ranked high on social cognition (the infants discriminated between the various conditions) and on prosocial behaviors (the infants smiled more and gazed longer at the social stimuli) (see also Legerstee & Varghese, 2001). As suggested earlier, if jealousy is the fear of losing a loved one to a rival, then one can expect that infants of attuned mothers have stronger social bonds and may exhibit approach, whereas infants who are ambivalently or insecurely attached may feel anger and are more anxious in their expressions (see Fearon et al., 2010).

To examine the role of maternal attunement in the expression of jealousy, we examined individual differences in EEG activation during these different conditions as a function of maternal attunement. It was expected that infants of attuned mothers would protest more during the dialogue condition, as indicated by greater relative left frontal activation. Maternal attunement was categorized as (1) warm sensitivity, (2) maintaining infant attention, and (3) responsiveness during the natural interaction condition (see Legerstee & Varghese, 2001; Markova & Legerstee, 2006). Infants were divided into high-attunement (HA) and low-attunement (LA) groups. If HA infants had stronger jealous reactions than LA infants, then we expected them to show greater maternal gazing and negative affect and also greater left frontal EEG activation during the jealousy condition compared with LA infants.

Analysis showed that there was greater maternal gazing in the dialogue condition compared with the monologue condition for both groups. In addition, infants of HA mothers showed greater positive affect in the natural interaction condition compared with all other conditions, confirming the Legerstee and Varghese (2001) data that infants of HA mothers overall ranked higher on prosocial behaviors.

Analyses of the EEG data indicated that infants of HA mothers showed significantly less frontal alpha power in the left hemisphere (i.e., greater activation) in the dialogue and natural interaction conditions and significantly greater activation in the right hemisphere during the monologue condition than infants of LA mothers.

Taken together, the studies reported here, including both behavioral and EEG data, confirmed the findings of Legerstee and colleagues (2010) that between 3 and 6 months of age infants showed greater maternal gazing during the jealousy condition. However, only infants with highly attuned mothers showed significantly greater positive affect during the natural interaction compared with all other conditions, including the jealousy condition. Furthermore, infants of highly attuned mothers showed greater left frontal activation during the jealousy condition, suggesting that they reacted more strongly when the bond they had with their mother was being threatened. Thus, the results support the socially precocious view of infant jealousy and indicate that social emotions are lateralized in the infant's developing brain. Finally, infants who received greater levels of maternal attunement showed greater lateralization of jealousy.

This is the first study showing that infants' brain reactions to jealousy-evocative situations are similar to those demonstrated by adults, suggesting that jealousy has its foundation early on in life. According to Panksepp (2010), separation anxiety is part of the old mammalian (social) brain. However, rejections (e.g., felt when experiencing the fear of losing a loved one to a rival) become manifest (albeit rapidly) through existential experiences of living in social worlds (Panksepp, 2010). Rejections and exclusions (as experienced during jealousy) is that social emotion whose adaptive value is to *counteract* severance of existing social bonds. Interestingly, the stronger the social bond, the more infants tried to reestablish this social bond through approach behaviors. An issue that needs to be addressed, however, is whether the feelings of the infants of the high-attuned mothers are more foundational than those of the low-attuned mothers. Variation in the expression of jealousy does not mean that jealousy is not based on a variety of primary, genetically ingrained, emotional processes (Panksepp, 2010).

Jealousy is an interesting phenomenon and fits the neuroconstructivist model well. Jealousy is founded on social loss, which is an aspect of the primate social brain (Panksepp, 2010). Both behavioral and neurological data show that jealousy becomes activated after infants have formed a social bond with a special person because they

do not display jealousy with a stranger (Legerstee et al., 2010). Jealousy is also dependent on development because it is expressed differentially as a function of attuned interactions with the caretaker.

In this chapter, I have reviewed a range of studies to support the idea that infants have social brains that prepare them to interact with conspecifics. In particular, I have argued that infants are born with a social brain by providing behavioral and neurological evidence for the development of jealousy in infants ages 3–6 months. Infants show that they come prepared to manifest jealousy soon after birth because from birth infants are attracted to people, form social bonds, engage in triadic relationships, and have an awareness of goals. That infants are able—so early in life—to experience these intersubjective transactions suggests that love and loss are part of the primate social brain, and that through bonding with conspecifics infants develop an awareness of simple mental states such as emotions, attention, and intentions, which allows for experiences such as jealousy.

Although there has been some indication that infants get upset when their parents ignore them for each other (Fivaz-Depeursinge et al., 2010) or in favor of a book or a doll (Hart et al., 2004), these studies did not focus on the *reason* why infants got upset. To control for the possibility that infants are reacting to lack of attention rather than jealousy (fear of losing a loved one to a rival), infants' reactions while being ignored by a familiar person with whom they have developed a social bond (mother) versus one with whom they do not have a social bond (female stranger) need to be examined. The behavioral and neurological data we collected indicate that infants only become upset when they are excluded by a loved one in favor of someone else. Thus, it appears that already between 3 and 6 months infants feel the pain of social loss that adults speak of when being excluded by a loved one.

Increasingly, developmental research is beginning to address the ontogeny of sociocognitive development and to describe its function and developmental trajectory through examining the predispositions of the very young infant and relating them to later complex abilities. As the data revealed, infant sociocognitive development is complex, involving a multifactorial interplay between innate predispositions and environment. In addition, many social processes, including such complex constructs as emotions and theory of mind, are indirect and cannot be mapped directly onto neural systems (Pluess et al., Chapter 4, and Knafo & Uzefovsky, Chapter 5, this volume). For instance, an important developmental milestone occurs when infants change from sharing attention with others in dyadic (face-to-face) situations to coordinating attention between people and the environment during triadic interactions. Legerstee and colleagues (2007) showed that variability in maternal care introduced individual differences in this development. We replicated the influence of maternal care with our jealousy studies. However, this research does not make clear the individual contributions of the infants. If development is a complex, dynamic process, where genes, parenting, and age interact in affecting individual differences, then research addressing the brain structures of both mothers and infants that support such change needs to be conducted, allowing for an examination of this dynamic perception action coupling between interacting agents. The brain permits us to learn continuously. It is important to know how, with development, the brain changes as a function of environmental input and how subsequent learning changes the brain over

time (Karmiloff-Smith, in press). This knowledge should enable us to contribute to the development of new theories of developmental social neuroscience and the elaboration of existing theories.

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