Neonatal imitation and its sensory-motor mechanism

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Abstract:

A developmental approach is critical to understanding mirror neurons and debates surrounding their properties, plasticity, function, and evolution. The presence of inter-individual differences in early social competencies, such as neonatal imitation, are indicative of the complex nature of interactions among genetic, epigenetic, and non-genetic (environmental) factors in shaping action-perception brain networks. In the present review, we propose that three aspects of early social development may explain variability in neonatal imitation, specifically (1) individual differences in sensory-motor matching skills, underpinned by mirror neurons, functioning from birth and refined through postnatal experiences, (2) individual differences in social engagements, with some infants demonstrating stronger preferences for social interactions than others, and (3) more general temperamental differences, such as differences in extroversion or reactivity. We present findings and propose future directions aimed at testing these possibilities by examining individual differences related to imitative skill. Neonatal imitation is a useful tool for assessing infants' sensory-motor matching maturity, social motivation, and temperament, particularly when used with a mindfulness of infants' changing social motivations and expectations. The presence of an action-perception mechanism at birth can be better understood by considering the complex interactions among infants' social competences, sensory-motor skills, environmental influences, and individual differences in social interest and temperament.

In recent years, a developmental approach has been recognized as being critical to understanding mirror neurons and debates surrounding their properties, plasticity, and especially their proximate and ultimate functions (e.g., Del Giudice et al. 2009; Ferrari et al. 2013; Lepage & Théoret 2007; Simpson et al. 2014a). This interest is, at least in part, due to the fact that, during development, infants' brains undergo several changes, which provide them with the cognitive capacity to sustain complex forms of social behavior. In particular, the cortical motor system appears to be involved in action understanding and imitation. Second, it is important to understand not only the basic brain mechanisms that support such behaviors and skills from birth, but also the extent to which early experience shapes such networks during development.

Work on postnatal development carried out in human and nonhuman primates revealed the presence of early imitative skills and complex mother-infant interactions, useful for understanding how action-perception mechanisms operate at birth and how early experience might affect the neural circuitry that makes such complex behaviors possible. The presence of inter-individual differences in early competences highlights the need to explore the contributions of, and interactions between, action-perception brain networks, present from birth, and postnatal environments.

The neonatal period is a unique, sensitive, and experience-expectant time in development (Nagy 2011). Mothers engage in complex exchanges with newborns, including mutual gaze, body contact (e.g., kisses), and exaggerate facial and vocal expressions, in humans (Stern 1985; Trevarthen 1974; Tronick 1989) as well as in at least some Old World nonhuman primates (e.g. rhesus macaques: Ferrari et al. 2009a; gelada baboons: Mancini et al. 2013; chimpanzees: Bard 1994; Bard et al. 2005). Such complex, face-to-face newborn-mother interactions may occur in other nonhuman primate species as well, although we are unaware of any published reports.

During such exchanges, some infants exhibit neonatal imitation, or the matching of others' actions, while some infants do not (Ferrari et al. 2009b; Heimann 2002; Paukner et al. 2011), Figure 1. It still remains unclear, however, whether these early imitative skills reflect meaningful individual differences, and if so, how exactly these individual differences may inform us about the underlying action-perception mechanism. The present review focuses on individual differences in imitative skill, since evidence of neonatal imitation has been reviewed elsewhere (e.g., Meltzoff & Moore 1997; Nagy et al. 2012; Oostenbroek et al. 2013), including best practices for eliciting imitation (Simpson et al. 2014a), comparisons of imitation in humans and macaque newborns (Paukner et al. 2013), and tests of its plasticity (Jacobson 1979; Nagy et al. 2014; Simpson et al. 2014a; Vanderwert et al. under review). We discuss rhesus macaques specifically, in part, because of their similarities with humans in early mother-infant interactions (Ferrari et al. 2009a) and their ability to imitate from birth (Ferrari et al. 2006). It is worth noting that rhesus macaques are not the only nonhuman primate species capable of neonatal imitation; neonatal imitation has also been empirically demonstrated in chimpanzees (Bard 2007; Bard & Russell 1999; Myowa-Yamakoshi et al. 2004). In addition, rhesus macaques, relative to chimpanzees, are more easily bred in captivity, providing the large sample sizes necessary for the study of individual differences. Individual differences in imitative skill, to our knowledge, have only been explored in humans and rhesus macaques (for a review, see Simpson et al. 2014a). Such variability in imitative skills might be explained by some

combination of (1) individual differences in sensory-motor matching skills, underpinned by mirror neurons, functioning from birth and refined through postnatal experiences (Ferrari et al. 2013), (2) individual differences in social engagements, with some infants demonstrating stronger preferences for social interactions than others, and (3) more general temperamental differences, such as differences in extroversion or reactivity. This list is not intended to be exhaustive[1], but rather, reflects three areas of individual differences that we propose may explain significant variability in neonatal imitation. In the present chapter, we propose that these aspects of early social development—sensory-motor matching skills, social motivation, and temperament—may explain variability in neonatal imitation. We suggest that the presence of an action-perception mechanism at birth can be better understood by taking into account the complex interactions occurring during development between infants' social competences, in part a cause and consequence of their sensory-motor skills, and the effects of different experiences and environmental inputs on individual differences already present from birth (e.g., social interest, temperament). We also present some findings and propose future directions aimed at testing these possibilities by examining individual differences related to imitative skill.

Sensory-motor matching skills related to neonatal imitation

Electroencephalography (EEG) studies reveal that during infants' execution and observation of actions, specific frequency bands within the alpha range (5-9Hz) desynchronize (Lepage et al. 2006; Marshall & Meltzoff 2011; Marshall et al. 2011; Saby et al. 2012; Southgate et al. 2009). This suppression, termed the mu rhythm, is associated with the activation of mirror neurons areas—i.e., inferior frontal gyrus, ventral premotor cortex, posterior parietal lobe (Arnstein et al. 2011)—and thus may be an indicator of mirror neuron activity (Coudé et al. 2014; Marshall & Meltzoff 2011; Pineda 2005; Vanderwert et al. 2013). Indeed, in newborn macaques, the mu rhythm desynchronizes during the observation and imitation of facial gestures (Ferrari et al. 2012a). The mirror neuron mechanism, therefore, may be the basis for human and nonhuman primate infants' capacities to tune their own behavior with that of their mothers' through complex face-to-face matching behaviors (Ferrari et al. 2009a). If imitation performance reflects the presence of a sensory-motor mechanism, then we can better understand the functioning of this mechanism by studying newborns' imitation skills.

Previous work suggests that motor experience affects the activation of the mirror neuron system specifically during action observation. In adults, several studies show links between action skill and action observation (e.g., humans: Cannon et al. 2014; Calvo-Merino et al. 2005; Marshall et al. 2009; Orgs et al. 2008; and monkeys: Umiltà et al. 2008; Rochat et al. 2010). How these links emerge developmentally, however, remain largely unresolved, despite several recent experimental attempts in human infants (for a review, see Hunnius & Bekkering in press). For example, the magnitude of mu rhythm desynchronization during action observation appears modulated by action expertise. Eight-month-old infants given one week of training to shake a particular rattle subsequently showed attenuated power in the mu band when hearing the rattle sound compared to control sounds, and the amount of training correlated with the degree of attenuation (Paulus et al. 2012). Similarly, 14- to 16-month-old infants exhibit stronger desynchronization while viewing crawling compared to walking, which appears to be related to an infant's crawling experience (van Elk et al. 2008). Only recently have

studies begun to directly assess infants' motor skills to see whether they are associated with cortical activity during action observation. In one study, 4- to 6-month-old infants' cortical activation (in the posterior superior temporal sulcus-temporoparietal junction region) during observation of hand movements correlated with infants' fine motor skills (Lloyd-Fox et al. in press). However, in this study, no goal-directed actions were explored; rather, they assessed fine motor skills generally and measured whether they may be related to cortical activity while viewing modeled hand actions that were not goal-directed (i.e., opening and closing of fingers to form a fist). In this study, near-infrared spectroscopy was used to measure cortical activity; it is therefore unclear whether individual differences in activity reflect activity of mirror neurons, as this method does not allow for the degree of specificity necessary to ensure measurement specifically of the mirror neuron system. We recently addressed these issues in a study in 9-month-olds, in which we found desynchronization over motor-related regions during action observation that were associated with action competence: infants with stronger reaching-grasping skills exhibited stronger mu suppression while viewing reaching-grasping actions (Cannon et al. under review). Together, these studies provide evidence for an early emerging neural system integrating one's own actions with the perception of others' actions.

To date, no published studies have tested the prediction that human newborns with stronger imitative skills would likewise exhibit greater mu suppression during action observation. Specifically, we would predict that infants with stronger facial gesture imitation would exhibit greater desynchronization when viewing those same facial gestures. If so, this would suggest that neonatal imitation relies on sensory-motor skills, and that individual differences in the maturity or strength of mirror neurons may underpin individual differences in behavioral measures of sensory-motor matching. One study from our lab provides some indirect evidence of this effect in newborn macaques. We assessed whether experiences in the first three days of life can modulate macaque newborn imitation and mirror neuron activity. We found that 3-day-old macaque infants reared by their biological mothers, compared to nursery-reared infants, were more likely to imitate familiar gestures (Figure 2) and exhibited greater mu rhythm desynchronization while viewing familiar gestures (Ferrari et al. 2012b), suggesting that socially enriched early experiences, even in the first few days following birth, may increase sensitivity of the mirror mechanism.

If neonatal imitation relies on a functioning sensory-motor matching system, then other behaviors that also require sensory-motor matching might be associated with neonatal imitation. For example, the ability to recognize the correspondence between one's own actions and another individual's actions—or imitation recognition—appears to require such a neural mechanism. Instead of translating visual input into motor output, imitation recognition requires the translation of motor output into a matching visual representation and recognizing the motor-visual correspondence. Adult nonhuman primates show evidence of imitation recognition (Haun & Call 2008; Paukner et al. 2005, 2009), as do infant monkeys starting in the second week of life (Sclafani et al. in press; Simpson et al. 2014c). Human infants similarly show early preferences for contingent responses (for a review, see Nadel 2002) and 14 months old infants recognize imitation (Agnetta & Rochat 2004), but it is unclear whether human neonates are sensitive to being imitated.

In order to test a possible association between neonatal imitation and imitation recognition, we examined whether infant macaques' imitative skill in the first week of life could

predict their gesture rates in an imitation recognition task at 2 to 4 weeks of age (n = 27). Using a standardized neonatal imitation task (Paukner et al. 2011), we calculated the strength of each infant's LPS imitation skill (for details, see Sclafani et al. in press). In the imitation recognition task, a human model imitated the infant's mouth movements for 2 minutes, followed by a 2 min still-face. In a non-contingent control condition, a human model opened her mouth five times every 10 seconds for 2 min, followed by a 2 min still-face. Therefore the imitation condition included structural and temporal matching whereas the control condition presented lipsmacking gestures simply as a repetitive response. We found that the strength of LPS and TP imitation skill in the first week of life was positively associated with the frequency of infants' LPS and TP gestures during the imitation period in the fourth week of life, Figure 3, but not in the control condition or still-face periods (unpublished data). In addition, while there was consistency between weeks 2 and 4 in how infants responded to being imitated (e.g., LPS frequency in week 2 and 4 were correlated), there was no association between weeks 2 and 4 in their gesture frequency in response to the still face (unpublished data). These results are consistent with our hypothesis that neonatal imitation and imitation recognition may both be behavioral measures for assessing individual differences in sensory-motor matching. In addition, since macaque infants appear relatively more engaged by imitation recognition after the first week of life, this paradigm might be a promising measure to utilize with older infants. To our knowledge, this imitation recognition measure has not yet been used with human newborns.

Stability in imitative skills across ages and paradigms

The mirror mechanism has been suggested to play a key role in social interactions and several scholars have proposed that its dysfunction may lead to impaired social competence, such as autism. In humans, there is evidence that the hypofunctioning of mirror neurons may be associated with diminished social competence (e.g., Enticott et al. 2012; Iacoboni & Dapretto 2006). For example, an fMRI study found that autistic children had reduced mirror neuron activity during imitation, which was inversely correlated with the severity of their autism (Dapretto et al. 2006). Given that individual differences in imitation/social competence are related to individual differences in mirror neuron activity in autism, such links may also exist in typically developing populations; therefore, some of the interindividual differences in neonatal imitation might be associated with individual differences in the mirror system. The capacity to be better tuned or more interested in actively engaging with social partners might depend on the strength of such a system.

In addition to the developmental maturity or strength of the system, social motivation may also affect the capacity of infants to be more attentive to social stimuli, thus leading some infants to search for the social stimuli and, ultimately, impacting their behavioral matching response. Infants' differential social interest may lead to differential experiences, giving them varied opportunities to regularly exercise the system. It is therefore important to understand how neonatal imitative responses reflect a behavioral trait linked to a more stable aspect of temperament, such as social motivation and social engagement. To these ends, we carried out a variety of modifications to our standard neonatal imitation assessment, to determine whether there are better ways of assessing individual differences in neonatal imitation, as well

as to examine whether individual infants consistently demonstrate (or fail to demonstrate) imitation across a variety of tasks.

If neonatal imitation is influenced by an infant's motivation to interact with others, we would expect stability in imitative skill; that is, infants who imitate in the first week of life are also likely to imitate in the second week of life. Previous work with human infants has shown stability in imitative responses from 2- to 3-days of age, to 3-weeks of age (Heimann et al. 1989), however previous attempts with infant macaques failed to provide any evidence of imitative ability in the second week of life (days 13-15, Ferrari et al. 2006). We hypothesized that the testing environment might play an important role: a more familiar (home environment) might increase imitation levels compared to an unfamiliar testing room, particularly in the second week of life. Thus, it is possible that in previous studies, macaque infants failed to show imitation due to an increase in anxiety associated with novel environments. To test these predictions, we presented nursery-reared macaque infants (n = 16) with standard imitation assessment at 1 to 12 days old. We found no evidence that testing in the home cage increased imitation. In addition, infants who imitated in the first week of life were not consistent imitators in the second week of life. One possibility is that neonatal imitation is not reflecting a stable individual difference, but something that is subjected to random fluctuations and therefore may be related to an infant's current state; however, this seems unlikely as infants demonstrate response specificity (i.e., match specific actions; e.g., Meltzoff & Moore 1977, 1989; Nagy et al. 2012, 2014). Another interpretation of this finding is that imitation simply declines by the second week of life in macaques, making the neonatal imitation period significantly shorter compared to human infants. This seems a possibility, especially given the faster rates of development in macaque newborns relative to humans (Clancy et al. 2001; Workman et al. 2013). In addition, human infants likewise begin to show declines in certain types of neonatal imitation, such as facial gestures, after the first month of life (e.g., Fontain, 1984). It is also possible that, after engaging in this task every other day for the first week, infants become less interested with this type of social interaction. In particular, experimentally timed and controlled interactions with the model may create situations rather different from natural face-to-face caregiver-infant interactions, and may reduce imitation rates (Bard 2007; Ullstadius 1998). After all, imitation is both a cognitive and a social phenomenon (Maratos 1982), so failure to exhibit attuned and responsive behaviors may decrease infants' motivation to interact. This interpretation seems to find also support in one study on mother-reared rhesus macaques (Ferrari et al. 2009a), in which infants displayed imitative lipsmacking response after mother's solicitation in the second week of life. This finding therefore suggests that a lack of early maternal solicitation might decrease infants' interest and response towards facial stimuli.

To address the above mentioned limitations, we presented macaque infants with an unstructured neonatal imitation assessment (adapted from studies with human neonates, Kugiumutzakis 1999; Nagy & Monar, 2004; Bard, 2007; Bard & Russell 1999), which is more novel, less rigid, and the pace is geared to the infant's responsiveness. Unlike the structured imitation task, the unstructured task includes more turn taking and is more reflective of a natural social interaction. Previous studies suggest that, in both humans and macaque monkeys, only about 50% of neonates consistently imitate facial gestures in structured assessments (Ferrari et al. 2009b; Heimann 2002; Paukner et al. 2011). In contrast,

approximately 80% of human infants imitate during unstructured assessments (unpublished dissertation data: Kugiumutzakis 1985). Unstructured neonatal imitation, compared to structured neonatal imitation, also increases the number of gestures imitated by chimpanzee newborns (Bard 2007). We used the same actions and control conditions as in our previous structured imitation assessment (Paukner et al. 2011), and macaque infants (n = 20) were tested every other day in the first week of life, and one day in the second week of life (between days 10-12). We adjusted the timing of the session to mimic natural macaque mother-infant interactions, which occur in frequent, short bouts (i.e., 5 sec action, 5 sec pause, repeated; see Ferrari et al. 2009a, for a description of naturally-occurring macaque mother-infant face-to-face interactions). First, we tested whether there were higher rates of imitation with the unstructured paradigm compared to the structured paradigm in the first week of life (unpublished data). Since the unstructured paradigm resulted in different test periods and response measures, there was a less strict criterion for being an imitator: infants had to produce at least one matching gesture in the majority of test sessions (in at least 3 of the 5 sessions). Using this criterion, 100% of infants were LPS imitators and 90% were TP imitators in the unstructured paradigm (overall across days 1-12). Interestingly, imitation lasted through the second week of life (80% of infants imitated LPS and 90% of infants imitated TP on day 10-12), whereas it decreased with the structured paradigm (e.g., LPS imitation down to 33% of infants on day 7, no imitation on D14; Ferrari et al. 2006). The results suggest that older infants may be more responsive to this unstructured paradigm. Furthermore, we found positive associations between infants' performance in the unstructured and structured tests. Assessing the mean gesture frequency across all test days, we found correlations between responses in the structured and unstructured tests for LPS matches (LPS in LPS condition) r = .44, p = .050, and TP matches (TP in TP condition) r = .67, p = .001, Figure 4. These results suggest there is some consistency in infants' imitative skill across these two different paradigms, consistent with the proposal that neonatal imitation reflects meaningful and stable individual differences. However, it remains unclear whether such differences may be a reflection of infants' sensory-motor matching maturity, motivation to interact with others, temperament, or some combination of these factors. Nonetheless, neonatal imitation testing is a valuable tool for exploring such questions. In addition, these results highlight the need to use a variety of age-appropriate measures of imitation, e.g., flexible, game-like, or turn-taking paradigms with older infants that take into account changes in infants' expectations and motivations (Hanna & Meltzoff 1993; Kaplan & Oudeyer 2007; Meltzoff & Moore 1992).

Imitative skill, social motivation, and social skills

Many researchers argue that it is important to examine whether neonatal imitation is predictive of later social and cognitive development (Heimann 1989, 2001; Heimann et al. 1989; Maratos 1998; Siller & Sigman 2004; Suddendorf et al. 2013) because, for example, it could be an early marker of later deficits in social skills (Paukner et al. in press; Simpson et al. 2014a). Variability in imitative performance may therefore reflect genuine individual differences, such as social interest. Only one published study examined neonatal imitation predictively in human infants: imitation at three ages—2 to 3 days, 3 weeks, and 3 months of age—predicted visual attention at 3 months (Heimann et al. 1989; Heimann 1989). Specifically, imitators had fewer looks away from their mother's face during a face-to-face interaction game at 3 months. During

neonatal imitation itself, macaque imitators show increased visual attention to the faces of human social partners (Simpson et al. 2014b), are better at recognizing human social partners (Simpson et al. 2013), and are better at remembering gestures and initiating social interactions after a delay, known as deferred imitation (Paukner et al. 2011), which hint at an association between imitation performance and social interest.

If imitation is indeed reflecting greater social interest, we might expect that imitators exhibit more frequent or more positive social behaviors, such as play with peers. When we examined nursery-reared macaque infants' (n = 135) first 5-minutes of social interactions, which in our lab occur at approximately 5-6 weeks of age, we did not find any significant effect of imitative skill (unpublished data). This included instances of giving or receiving aggression (e.g., bites, threats), duration of time grooming, playing (e.g., "play face", non-aggressive chasing, tagging, wrestling), and engaging in other social interactions, including being in proximity to others (within arm's reach) and giving or receiving any exploration (oral, pedal, or manual) of another animal. Although the novelty of situation might have diminished or masked the potential impact of early imitative skills, these data are consistent with the proposition that at this early age, imitators and non-imitators are equally interested in social interactions with peers.

Another prediction related to social motivation is that imitators might have better memory for social relative to non-social information. To test this hypothesis, we carried out a test of 40- to 50-day-old infants' (n = 48) working memory for social and nonsocial information, using methods used previously with human infants (Noland et al. 2010). We found no association between infants' imitative skill in the first week of life and their working memory for either social or nonsocial stimuli (unpublished data). Overall, both imitators and non-imitators demonstrated evidence of memory for both social and nonsocial stimuli, suggesting this particular task may be insensitive for detecting individual differences in social memory between these groups, perhaps because it was too easy (i.e., ceiling effect). In other words, neonatal imitative skill does not appear to be related to working memory at this age; however, again, it is difficult to draw any firm conclusions based on this null finding. It is our view that converging evidence employing other measures of social interest and competence is necessary before we can draw more firm conclusions about these associations.

This lack of a difference in performance between imitators and non-imitators, particularly for the social stimulus, may reflect the fact that there is no relation between imitative skill and working memory; however, tests of memory earlier in development do appear to be linked to imitation. For example, newborn macaques who imitate lipsmacking gestures appear to be better at deferred imitation, which is imitation after a delay, requiring infants to remember a gesture that was previously directed at them, and to perform that gesture when seeing a social partner with a neutral expression, suggesting imitators may be more capable or willing to initiate social interactions (Paukner et al. 2011). In addition to perhaps possessing better memory of a previously seen gesture, infants who are imitators also appear to have better memory for the specific person who made the gesture. Specifically, macaque infants' lipsmacking imitation is positively correlated with lipsmacking when a familiar person returns after a brief delay, but not when this person is novel, suggesting that imitators may be better at recognizing social partners (Simpson et al. 2013). Between 10-28 days of age, imitators, compared to non-imitators, exhibit more mature patterns of looking towards faces,

with more looking to eye region (Paukner et al. in press). Imitators are also more visually attentive during neonatal imitation sessions, compared to non-imitators (Simpson et al. 2014b); therefore, increased social motivation may be responsible for their better performance. Nonetheless, these latter findings during the early neonatal period are consistent with the notion that imitative skill is reflective of infants' interest in social interactions within the newborn period. Participating in imitative exchanges may increase infants' social interest, or social interest levels prior to such interactions may predict the degree of neonatal imitation. Studies of infants' early visual attention preferences, such as their relative interest in social and nonsocial stimuli (Pierce et al. 2011), could further test these predictions. Together, our findings thus far seem to suggest that while neonatal imitation predicts social interest and competence within the neonatal period, it does not predict behaviors later in development.

Imitative skill and temperament

Finally, there remains the possibility that differences in neonatal imitative skill are related not to specific social skills, but rather to general differences in behavioral dispositions (first proposed by Field 1982; also proposed by Heimann, 1998). For example, human infants who are highly fearful or withdrawn from their environment may be less likely to engage with stimulating objects or social partners, and thus may be less likely to imitate facial gestures (Peters-Martin & Wachs, 1984). In 13-15-month-old humans, imitation was positively associated with extraversion (Hilbrink, Sakkalou, Ellis-Davies Fowler & Gattis 2013), and imitative skill at 3 weeks was positively associated with activity level at 3 months (Heimann 2001). In addition, such links are particularly interesting given that, compared to typically developing infants, infants at heightened risk of developing autism (due to having a sibling with autism), or who later are diagnosed with autism, demonstrate lower rates of imitation (e.g., Charman et al. 1997) as well as exhibiting temperamental differences (Garon et al. 2009). Specifically, compared to typically developing children, high-risk infants express less positive affect, more negative affect, and exhibit difficulties in controlling their attention and behavior, while infants who later receive an autism diagnosis demonstrate reduced sensitivity to reward cues and higher levels of motor activity (Garon et al. 2009). Although it has been proposed that newborns with more sociable temperaments may be more likely to imitate (Simpson et al. 2014b; Suddendorf et al. 2013), we are unaware of any published studies to date that assessed the association between imitative skill and temperament in newborns. We assessed whether imitative skill in rhesus macaques may be related to temperament with two assessments, the first of which examined infants' sensitivity to novelty, believed to reflect a dimension of temperament, related to approach-avoidance or shyness-boldness (e.g., Clarke & Boinski 1995; Herrmann et al. 2011). We found that on day 7, non-imitators (n = 64), compared to imitators (n = 60), spent a greater amount of time exploring a novel environment (unpublished data). This finding is consistent with those of another study in which 3-month-old macaque infants (n = 32) were presented with a novel object in their home cage for 5 minutes, in which we found that imitators, compared to non-imitators, were slower to touch the novel object (Simpson et al. 2012). Thus is appears that imitators may be more fearful of novel situations and objects than non-imitators, a finding which we did not predict. Alternatively, it is possible that non-imitators may be more interested to objects than social stimuli, and these tests could reveal such preferences.

In order to test more directly whether imitation skill might be related to temperament, we also used a modified version of the Neonatal Behavioral Assessment Scale (Schneider & Suomi, 1992), to assess temperament, sensory, and motor skills from 7-30 days of age in nursery-reared macaque infants (n = 124), comparing imitators (n = 60) and non-imitators (n = 64) (unpublished data). In terms of emotional and self-soothing behaviors, we found that imitators more often self-mouthed (e.g., thumb sucking). There were also differences in infants' comfort-seeking behavior from caregivers. Non-imitators were cuddlier, and were rated as easier to console. Non-imitators exhibited more intense aversion to being on their backs, but also more easily calmed themselves, while imitators exhibited more continued distress. Similarly, in a separate sample of mother-reared infants (n = 33), imitators showed a trend of needing greater intervention to sooth, and exhibited more agitated behavior, compared to non-imitators. Together, these results suggest that there may be differences in temperament between imitators and non-imitators, although not in the direction we predicted, with imitators possibly being more reactive, fussy, and sensitive to novelty. Further studies are clearly needed.

Conclusion

A developmental approach is critical to understanding mirror neurons and debates surrounding their properties, plasticity, function, and evolution. The presence of clear inter-individual differences in early social competencies, such as neonatal imitation, are indicative of the complex nature of the interactions that occur among genetic, epigenetic, and non-genetic (environmental) factors in shaping action-perception brain networks (Ferrari et al. 2013). In the present review, we presented evidence suggesting an association between neonatal imitative skill and various other individual differences, including sensory-motor matching skill, social skill and motivation, and temperament. While these factors are unlikely to be the only contributors to variability in neonatal imitation[1], we suspect that they each contribute to this variation. How these processes differentially contribute across development, whether there exist sensitive periods, and the extent to which such skills are plastic, however, are questions that must be addressed in future work. Nonetheless, neonatal imitation is a useful tool for assessing infants' sensory-motor matching maturity, social motivation, and temperament, but should only be utilized with a mindfulness of infants' changing social motivations and expectations.

Footnote

1. There are, of course, other factors that might contribute to variability in neonatal imitation. For example, there may be genetically determined predispositions for neonatal imitation, which may be heritable. We are currently testing this in macaques by following individuals longitudinally to see whether imitators are more likely to have their own infants who are imitators (particularly, when infants are nursery-reared, to control for environmental effects).

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Figures

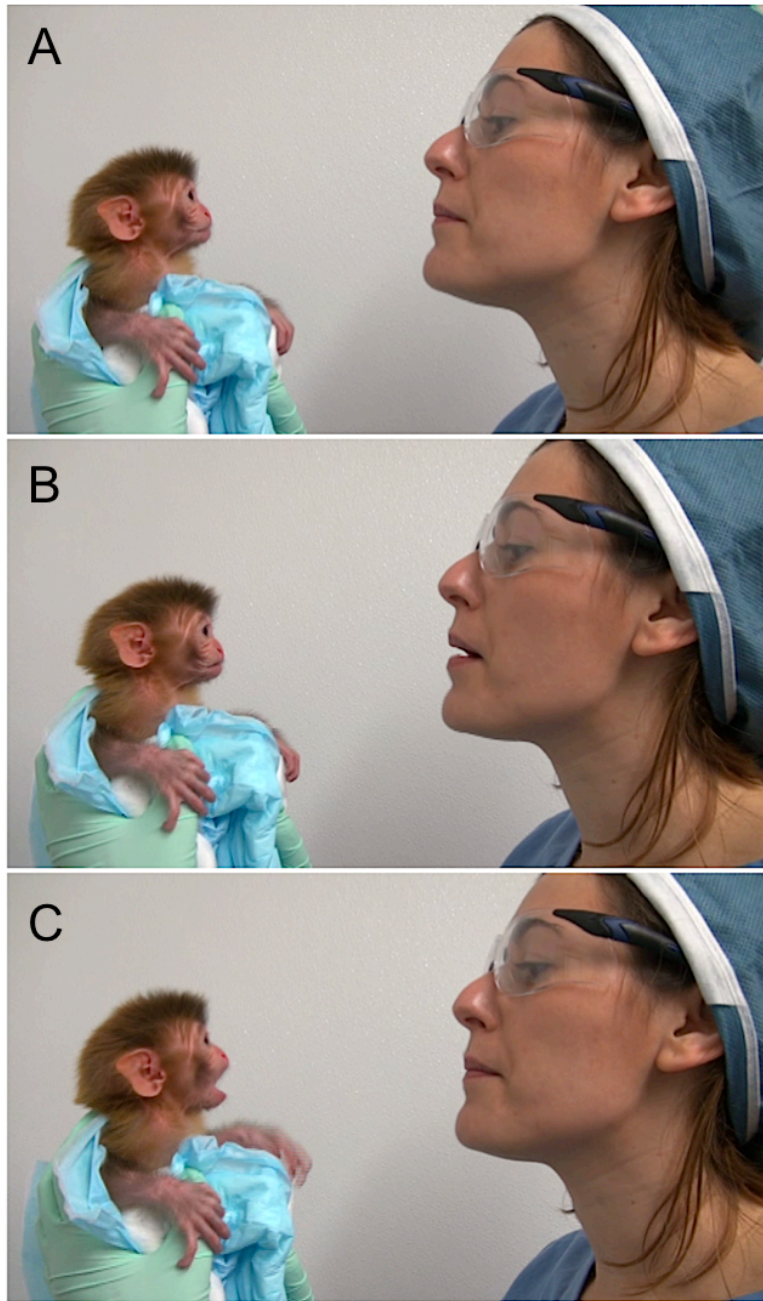Figure 1. Example of nursery-reared infant engaging in neonatal imitation.

Figure 1. A 3-day-old nursery-reared infant macaque watches a human model perform lipsmacking gestures (A, B); she then imitates lipsmacking gesturing (C).

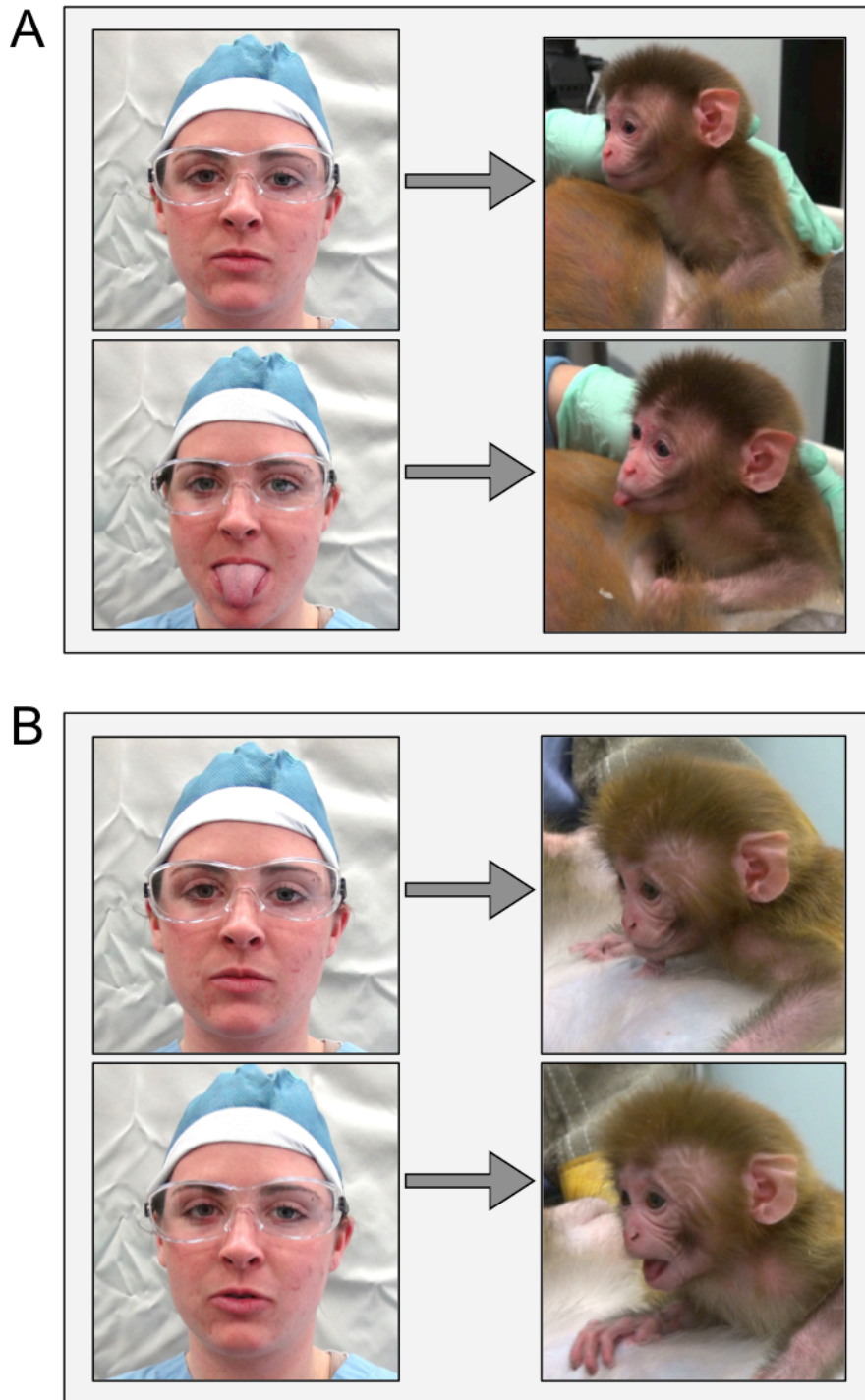Figure 2. Three-day-old mother-reared macaque infant imitation.

Figure 2. Models producing still-faces and facial gestures (left) and 3-day-old mother-reared macaque infants' facial gesture responses (right). Gestures imitated included tongue protrusion (A) and lipsmacking (B). Infants are tested while clinging to their mothers.

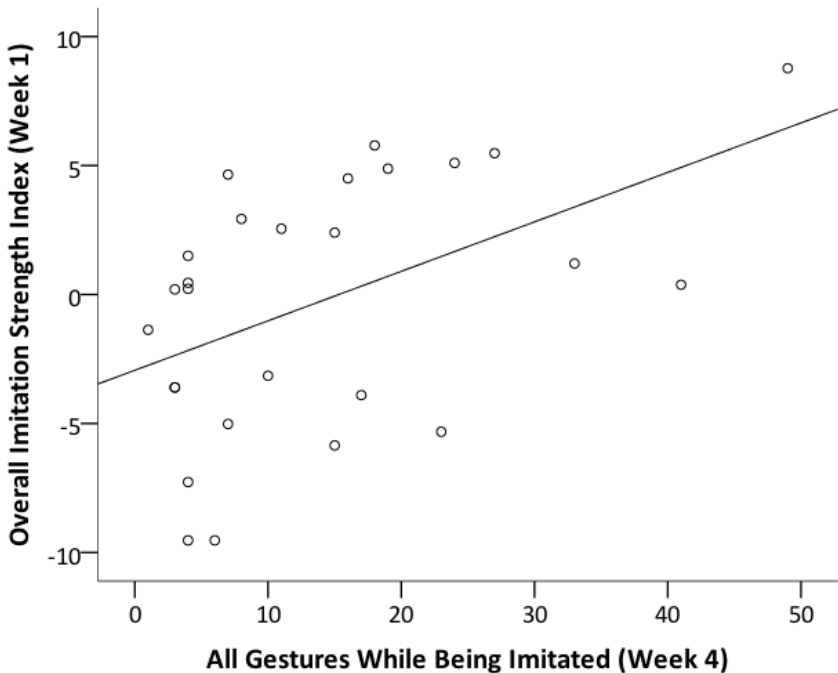Figure 3. Neonatal imitation predicted sensitivity to being imitated.

Figure 3. Infants' facial gesture neonatal imitation in the first week of life (days 1-8) predicted their facial gestures while they were being imitated in the fourth week of life (days 21-28), $r = .482$, $p = .011$.

Figure 4. Consistent responding in unstructured and structured neonatal imitation assessments.
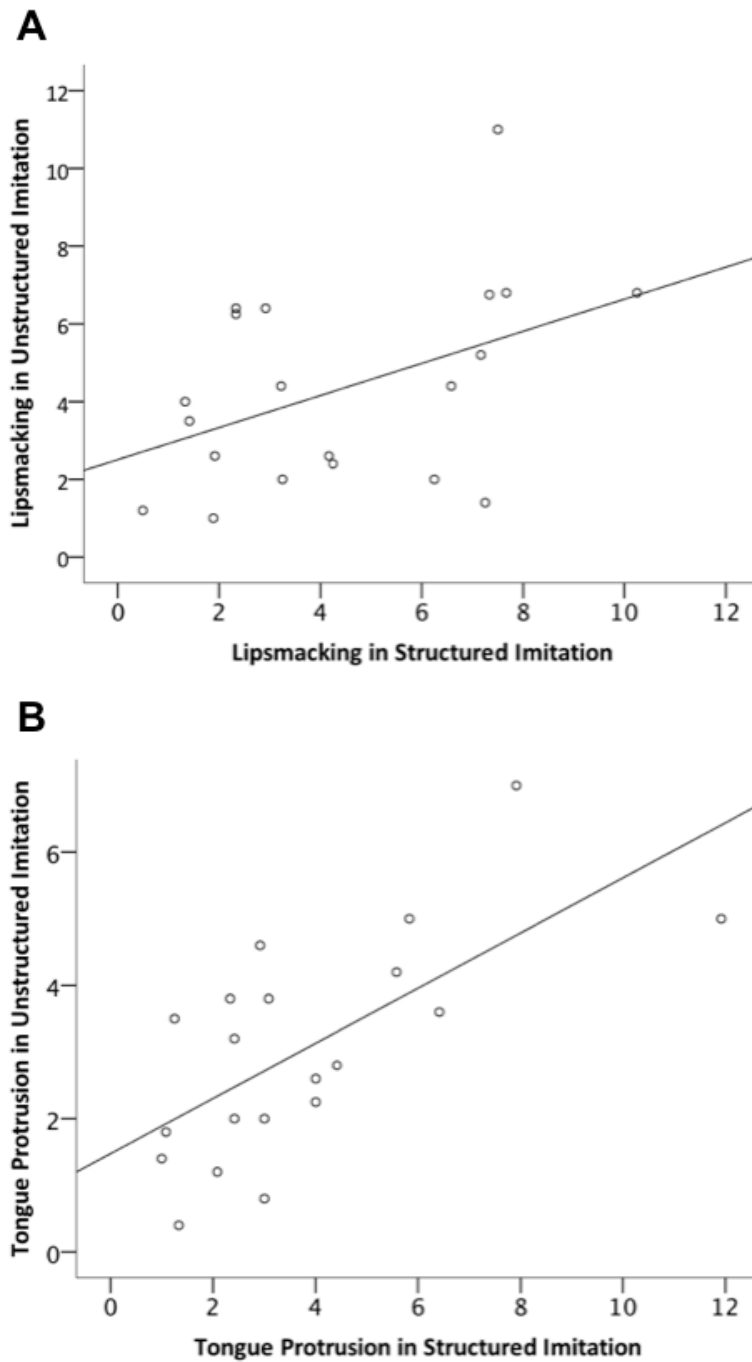
A

B

Figure 4. Facial gesturing was positively correlated in the unstructured and structured neonatal imitation tests for (A) lipsmacking in the lipsmacking condition, $r = .44$, $p = .050$, and (B) tongue protrusion in the tongue protrusion condition, $r = .67$, $p = .001$