Drivers of Social Cognitive Development in Human and Non-Human Primate Infants

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Abstract:
In this chapter, we highlight the benefits of a comparative developmental approach, not only for revealing which social cognitive capacities are unique or shared across species, but also for uncovering environmental influences and physiological underpinnings of social understanding in infancy. We discuss human and nonhuman primate infants' (a) recognition of, and selective attention toward, social agents, (b) affiliation toward conspecifics and similar others, and (c) basic action understanding, as three examples of important social cognitive skills. These skills appear foundational, emerging early in development, and are shared across species, suggesting they may be (some of) the precursors upon which later, higher-order social cognitive abilities are built. Throughout, we emphasize how comparative studies can reveal nuances not readily observable in humans alone, including their developmental stability or plastic, early environmental contributions that may support or hinder such skills, and their underlying neural and physiological mechanisms.

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From prosocial behavior to cultural learning and belief understanding, social cognitive skills are important for engagement in social interactions and learning from others. In this chapter, we review some probable foundational skills of social cognitive development in human and non-human primate (NHP) infants. We selectively discuss capacities that are early-emerging and shared across species, with the goal of illustrating the value of a comparative developmental approach in advancing our understanding of early social cognitive development. While this field is still in its infancy and much remains unknown, we think such an approach is useful for uncovering the proximate and ultimate mechanisms of early social capacities. In particular, we review early emerging skills related to infants' recognition of, and selective attention toward, social agents, infants' affiliation toward conspecifics and similar others, and infants' basic action understanding. Given the early ontological emergence and shared phylogeny of these skills, we suggest that they may make up some of the precursors upon which later, higher-order social cognitive abilities are built. Although these skills appear across species, and thus may be based in evolutionarily conserved systems, this does not imply that they are innate or impenetrable by experience. We review evidence suggesting that, in both human and NHP infants, a variety of experiences contribute to these early markers of social cognitive development, including face-to-face interactions, self-other comparisons, and motor experience. We also discuss how individual differences in early development, often overlooked in experimental work, provide a rich source of data for understanding variability across social-cognitive outcomes and how NHP studies are beginning to uncover some of the factors—e.g., experiential, epigenetic—that may underlie such differences. Finally, we outline future directions for the field. Though noting the challenges, we emphasize the important gains in understanding that can be accomplished by, for example, considering the role of emotions in social cognitive development and anchors of social cognitive skills in physiology.

The value of a comparative developmental approach for identifying foundational social cognitive skills

The first few chapters in this volume, as well as other recent work (for recent reviews: Machluf & Bjorklund, 2015; MacLean et al., 2012; Maestripieri & Roney, 2006), highlight examples of how animal studies can uncover evolutionary insights, revealing specific social cognitive abilities that may be shared or differ across species. Beyond these contributions, there are a number of additional reasons why developmental NHP studies are valuable. In particular, this chapter focuses on exploring the role that a comparative developmental approach may play in identifying foundational social cognitive abilities and the drivers of these early-emerging skills in human infants.

First, NHP developmental studies permit the use of unique approaches, utilizing methods that are not possible in human infants. For example, compared to humans, macaque newborns are precocious in their fine motor abilities (e.g., grasping; Sclafani, Simpson, Suomi, & Ferrari, 2015a), gross motor abilities (e.g., walking, climbing; Castell & Sackett, 1973), and visual acuity (Boothe, Williams, & Kiorpes, 1980; Ordy, Latanick, Samorajski, & Massopust, 1964; Teller, Regal, Videen, & Pulos, 1978). By one estimate, macaques' postnatal sensorimotor brain development is approximately four times faster than humans', such that a 4-year-old human is approximately equivalent to a one-year old macaque (Workman, Charvet, Clancy, Darlington, & Finlay, 2013). Because they develop more quickly, NHPs are a convenient model of development, especially for longitudinal studies that offer numerous advantages compared to cross-sectional designs (Klin & Jones, 2015). Furthermore, some methodologies used in human infancy research (e.g., eye tracking paradigms, electroencephalography) are currently not possible in human neonates (Morimoto & Mimica, 2005) but have been successfully implemented in NHP newborns (Ferrari, Vanderwert, Paukner, Bower, Suomi, & Fox, 2012; Hall-Haro, Johnson, Price, Vance, & Kiorpes, 2008; Paukner, Simpson, Ferrari, Mrozek, & Suomi, 2014; Vanderwert, Simpson, Paukner, Bower, Fox, & Suomi, 2015). Thus, NHPs offer a number of advantages as a model for the study of early postnatal visual

and neural social information processing.

A second advantage of NHP studies of development is that they allow experimental manipulations that cannot be carried out with human infants. Whereas the role of early interactions on social cognitive development and social functioning may be explored in human infants via naturally occurring individual differences in caregiving, it is impossible to attribute causal power to any such interactions since unobserved and uncontrolled factors are always a potential source of confound. The study of NHP infants allows for refined control of postnatal environments that is not ethically or practically feasible with human infants. For instance, systematically administered interactions in controlled early environments of NHP infants can begin to differentiate the roles of maturational, genetic, and environmental factors on infant social cognitive development (Bard, Bakeman, Boysen, & Leavens, 2014; Sugita, 2008). This approach can offer insights into the degree of plasticity and the nature and timing of potential sensitive periods in early development and provide causal evidence for environmental contributions that may support or hinder infant behavior, health, and social-cognitive development (Belmonte et al., 2015; Dettmer & Suomi, 2014; Dettmer, Suomi, & Hinde, 2014). Finally, just as alteration of early postnatal experiences is logistically complicated and ethically questionable in human infants but achievable in NHP infants, so too is the experimental manipulation and measurement of infants' physiology. Although ethical oversight and humane treatment of NHP infants is paramount, important research questions that rely on invasive sampling methods (e.g., blood, cerebral spinal fluid) or require the administration of drugs or substances not yet deemed safe for use in human infants (e.g., Simpson et al., 2014) can potentially be tackled by employing an infant NHP model.

These arguments emphasize the theoretical value of a comparative-developmental approach, but what has it actually contributed to our understanding of the development of social cognitive skills so far? In what follows, we review how findings with NHP developmental samples have helped identify common, early-emerging social cognitive capacities that are in accord with and build upon findings with human infants.

Identifying foundational skills of social cognition by combining developmental and comparative approaches

Both human and NHP infants are born into rich and complex social worlds, surrounded by social partners who act with objects and interact with conspecifics in a seemingly continuous stream of activity. Although primates in general appear to be born with the propensity to engage in the social world (Farroni et al., 2013; Johnson, Senju, & Tomalski, 2015; Sugita, 2008), they do not enter the world with a complete set of knowledge concerning the movement, actions, goals, and intentions of the social beings that surround them. A challenge for the field, then, is to identify the foundational skills from which broader social cognitive development grows, and to uncover the drivers of these skills. Whereas some researchers focus on socioemotional processing and highlight face and emotion processing (e.g., Choudhury, Blakemore, & Charman, 2006), recognition of prosocial behavior (e.g., Holmes, 2002), and moral reasoning (e.g., Smetana, 1983) as 'essential building blocks' for broader social cognitive functioning, others focus on recognition of others' actions and intentions (e.g., Saxe, 2006; Zwickel, White, Coniston, Senju, & Frith, 2011), the emergence of joint attention (e.g., Tomasello, 1995), and cultural learning (Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007; see Rochat, 2014 for a review of several of these topics). Given that many of these skills are early emerging in their ontogeny, they represent good candidates for identifying the foundational social cognitive functions that are precursors to more complex social cognitive functioning. Identifying these precursors and how they come about is critical for understanding social cognitive development more broadly. In this section, we describe the development of social cognitive skills that appear to be shared across humans and NHPs, including preferences for social stimuli (e.g., faces, biological motion), affiliation with and preference for similar others, and basic action understanding.

Recognition of social beings

From birth, infants recognize and preferentially attend to biological motion (Blakemore & Decety, 2001). Across a variety of species, infants exhibit preferences for biological motion patterns of conspecifics (i.e., one's own species) and heterospecifics (i.e., other species) relative to non-biological motion (Simion, Regolin, & Bulf, 2008; Vallortigara, Regolin, & Marconato, 2005), suggesting a broadly tuned animacy detection system. Sensitivity to biological motion may function to attract infants' attention to socially meaningful stimuli in their environment, from which they can then learn. Understanding how biological motion is identified and preferentially processed may, therefore, provide clues for identifying the mechanisms upon which action understanding is built.

The preference for attending to other social or animate individuals and their actions extends beyond preference for biological, relative to non-biological, motion. In fact, across a variety of stimuli, both typically developing human and NHP infants tend to selectively attend to social stimuli, relative to non-social stimuli (Bard, Platzman, Lester, & Suomi, 1992; Lutchmaya & Baron-Cohen, 2002). For example, human newborns prefer to look at face-like stimuli compared to other stimuli (Goren, Sarty, & Wu, 1975; Simion, Farroni, Cassia, Turati, & Dalla Barba, 2002; Valenza, Simion, Cassia, & Umilta, 1996), as do infant macaques (Paukner, Bower, Simpson, & Suomi, 2013; Sugita, 2008). We recently found that 3-week-old macaques look longer at faces than non-faces presented in complex 8-item visual arrays (Simpson, Jakobsen, Damon, Suomi, Ferrari, & Paukner, submitted). Further, both faces and human figures are quickly and easily detected and preferentially attended toward in complex displays when viewed by human adults and infants (Fletcher-Watson, Findlay, Leekam, & Benson, 2008; Gliga, Elsabbagh, Andravizou, & Johnson, 2009) and early preferential attention to social stimuli has been observed on a neural level in 4- to 6-month-old human infants (Lloyd-Fox, Blasi, Elwell, Charman, Murphy, & Johnson, 2013; Lloyd-Fox, Blasi, Everdell, Elwell, & Johnson, 2011). In human children, early attention toward and processing of social information has been linked to individual differences in later social cognitive abilities, such as theory of mind (e.g., Wellman, Lopez-Duran, LaBounty, & Hamilton, 2008), suggesting that this propensity to recognize and preferentially attend to social beings may provide an important basis for subsequent social cognitive development.

Further evidence for the foundational role of social orientation can be seen in cases where social cognitive development goes awry. Reduced sensitivity to social stimuli, including biological motion, is evident in humans with or at risk of developing Autism Spectrum Disorders (ASD), a developmental disorder that is largely defined by social cognitive deficits (Lloyd-Fox et al., 2013; Klin, Lin, Gorrindo, Ramsay, & Jones, 2009; Noland, Reznick, Stone, Walden, & Sheridan, 2010). This highlights the importance of understanding the development of these foundational abilities. The utility of early measures of social interest as markers for developmental disorders, such as ASD, however, remains to be determined. Recent developments in NHP models of ASD (e.g., Bauman et al., 2013; Bauman et al., 2014; Wilson & Weiss, 2015) offer promising opportunities to further explore early preferences for social information and their predictive power for identifying early disturbances to healthy social cognitive development.

Physiological mechanisms of social interest: Oxytocin

Recent research has identified one potential physiological underpinning of preferential attention toward social stimuli and social engagement. Oxytocin is a neuropeptide implicated as both a cause and consequence of social engagement. We know little about this neuropeptide in infancy in humans or other primates, but a small number of findings hint at an association between social interest and oxytocin. In human newborns, endogenous oxytocin levels in cerebrospinal fluid are associated with higher levels of social engagement (Clark et al., 2013). Both parents and infants exhibit increased salivary oxytocin following play interactions, and parent-infant affect synchrony is positively associated with increases in infants' salivary oxytocin (Feldman, Gordon, & Zagoory-Sharon, 2010). While there is great clinical

interest in the possibility of treating disorders with exogenous oxytocin (e.g., Guastella et al., 2010), this enthusiasm should be tempered by the fact that we do not yet understand whether or at what doses acute or chronic exogenous oxytocin is safe, particularly for young, vulnerable populations (Rault, Carter, Garner, Marchant-Forde, Richert, & Lay, 2013). NHP infants offer an excellent model for the study of oxytocin to assess its efficacy as well as safety. The acute nebulization of oxytocin appears to increase macaque infants' affiliative social behaviors (Simpson et al., 2014a). A number of outstanding questions remain, such as whether there may be ways of naturally increasing infants' endogenous oxytocin to positively influence social development (Crockford, Deschner, Ziegler, & Wittig, 2014; Feldman, Golan, Hirschler-Guttenberg, Ostfeld-Etzion, 2014). We think these promising approaches offer unique opportunities to begin to understand the physiological underpinnings and correlates of infant social cognitive development.

Affiliating with conspecifics and social group members

Whereas initial attraction to potential social partners appears rudimentary, based in an apparently shared physiology with NHPs, a step beyond detecting other social beings is identifying those who act in similar ways to ourselves, making mimicry recognition a useful early capacity for attracting us to potential social partners. The "Chameleon Effect"— subconscious mimicry of others' behavior—is a well-studied phenomenon in human adults that appears to promote affiliation between individuals (for recent review: Duffy & Chartrand, 2015), with important consequences for higher-order social cognitive skills, such as collaboration, moral behavior, and cultural learning (Lakin, Jefferis, Cheng, & Chartrand, 2003). Because mimicry tends to occur at a subconscious level, in order to better understand recognition of mimicry, researchers must measure behaviors during or following mimicry that imply recognition of mimicry, rather than asking participants about their explicit awareness of having been imitated or mimicked.

In accord with the evolutionary benefits proposed by Lakin and colleagues, evidence of imitation recognition has been reported in both human and NHP infants. In one test of imitation recognition, human infants were presented with two individuals, each with an identical toy. One model interacted with the toy in the same way as the infant did with her toy, whereas the other model interacted with the toy in a non-matching way, acting independent of the infant's actions. Using this task, by 9 months of age, human infants tended to look and smile more at the model who produced matching actions, suggesting some degree of imitation recognition and subsequent desire to affiliate (Meltzoff, 1990; Meltzoff & Moore, 1999). There are considerable developmental changes in imitation recognition beyond this age. By 18 months, human infants not only recognize and prefer others who produce similar gestures and movements as themselves, but they also prefer to interact with and copy the subsequent toy choices of individuals who display similar preferences as the child (by matching the child's object-directed actions toward specific toys; Gerson, Bekkering, & Hunnius, submitted). The recognition of matching goal-directed actions between self and other is an important achievement in that it allows children to identify those who share their goals and preferences (rather than just movements), thus acting as a marker of similar others who might be useful resources for social learning and cultural development and also potentially playing a role in future action understanding.

NHP adults similarly recognize when they are being imitated and display increased affiliation towards individuals who imitate them (Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005; Paukner, Suomi, Visalberghi, & Ferrari, 2009). To assess imitation recognition in newborn NHPs, we carried out a study in which a human model imitated a macaque infant's mouth movements. For example, if the infant protruded her tongue, then the human model did as well. The infant's behavior during and after being imitated was compared to a non-contingent control, in which the model opened her mouth in a non-contingent manner relative to the macaque infant (Sclafani, Paukner, Suomi, & Ferrari, 2015b). We found that macaque newborns recognized when they were being imitated and displayed increased affiliative behaviors (e.g., facial gestures, looking at social partner, spending time in proximity to social partner) to a

contingent imitator relative to a non-contingent control. We do not currently know is whether NHPs, like human infants in Gerson and colleague's research (submitted), are sensitive to matching of object-directed actions, and when such a skill might develop. Exploring this question in NHP infants, who are motorically more advanced than human infants, may reveal these capacities emerge earlier because, although humans at birth possess a relatively precocial (i.e., maturationally advanced) brain, much like macaque infants, this precociality is hidden within a body that is otherwise quite immature relative to macaques of the same gestational age (Clancy, Darlington, & Finlay, 2001). Thus, testing these capacities in a NHP with more advanced motor skills may offer insights into the development of self-other matching capitates. Together, research to date suggests that imitation recognition, an important skill for identifying similar others with whom to affiliate, emerges early and is shared across human and NHP species.

Basic action understanding: Understanding goals and intentions

Beyond recognizing when others' behavior matches one's own, understanding the goals and intentions of others is essential to learning from and collaborating with others. An initial understanding of the goals and intentions of others' actions is a necessary precursor to moral reasoning, theory of mind, and cultural learning (see Woodward, Sommerville, Gerson, Henderson, & Buresh, 2009). As human adults, it is easy to assume that an infant who responds to a social bid (e.g., a person speaking to them) by babbling and looking toward the speaker shares similar knowledge about the intent of the speaker as we do as adults (i.e., the speaker likely intends to engage in a social interaction). Alternatively, however, the child may initially be attending to perceptual features of the actor's communicative signals without any identification of the intent behind the actions. Sensitive paradigms are needed, therefore, in order to uncover when an infant (whether human or NHP) is responding based on perceptual cues versus responding based on deeper levels of social understanding, such as knowledge of the person's goals. Through a combination of carefully controlled research paradigms, we now have evidence that young human infants do, in fact, recognize the basic goals and intentions of others' actions in the first year of life.

In a now classic experiment, using a habituation paradigm, Woodward (1998) found that six-month-old human infants recognized that the goal of a reaching action (i.e., the relation between the person acting and the object toward which she reached) was more important than the physical instantiation of the action (i.e., the physical location toward which the person reached). Human infants' recognition of others' goals has now been identified in imitation paradigms, eyetracking paradigms, and other controlled measures of overt behavior (see Woodward et al., 2009, for a review).

An understanding of others' actions was previously thought to be one of the differentiating factors between humans and other species (Tomsello & Rakoczy, 2003; Wobber & Santos, 2014). Recent evidence indicates, however, that NHP adults and human infants share similar basic action understanding capabilities. For example, common marmosets detected violations in goal-relations when a reaching action was carried out by a conspecific but not by an inanimate object (Burkart, Kupferberg, Glasauer, & van Schaik, 2012; for similar results in non-primates: Marshall-Pescini, Ceretta, & Prato-Previde, 2014). Further, both human infants and adult NHPs (great apes and macaque monkeys) are sensitive to the efficiency of goal-directed actions when tested in a looking time paradigm (Gergely, Nadasdy, Csibra, & Biro, 1995; Kano & Call, 2014; Rochat, Serra, Fadiga, & Gallese, 2008) and both human infants and adult capuchin monkeys detect the difference between intentional and unintentional actions and respond differentially when an experimenter is 'unwilling' versus 'unable' to give them an item (Behne, Carpenter, Call, & Tomasello, 2005; Phillips, Barnes, Mahajan, Yamaguchi, & Santos, 2009). To date, we know relatively little about the developmental emergence of action understanding in infant NHPs. This gap in our understanding is significant, as NHP infant research in this area has the potential to clarify the environmental contributions and mechanisms that support action understanding in ways that go beyond what can be addressed in humans alone. As a step in this direction, progress has recently been made in

identifying physiological underpinnings of action perception that may be related to action understanding in both human and NHP infants, which we review next.

Physiological mechanisms of action understanding: Mu Attenuation

Compared to studies in humans, animal studies allow greater precision in addressing certain questions about the brain, because they allow us to measure neural activity at a single cell level (Zhang, Smith, & Chino, 2008). This level of analysis can be particularly powerful when combined with an understanding of each species' behavioral and cognitive capacities, increasing the translational value for models of the human brain (Hall-Haro et al., 2008). Links between the perception and production of action on a neural level were first discovered in rhesus macaques using single-cell recording in parietal areas and the premotor cortex (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Since the initial discovery of mirror neurons, shown to fire during both the production and perception of goal-directed actions, less invasive techniques have been developed to study action-perception link in both humans and NHPs across ontogeny. The mu rhythm, found in electroencephalography (EEG), is considered a marker of mirror system activity in the brain (Cuevas, Cannon, Yoo, & Fox, 2014; Vanderwert, Fox, & Ferrari, 2013). The mu rhythm is in the same frequency ranges as the alpha rhythm (i.e., approximately 8-12 Hz in human adults, 6-9 Hz in human infants, and 5-7 Hz in neonate macaques) but is measured over central electrodes and decreases in power (often termed mu attenuation) during the production and perception of goal-directed actions, which is taken as an indication of increased mirror activity (Coudé et al., 2014; Cuevas et al., 2014; Vanderwert et al., 2013).

Studies measuring mu rhythm activity report that macaque infants appear to already possess a functioning mirror system from the first week after birth (Ferrari et al., 2012), enabling them to represent others' actions in a similar neural format to that used in the planning and execution of their own motor actions. This system is malleable and responds to changes in the infant's environmental circumstances. For example, we found that three-day-old infant macaques being reared by their mothers showed stronger mu attenuation in response to facial gestures than infants who grew up without a mother figure (Vanderwert et al., 2015). Moreover, the ability to produce different actions modulates the mirror system such that neural correlates of motor activity (i.e., mu attenuation) become active during the perception of recently learned actions. For example, in human infants, the experience of walking is related to the degree of mu attenuation found when infants observed videos of other children walking (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008), and human infants' reaching and grasping competence was related to mu attenuation when observing a model perform a reaching and grasping action (Cannon, Simpson, Fox, Vanderwert, Woodward, & Ferrari, 2015). Beyond revealing correlational links between action production and neural correlates of action perception, in a recent intervention study, we directly contrasted the effects of active versus observational experience on mu attenuation during perception of actions and their consequences in 10-month-old human infants (Gerson, Bekkering, & Hunnius, 2015). In this experiment, infants who gained active experience performing a novel tool-use action subsequently showed stronger mu attenuation during the perception of the effects of those actions (i.e., sounds associated with the learned action) compared to the effects of actions (sounds) with which they had received similar amounts of observational experience. Similar to van Elk et al. (2008) and Cannon et al. (2015), variability between infants was meaningful: infants who better learned the motorically trained action showed greater mu attenuation following training when listening to the sounds associated with the learned action. Studies in motorically precocial NHP newborns can further clarify these relations, especially by disentangling experience-independent mirror system differences from those driven by differential experiences (e.g., opportunities to practice reaching-grasping). The neural findings discussed in this section closely parallel behavioral findings concerning unique effects of active experience on action perception discussed below (see *Effects of experience on basic action understanding*) and highlight the importance of considering individual differences in action experience and perception.

Summary and other possible foundational skills of social cognitive development

To recap, we summarized a range of foundational social cognitive abilities that are shared among humans and NHPs and reviewed extant research on the developmental origins of these skills. In accord with theoretical frameworks emphasizing the foundational importance of agency detection and recognizing similar others (e.g., Macrae & Bodenhausen, 2000; Meltzoff, 2002; Rochat, 2014; Zwickel et al., 2011), we suggest that recognizing other agents and affiliating with them are primitive, early-emerging social cognitive skills that are likely shared to some degree across species. We find impressive action understanding skills in both human infants and in adult NHPs (e.g., Phillips et al., 2009; Woodward et al., 2009), with open questions remaining regarding infant NHP capabilities. The evolutionarily shared origins of basic action understanding that we cite as foundational are in accord with perspectives that cite action understanding and intentionality as building blocks of social cognitive development (e.g., Meltzoff, 2002; Rochat, 2014, Saxe, 2006). Although we believe that these capacities are strong candidates for being critical skills for forming the basis of social cognitive development, given their early emergence and shared evolutionary roots, we do not suggest that these are the only possible contenders. Our analysis thus far has focused on those areas of social cognition for which comparative developmental research has allowed new insights into shared capacities to date, but this field is still in its relative infancy and there is much to be discovered. In this review we did not emphasize some areas cited by others as critical to social cognition, such as joint attention development, theory of mind, moral reasoning, and emotional perspective taking (e.g., Choudhury et al., 2006; Smetana, 1983; Tomasello, 1995), but this does not suggest that these skills are unimportant for social cognitive development. Rather, their emergence has been less well-studied in both human and NHP infants, leaving open questions regarding whether some of these skills may emerge from or arise independently of the initial, foundational skills discussed above, and which are common across species (see, for example, Hermann et al., 2007; Saxe, 2006, for discussions).

Experience profoundly shapes foundational social cognitive skills in human and NHP development

The fact that the above-reviewed foundational skills are shared across species speaks to their importance evolutionarily, but it does not necessarily imply that the maturational and experiential drivers of social cognitive development are identical across humans and NHPs. It is important to consider how these skills come about and how the shared or divergent experiences of infants influence their emergence. Social cognitive skills do not develop in a vacuum – every day, infants are exposed to a variety of social others as well as other environmental conditions that can affect their development. In this section, we focus on the role different experiences play on the foundational social cognitive skills discussed in the previous section. Although group effects or population-level patterns are important for identifying the drivers of typical development, they often leave out the rich information that comes from what might otherwise be considered noise in the data: the individual differences that exist in terms of infants' postnatal environments and their social cognitive knowledge and skills. Throughout this section, we emphasize the role of individual differences in infants' early environmental experiences and their relations to the emergence of foundational social cognitive skills.

Effects of experience on recognition of and preference for social others

Human infants exhibit preferences for faces and biological motion (Simion, Di Giorgio, Leo, & Bardi, 2011). The extent to which these early interests are broad, for animate stimuli in general, or specific to evolutionarily relevant (e.g., own-species) motion, is difficult to test in humans. Because human infants are exposed to other humans from birth, it can be difficult to disentangle the postnatal contributions of experience-dependent (i.e., perceptual attunement; Maurer & Werker, 2014) and experience-independent biases (i.e., evolutionary predispositions; Scherf & Scott, 2012). In contrast, it is possible to rear NHP

infants without exposure to members of their own species and thus unravel the potential contributions of personal experience and maturational processes from evolutionary adaptation. We recently found that rhesus macaque infants, at only 3 weeks of age, are efficient at detecting faces in complex heterogeneous arrays of distractor images, and do so broadly, for both conspecific and heterospecific faces (Simpson et al., submitted). We additionally found that it was only after more extensive socialization with peers, at 3 months, that the infants exhibited an own-species bias in their face detection capacities. However, it is difficult to know whether the own-species specialization at 3 months is due to experience, maturational processes, or some combination of both. To address this question, more controlled experiments are necessary. For example, in one study, Japanese macaque monkeys were reared without exposure to faces of any kind for the first 6 to 24 months of life, and were tested on their preference for own-species faces, human faces, or non-face objects (Sugita, 2008). This revealed that, prior to face exposure, infants had broad face processing skills, including preferences and the capacity to recognize individuals within a species. In addition to an early attraction to faces, infants also exhibit early biases to biological motion. However, while own-species face specialization has been explored, to at least some extent, we know little about whether there may be own-species biases in the detection and processing of biological motion. Future work could employ similar designs to those used with face processing in NHPs to assess whether there is also own-species specialization in the detection and processing of biological motion, and if so, whether such biases appear prior to infants' exposure to conspecifics. To date, there are no published reports on own-species bias in human or NHP infants, so it remains untested whether there even is such specificity or whether it only emerges through social experience.

To directly address whether experience engaging in social interactions influences subsequent social interest and social processing, we randomly assigned neonate macaques to either receive daily face-to-face interactions with caregivers or receive other forms of interaction (i.e., touch without eye contact). We assessed whether this early social experience influenced NHP infants' social interest and skills. By the end of the first week of life, NHP infants in the face-to-face interaction group exhibited superior neonatal imitation compared to the control groups (Simpson, Murray, Paukner, & Ferrari, 2014b). By 1 to 2 months of age, infants in the face-to-face interaction group exhibited stronger preferences for social compared to non-social videos and spent more time in social contact with peers during social interactions (Dettmer, Kaburu, Paukner, Simpson, Ferrari, & Suomi, in prep). Thus, early engagement in face-to-face interactions seems to hone NHP infants' interest in and processing of social stimuli and interest in interacting with social others. This may have subsequent effects on further social cognitive development, including action understanding and cultural learning.

Despite the experience-expectant nature of engagement in social interactions, there is variability in the quality and quantity of these face-to-face interactions across individuals. Natural variations in social interaction quality may, in part, stem from inter-individual differences in social motivation on the part of either the parent or the infant (Chevallier, Kohls, Troiani, Brodkin, & Schultz, 2012). Neonatal imitation varies considerably across individuals in both humans and NHPs with approximately half of newborns of both species imitating facial gestures (Ferrari, Paukner, Ionica, & Suomi, 2009; Heimann, 2002). Individual differences in terms of how engaged infants are in neonatal imitation appear to be related to both prior and subsequent social experiences. For example, at only three days of age, macaque infants exhibit individual differences in behavioral mirroring responses (i.e., neonatal imitation) that appear to be driven, in part, by infants' early social experiences (Vanderwert et al., 2015). Specifically, NHP infants reared by their mothers exhibited stronger neonatal imitation compared to infants reared by human caregivers.

Another proposed explanation for the variability in neonatal imitation is that NHP neonatal imitation reflects, at least in part, individual differences in sensorimotor matching skills (for a recent review, see Simpson, Paukner, Suomi, & Ferrari, in press). A few reports have already found links between neonatal imitation and other aspects of social engagement and social cognitive development. For example, in

human infants, neonatal imitation at 2-3 days and at 3 weeks of age is negatively related to the frequency of averted eye gaze during a social interaction at 3 months (Heimann, 1989; 2002). In macaques, neonatal imitators, but not non-imitators, appear to recognize when, after a 1-minute-break, there is a change in the social partner with whom they are interacting (i.e., produce fewer communicative gestures to a novel vs. familiar human) during neonatal imitation assessments (Simpson, Paukner, Sclafani, Suomi, & Ferrari, 2013). Monkey imitators, compared to non-imitators, also exhibit more mature face viewing patterns, such as spending a greater proportion of time fixating on the eye region at 2- to 3-weeks of age (Paukner et al., 2014). Recently, we found that variation in the performance of facial gesture imitation in the first week of life predicts gaze following—the ability to follow where another individual is looking in space— in macaque infants at 7 months of age (Simpson, Maloney, Ferrari, Suomi, & Paukner, submitted). Individual differences in imitation recognition are also associated with later-emerging and more complex social cognitive skills in humans (e.g., gaze following capacity; Agnetta & Rochat, 2004) and NHPs (e.g., chimpanzees; Pope, Russell, & Hopkins, 2015).

These findings suggest that infants may possess a relatively plastic early system for encoding socially relevant actions, which is malleable as a function of infants' social interactions in the first days of life. Social interest is foundational for further social cognitive development, as initial attention to conspecifics or other agents is a precursor to learning from or about others. This work suggests that extremely early experiences in infancy may influence both within and across species differences in this foundational phenomenon. Therefore, any differences found between species may partially be due to systematic differences in early interactions rather than innate differences between species. The specific timing and nature of the interactions—e.g., mutual gaze, facial gestures, tactile/proprioceptive stimulation—that individually or in combination support the development of social interest, remain unexplored in humans or NHPs, and is essential to better understanding this foundational propensity.

Effects of experience on recognition of, and affiliation with, conspecifics and group members
According to Meltzoff's "like me" framework, "the bedrock on which commonsense psychology is constructed is the apprehension that others are similar to the self" (Meltzoff, 2007, p. 27). Meltzoff suggests that the recognition of others as similar to the self is a starting point for social cognition and begins in the first weeks of life with neonatal imitation. How might these self-other comparisons operate to help infants identify similarly acting others? We have proposed that relational comparison of one's own actions and goals and those of a social partner is one route to identifying others who share similar action tendencies (Gerson, 2014; Gerson et al., submitted; Gerson & Woodward, 2009). Relatedly, Barresi and Moore (1996) proposed that the physical alignment of one's own and others' actions during joint attention allows human infants to form an analogy between self and the other. Because the infant's actions and attentional states are physically co-present with the actions and attentional states of another individual, this allows the infant to compare these states and thus infer that the other individual likely possesses similar attentional and intentional states as oneself. There is limited empirical evidence that human infants use this route to recognize similar others and, as far as we are aware, such evidence is virtually non-existent in NHP infants. Although some theoretical frameworks are consistent with the notion that experience with self-other comparisons is important for recognition of similar others in human infants (e.g., Baressi & Moore, 1996; Meltzoff, 2007), experimental work delineating the ways in which this process might be implemented is needed. We have further suggested that self-other comparisons during instrumental actions (e.g., goal-directed reaches) facilitate human infants' understanding of the goals of novel actions, and we have found initial evidence for the role of this experience in action understanding, as discussed below (Gerson, 2014; Woodward & Gerson, 2014).

Effects of experience on basic action understanding

An important question for social cognitive development is when and how infants begin to understand others' actions when they engage in early, formative social interactions or simply observe social beings around them. As described above, research indicates that human infants begin to recognize the goals of others' actions in the first year of life (Woodward et al., 2009) and that adult NHPs similarly recognize humans' goal-directed actions as directed toward particular objects (e.g., capuchin monkeys; Drayton & Santos, 2014). Little is known about the developmental mechanisms underscoring this understanding in NHP, but consistent with the action-perception links observed across species on a physiological level, increasing evidence indicates that one route via which human infants begin to understand others' goals is by acting as intentional agents in the world themselves.

At three months of age, human infants can reach objects directly in front of them but have little control over their movements and cannot intentionally reach for, grasp, and pick up chosen objects. At this age, there is also no evidence that they naturally recognize the goals of others' reaching actions (Woodward, 1998). In order to address the origins of action understanding in human infants, Sommerville and colleagues (Sommerville, Woodward, & Needham, 2005) manipulated the action experience of 3-month-old infants and measured their subsequent understanding of others' actions. When infants were given experience using Velcro mittens with which they could procure and move objects, and hence gain object-directed motor experience, they subsequently demonstrated an understanding of the goal of a reaching action in a habituation paradigm. This change in goal-directed action recognition could be a function of the infant's first-hand experience producing the actions or, perhaps less convincingly for the role of active motor experience, a consequence of infants having visually perceived the object-directed actions (regardless of whether the infants themselves were the agents of those actions). In order to distinguish between these two possibilities, we assessed the action understanding of two groups of 3-month-old infants: a group trained with Velcro mittens and a group exposed to a matched amount of experience observing mittened actions without the opportunity to act on the objects with mittens themselves (Gerson & Woodward, 2014a). Infants who received active mittens training, but not those who received matched observational training, demonstrated recognition of the goal of a reaching action when tested in a habituation paradigm, supporting the view that action understanding is more strongly influenced by motor, relative to visual, experience in young, human infants. Similar unique effects of motor experience have been found for more complex actions at older ages (Gerson, Mahajan, Sommerville, Matz, & Woodward, 2015; Sommerville, Hildebrand, & Crane, 2008) and for neural activity during action perception, as discussed above (*Physiological mechanisms of action understanding: Mu Attenuation*).

Although we may attempt to give infants qualitatively different experiences via training, the ways in which infants participate in these different experiences is not homogenous. For example, when given the opportunity to reach and grasp with sticky mittens, as described above, human infants vary in the extent to which they carry out reaching-grasping actions during this training. Individual differences in infants' production of object-directed actions during mittens training (i.e., the amount of time they spend producing object-oriented, intentional movements during the brief training session) is related to subsequent individual differences in action understanding, as assessed via a habituation paradigm (Gerson & Woodward, 2014b; Sommerville et al., 2005). In two experiments, infants who produced more object-directed actions during a short training session showed a stronger novelty response to a change in goal-relation. Using yoked scripts, each infant in the observational condition was matched to an infant in the active condition, and the variability in experience produced (or observed) was matched between yoked pairs (Gerson & Woodward, 2014ab). Despite this match in variability, we found no relation between the amount of observational experience received and goal understanding. This finding suggests that, despite possible variability in natural tendencies to attend to goal-directed actions (e.g., social interest), individual differences in observational experience play less of a role than variability in motor experience on action understanding at this developmental stage.

Thus, at the origins of basic action understanding, active motor experience has a qualitatively unique influence on action understanding in human infants. Research manipulating active and observational

experience with actions learned later in infancy have mirrored these findings and further emphasize the importance of examining individual differences in action production and perception in human infants (e.g., Gerson et al., 2015). Whether active experience similarly influences action understanding in NHPs remains an open question. Identifying the drivers of action understanding can help us understand how and why certain aspects of action understanding are shared between human and NHP species and how the pace and patterns of development compare between species (Wobber, Herrmann, Hare, Wrangham, & Tomasello, 2014). Evidence described above indicating that early interactional experiences (e.g., lipsmacking during face-to-face interactions) influence neural motor activity during perception of these actions in neonate NHPs (Vanderwert et al., 2015) is consistent with the notion that active experience influences action perception in NHPs, but behavioural measures of their action understanding following motoric training are needed to directly address this issue.

Although motoric experience is highly beneficial to action understanding (relative to observational experience) early in human infancy, it is clearly not the only route through which infants and young children learn about the goals of others' actions. Research indicates that human infants' initial goal understanding gained via motoric experience is limited to the context in which the action was learned (Gerson & Woodward, 2014a). Again, a lack of research on action understanding in NHPs limits our ability to discuss the possible constraints or breadth of potential action understanding in this species. The limits seen in human infants would constrain the ability to recognize the goals of actions that infants or children have not produced with matching kinematics and objects. Clearly, other drivers must allow individuals to generalize beyond this basic understanding. We suggest that self-other comparisons, discussed as a driver of recognition of similar others above (*Effects of experience on recognition of similar others*), also helps human infants generalize their initial action understanding, as discussed below. We raise the question of whether this could also be the case in NHPs.

Action understanding and experience with self-other comparisons

In a series of experiments, we examined whether the ability to engage in self-other comparisons helped 7- and 10-month-old human infants understand and imitate the goal-relation underlying an action with which these infants had no prior motor experience. We found that infants who reached for a toy with their hand at the same time they saw an experimenter reach for the same toy with a tool could compare the matching goal-relation between their own and the experimenter's actions and subsequently recognize and match the goal (i.e., the toy chosen) of the experimenter's tool-use actions without having gained motoric experience manipulating the tool (Gerson & Woodward, 2012, 2014c). That is, infants recognized that when they reached for a toy with their hand, the goal-relation between themselves and the toy matched the goal-relation between the experimenter and the toy despite the experimenter using a tool to perform the action. More importantly, infants then transferred this understanding of the goal-relation of the tool-use action in order to match an experimenter's goal-object (toy-choice) when she chose between two toys using the tool. Thus, comparisons between self- and other-produced actions allowed human infants to overcome perceptual and kinematic dissimilarities between actions and to recognize the matching underlying goal structure of an action with which they had motor experience and an action that was motorically unfamiliar.

Findings in NHPs are consistent with the possibility that a similar mechanism might exist, at least on a physiological level, in primates: monkeys who had never acted on tools themselves but had retrieved food from tools with their hands while an experimenter held the food with a tool (during daily feeding routines) subsequently showed neural activity in the ventral premotor area F5 when the monkeys observed tool-use actions (Ferrari, Rozzi, & Fogassi, 2005). The authors suggest that the motor systems of these NHPs adapted to incorporate the tool-use action via purely visual experience. An alternative hypothesis is that the co-occurrence of the monkey's grasping action (a motorically familiar action) and the experimenter's tool-use action (a motorically unfamiliar action) could have provided an opportunity for comparison and

for the motor system to adapt to this motorically unfamiliar action. Future research examining behavioral action understanding in NHPs and controlling for confounding factors in the hypothesized driver of the above-described finding could help illuminate this possibility.

The breadth and constraints of self-other comparison as a generalization mechanism of action understanding have yet to be defined (see Gerson, 2014; Woodward & Gerson, 2014, for discussion). Broadening infants' initial understanding of goal-directed actions is critical for developing action understanding capacities beyond basic intention understanding with regards to specific object-directed actions. Human infants and young children go on to recognize systematic preferences, desires, and beliefs across events and eventually distinguish between their own and others' mental states. Gaining a better understanding of the experiences that drive this generalization is critical for identifying whether, when, and why humans and NHPs diverge in their capacity to understand others. Whether a comparison of produced and observed actions facilitates goal understanding in NHPs is currently unknown but is an interesting avenue for future investigation.

Together, these findings suggest that early visual, motoric, and social experiences can profoundly influence the expression of these foundational social cognitive behaviors early in development (Raby, Lawler, Shlafer, Hesemeyer, Collins, & Sroufe, 2015). They identify key factors that drive development of these skills and emphasize the importance of considering individual differences when studying environmental factors and social cognitive outcomes. Although the skills reviewed are foundational and are present early in typically developing human and NHP infants, they do not arise independent of environmental experiences. Considering these experiences provides a richer understanding of these capacities and how they might further influence subsequent social cognitive development. Early mother-infant face-to-face interactions appear foundational to initial social interest, setting the stage for more refined social skill development, including specializations to process own-species stimuli, as well as higher-level social comparisons and action understanding capacities.

Future Directions

The integration of NHP and human developmental research has strengthened our understanding of the early-emerging social cognitive skills that are shared across human and NHP species. Still, the ability to identify foundational social cognitive phenomenon using a comparative developmental approach is challenging and limited. Below, we first discuss several challenges to using this approach in future research. Then, we discuss why the challenges should be overcome in order to further investigate the foundational abilities underscoring social cognitive development. We review some potential fundamental social cognitive capacities that remain to be examined and the additional driving factors that could emerge from future research.

What are the challenges and limitations of a comparative developmental approach?

One area in which little work has been done, but that we think may offer a unique and informative perspective, is in the adaptation of paradigms used to assess social cognitive development in human infants and children to assess the same underlying constructs in NHP infants. Currently, the comparisons we can make between species largely rely on isolated lines of research within each species. Neonatal imitation across NHP and human neonates is a prime example, however, of how similar methodologies can be used across species to uncover commonalities. Human experimental paradigms and methods may be adapted for use with NHP species in a way that is developmentally (and species) appropriate. For example, we know very little about NHP infants' understanding of goal-directed actions (but for adult NHPs see, e.g., Drayton & Santos, 2014; Tomasello, Call, & Hare, 2003; Wood, Glynn, Phillips, & Hauser, 2007), and paradigms used with human infants, such as motor training, looking time studies, and eyetracking, can be adapted for use with infant NHPs to address this issue (e.g., by making the stimuli

used in the studies more motivating and relevant for NHPs). Similarly, comparisons between familiar and unfamiliar actions facilitate the generalization of initial action understanding in human infants, but whether this benefit extends to NHPs can be addressed with research allowing NHPs to compare their own actions with novel actions produced by others. The first step in building this bridge between comparative and developmental research is cross-talk between human and animal researchers. Barriers between fields, created through field-specific language, journals, and conferences, can be broken down if researchers on both sides recognize the shared theoretical and methodological interests of animal and human researchers studying development, as demonstrated in this chapter.

Given the different capacities and motivations across species, there are, of course, limitations in the extent to which specific paradigms can be adapted for use with different species. For example, research investigating adult NHP action understanding has revealed that skills displayed by human infants in cooperative or neutral atmospheres were initially thought to be absent in primates until the primates were placed in a competitive atmosphere (Hare, Call, Agnetta & Tomasello, 2000). Although this divergence in motivations is incredibly telling (Tomasello, Carpenter, Call, Behne, & Moll, 2005), it can also lead to misrepresentation of abilities if not accounted for in adaptation of paradigms. In addition, when a species fails to demonstrate a certain capacity (i.e., null results), interpretations should be stated cautiously and with recognition of possible limitations, as one reason for null findings could be that the task was not sensitive enough to detect the animal's (or human's) ability (for an example in humans: Kolarik, Cirstea, Pardhan, & Moore, 2014). Claims that certain capacities are unique to humans should always be met with skepticism; indeed, as reviewed here, many capacities originally thought to be uniquely human were later found to be shared across species. These and other challenges have been summarized elsewhere (e.g., MacLean et al., 2012). Nonetheless, cross-disciplinary collaborations, and especially collaborations between groups who study human development and those who study development in other species, can allow us to obtain a more complete understanding of developmental processes.

Finally, it is worth noting that while most infant NHP studies of social cognition have been carried out in rhesus macaques and great apes (primarily chimpanzees), the field could benefit from a widening of the diversity of NHP infants studied (Hecht, Patterson, & Barbey, 2012; Shettleworth, 2009), better capturing how differing ecologies and social structures shape individual ontogenies (Bard & Leavens, 2014). Although NHPs are worth understanding in their own right, here we focus on their relevance for understanding humans. NHP studies are, of course, only a small collection of a broader diverse animal kingdom full of eclectic social cognitive skills (for a historical overview, see Burghardt, 2013). Expanding the comparative developmental approach highlighted throughout this chapter to additional species could further feed our understanding of the foundational forms of social cognition and how different kinds of experiences shape these.

Are there additional foundational social cognitive skills?

As reviewed in the introduction, researchers with differing perspectives have proposed a variety of additional social cognitive capacities as potential "building blocks" of social cognition. Whereas many of these capacities develop later in life than the reviewed skills in this chapter (e.g., emotional perspective taking, Choudhury et al., 2006; joint attention, Tomasello, 1995; theory of mind, Meltzoff, 2002, Saxe, 2006), some researchers have claimed that others (e.g., face recognition, Rochat, 2014; moral reasoning, Smetana, 1983) are early-emerging or even innate (face processing, Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000; moral reasoning, Hamlin, 2013). Whether these additional early-emerging capacities are shared across species in infancy and whether they share similar trajectories based on species common experiences is a topic of debate (e.g., Killen & de Waal, 2000). If shown to be common to humans and NHPs and early-emerging, the role these capacities might play in forming the foundations of subsequent social cognitive development should be further considered.

The fact that some capacities generally emerge earlier than others does not necessarily imply that the earlier developing skills are more important to adult functioning, but it does bring into question whether the capacities gained later in development may, in part, be built upon individual or a combination of foundational, early-emerging skills. How later developing, higher-order social cognitive skills emerge from initial skills is an important question for future research and may speak to how and when differences between species emerge. Below, we discuss a couple domains and techniques that we believe could be fruitful areas in which to further explore the foundations of social cognitive development using a comparative developmental approach.

The role of emotions in social cognitive development

Emotions are intricately linked to sociality, both driving and being modulated by engagement in social interactions. The role of emotions in social cognitive development has been highlighted in adolescent humans (e.g., Choudhury et al., 2006), but is relatively unexplored in early infancy. There is a similar lack of studies in NHP infants, partially attributable to the fact that, historically, emotions were considered outside the realm of study in animals. However, work in recent decades has made great strides in the objective study of both positive and negative emotions in animals (for a review: de Waal, 2007). Affect likely plays an important role in modulating early social interactions in both humans and NHPs (e.g., Bard et al., 2014; Clay & de Waal, 2013; Parkinson, 2012). Unfortunately, a review of all of these factors is outside the scope of this chapter. Instead, we next focus on a promising new tool that we suggest could yield new insight into the role of emotions in social cognitive development in both humans and NHPs.

Infrared thermography, which allows measurement of skin temperature (an index of arousal), is one measurement tool that could provide important information regarding the role of emotions in early social information processing (Clay-Warner & Robinson, 2014). Face temperature changes in human infants are related to both positive (mother-infant play; Nakanishi & Imai-Matsumura, 2008) and negative (mother-infant separation: Mizukami, Kobayashi, Ishii, & Iwata, 1990) emotional states, and mothers and infants exhibit synchronous changes in their facial temperature during interactions (Ebisch, Aureli, Bafunno, Cardone, Romani, & Merla, 2012). Despite its potential to measure affect within social interactions, we know of no studies to date that use thermography in infants to explore physiological arousal as it relates to social cognition. This tool could be useful to non-intrusively measure emotional reactivity in human and NHP infants during their first social interactions in the neonatal period, providing a window into nonverbal infants' early emotions. For example, thermography could assess emotion contagion, such as contagious crying, proposed to be one of the earliest measures of empathy and foundational for social understanding (Geangu, Benga, Stahl, & Striano, 2010). It could also be used to assess arousal during neonatal imitation, a meaningful early marker of social skill, in order to confirm that increased arousal does not solely account for infants' apparent imitative responses (Nagy & Molnar, 2004).

The contribution of epigenetic approaches

We are just starting to understand the cognitive drivers of social cognitive development, but we still have a poor grasp on how these cognitive mechanisms are anchored in physiology. Some progress has been made in the field of epigenomics, where mental and physical health outcomes have been related to significant methylation changes (Kaufman, Plotsky, Nemeroff, & Charney, 2000; Power et al., 2007). Specifically, in humans, epigenetic mechanisms of pathogenesis have been implicated in several central nervous system diseases, including neurodevelopmental disorders of cognition involving learning and memory (e.g., fragile X mental retardation and Rett syndrome). Furthermore, neurogenerative disorders of aging such as Alzheimer's disease also show derangement of epigenetic mechanisms (Day & Sweatt, 2011), and a glucocorticoid receptor promoter in the hippocampus appears to be significantly altered in response to adverse upbringing (McGowan et al., 2009). Even in typical development, methylation patterns of brain structures have been found to vary considerably both within and between individuals

15

(Davies et al., 2012). Most animal work in this area is done using rodent models, including generating and maintaining experience-driven behavioral change (Levenson & Sweatt, 2006). For example, rodent studies have shown that contextual fear conditioning changes methylation of memory-related genes expressed in the hippocampus, implicating methylation and demethylation as a molecular mechanism underlying learning and memory (Day & Sweatt, 2011).

However, given the advanced cognitive skills discussed in this chapter, rodent models may be insufficient to address the role of epigenetics in social cognitive development and NHP work may be fruitful (see, for example, see Hopkins, Reamer, Mareno, & Schapiro, 2015; Leavens, Hopkins, & Bard, 2005; Phillips et al., 2014). What we know to date is that, similar to humans, early life adversity in NHPs affects methylation patterns in the prefrontal cortex (Provençal et al., 2012). What is still lacking is an understanding of how neurons generate epigenetic marks in response to the development of a specific cognitive skill (Day & Sweatt, 2011). Future studies may determine how DNA methylation is regulated and translated into changes in the neural circuit, thereby taking us beyond the overly simplistic discussion of nature/nurture contributions and leading to deeper insights into how multiple processes bi-directionally interact, and, ultimately, shape cognitive performance and social cognitive development. Gaining a more nuanced and complete understanding of these forces will require collaborations across disciplines with specializations at various levels (e.g., genetic, neural, behavioral) and the use of animal models that allow for control over some of these factors (e.g., genetics, environments) that cannot be controlled in humans (Gottlieb, 2007).

Conclusion
Through the exploration of research lines addressing social cognitive development in both human and NHP infants, we discussed early-emerging, shared capacities in a variety of social cognitive abilities that we believe are important precursors to further social cognitive development. Beyond simply revealing which capacities are unique or shared across species, NHP studies of infant social cognitive development are exceptionally well positioned to reveal insights about environmental contributions to the development and physiological underpinnings of social cognitive development. They also offer unique opportunities to explore development in visually and motorically precocious species, opening up avenues for research that are not possible in human infants alone.

Although NHP infant studies are challenging on a number of fronts—requiring long-term resource investment and careful ethical considerations—we presented some examples of ways in which such studies are invaluable in their advancement of basic and applied research questions. This perspective can provide new insights into the roots of human social cognition because, rather than assuming that language or culture are the unique drivers of human social cognition, studies in NHPs allow us to test whether certain abilities may develop independent of these influences. In summary, studies of social cognitive development in human and NHP infants can each inform the other, providing a more holistic approach to the study of the foundational skills and drivers underlying social cognitive development across species.

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