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Accepted Version

Simpson, E. A., Murray, L., Paukner, A. and Ferrari, P. F. (2014) The mirror neuron system as revealed through neonatal imitation: presence from birth, predictive power, and evidence of plasticity. Philsophical Transactions of the Royal Society B, 369 (1644). pp. 1471-2970. ISSN 1471-2970 doi: https://doi.org/10.1098/rstb.2013.0289 Available at http://centaur.reading.ac.uk/36545/

The mirror neuron system as revealed through neonatal imitation: Presence from birth, predictive power, and evidence of plasticity

Elizabeth A. Simpson
Department of Neuroscience, University of Parma, Italy

Lynne Murray
School of Psychology and Clinical Language Sciences, University of Reading, UK, and
Department of Psychology, Stellenbosch University, South Africa

Annika Paukner
Eunice Kennedy Shriver National Institute of Child Health and Human Development,
Poolesville, Maryland, USA

Pier F. Ferrari
Department of Neuroscience, University of Parma, Italy

Author note
Corresponding author: Elizabeth A. Simpson, email: simpsonea@mail.nih.gov.

Abstract

There is strong evidence that neonates imitate previously unseen behaviors. These behaviors are predominantly used in social interactions, demonstrating neonates' ability and motivation to engage with others. Research on neonatal imitation can provide a wealth of information about the early mirror neuron system (MNS): namely, its functional characteristics, its plasticity from birth, and its relation to skills later in development. Though numerous studies document the existence of neonatal imitation in the laboratory, little is known about its natural occurrence during parent-infant interactions and its plasticity as a consequence of experience. We review these critical aspects of imitation, which we argue are necessary for understanding the early action-perception system. We address common criticisms and misunderstandings about neonatal imitation and discuss methodological differences among studies. Recent work reveals that individual differences in neonatal imitation positively correlate with later social, cognitive, and motor development. We propose that such variation in neonatal imitation could reflect important individual differences of the MNS. Although postnatal experience is not necessary for imitation, we present evidence that neonatal imitation is influenced by experience in the first week of life.

Keywords: neonatal imitation, newborn, social development, mother-infant interaction, mu suppression, sensorimotor

Introduction

In the last few decades, human and nonhuman primate research has brought great insights to our understanding of the brain mechanisms that connect action and perception, and such work has begun to illuminate the nature of how these mechanisms support important cognitive processes and behaviors [1-2]. In particular, parietal-frontal circuits support several functions, such as space and object coding, action recognition, and imitation [3-5]. Neurophysiological experiments on mirror neurons in monkeys demonstrate that even at the single cell level, sensory information is processed and translated into a motor format, thus facilitating the coupling between sensory and motor codes. Such studies have contributed to our understanding of how social interactions depend on mirroring mechanisms embedded in parietal-premotor circuits. According to the mirror neuron hypothesis, observed actions are understood in terms of one's own action programs. This action-perception system allows individuals to understand others' actions as if they were performing those same actions themselves. (It is necessarily the case that, in order for an individual to be capable of reproducing (imitating) an action, that action must be in the individual's motor repertoire.) In fact, several brain imaging experiments in human adults have revealed that the mirror neuron system (MNS) is activated during the observation and imitation of simple and complex actions [6-8].

These issues have also been explored in infant development using less invasive techniques, such as electroencephalography (EEG). EEG studies reveal that during the execution and observation of actions, specific frequency bands within the alpha range (9-13 Hz in the adult and 5-9Hz in infants) desynchronize in newborns [9-12] and older infants [13-15]. 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) [16] and thus may be considered a marker for mirror neuron activity.

One research arena that is particularly well suited for investigating fundamental characteristics of the mirror mechanism is that of early imitation. Recent work has addressed this issue in an EEG study of newborn macaques [17]. This study revealed that the mu rhythm desynchronizes during the observation and imitation of facial gestures such as lipsmacking (LPS), an important communicative gesture in macaques. The mirror neuron mechanism, therefore, may be the basis for human and nonhuman primate infants' capacities to respond appropriately to their mothers and to tune their own behavior with that of their mothers' through elaborate face-to-face communicative signals and matching behaviors. Indeed, infants recognize and respond to social signals from birth, and are born with the ability to engage in social interactions. Newborns' early imitative capacities, insofar as they indicate a functioning mirror neuron system, can be informative about the early development of this system, including its innateness, plasticity, and individual differences.

In the present paper we assess the current understanding of early sensorimotor development in human and nonhuman primate infants, focusing on the evidence for an action-perception and mirroring mechanism operating at birth [17,18-20], instantiated in neonatal imitation. Neonatal imitation refers to the ability of infants to match others' actions in the first four weeks of life. We argue that complementary behavioral and neural studies are necessary for understanding the early functioning and developmental changes of the MNS. In the current review we examine the evidence for the phenomenon of neonatal imitation, in both experimental and natural contexts, addressing common criticisms, and proposing best practice procedures for eliciting imitation in the laboratory. We examine whether early individual differences in experience (e.g., culture) influence infants' imitation and whether individual differences in imitation are related to later developmental outcomes.

Historical and recent observations of neonatal imitation

Human infant imitation has been studied for almost a century [21-23]. Early reports were primarily anecdotal or uncontrolled observations [22,24-25]. Maratos found that 1-month-olds imitated tongue protrusion (TP), mouth opening (MO), and head shaking [26-27]. Imitation in newborns was subsequently confirmed by Meltzoff and Moore [28-29], in their seminal, well-controlled experiments, and thereafter found in infants as young as 45 minutes after birth [29-30]. Importantly, Meltzoff and colleagues demonstrated that infants could identify the particular body part producing the modeled action, as well as the particular action pattern of that body part [28,31-32]. In addition to facial imitation, neonates only 3- to 96-hours old also appear to imitate finger movements (e.g., [33], [34]). These studies, and others (Table 1), provide strong evidence that neonatal imitation is present from birth. This evidence suggests newborns are capable of perceptual-motor coordination and cross-modal matching (i.e., matching the visual perception of the model with the proprioceptive experience of performing the action themselves), as well as demonstrating that newborns already possess complex social and cognitive skills.

Neonatal imitation has also been observed in nonhuman primates, including chimpanzees [52,55], and rhesus macaques [18]. In fact, the phenomenon appears very similar in humans and macaques [56]. In both species, neonatal imitation of facial gestures is elicited in the laboratory most easily in the first few weeks after birth (compared to later in development) and mothers imitate facial gestures of infants more than infants imitate mothers. Additionally, in both species there are large individual differences in imitative skills; that is, some infants consistently imitate while others do not, which may be a reflection of infants' social predispositions (e.g., [57-59]). Though not yet tested in humans, recent work demonstrates that macaque newborns recognize when others imitate them [60], suggesting action observation and execution are intricately linked.

Laboratory-based experimental investigations are, of course, limited in their ecological validity, as they only show what infants are capable of imitating in a somewhat artificial environment. Experimental control of the model (e.g., producing a passive face, gesturing on a fixed schedule, displaying more than one action to be imitated) may reduce imitation rates, creating situations rather different from natural face-to-face caregiver-infant interactions [52,61]. After all, imitation is both a cognitive and a social phenomenon [27], so not exhibiting socially appropriate behaviors may decrease infants' motivation to engage. Complementary approaches include observing infants in less structured neonatal imitation paradigms (e.g., allowing models to adjust the timing or type of response as a function of infants' responses [52,61]), and observing infants in natural interaction settings, such as mother-infant face-to-face play. The latter in particular can shed light on what infants actually do during typical social interactions with caregivers (e.g., [62-65]), and reveals the types of behaviors infants naturally imitate, how often they do so, and how parents contribute to this skill.

Human mothers engage in complex, emotional, two-way face-to-face exchanges with their newborns, including mutual gaze and body contact (e.g., hand-body contact, kisses), and exaggerated maternal facial and vocal expressions [63,65-66]. There is a fundamental motivation on the part of both the parents and newborns to be in social engagement with each other, reflected in their preferential responses to faces and eye contact [67-73]. Even neonates show myriad facial expressions and gestures when in face-to-face contact. These include different facial expressions of emotion, lip and tongue movements, and active shaping of the mouth, which are unconnected to clearly internal 'biological' events (e.g., digestion; [74]). This expressiveness provides a rich corpus of behaviors that helps adults understand the nature of infant needs and experience. Mothers are sensitive to neonates' rare moments of alertness, and although such times are infrequent (15-20% of time observed), mothers choose them to socially engage with infants, otherwise providing relatively little social stimulation [75]. Human mothers initiate active engagements with clear 'greeting' and 'marking' behaviors, and also imitate infants' expressions, including vocal and facial expressions, immediately after birth and in the first months of life (e.g., [76-78]). Similar mother-infant interactions also occur in rhesus macaques [79] and gelada baboons [80]. For example, macaque mothers direct lipsmacking (LPS)—an affiliative facial gesture—at their infants, often in an exaggerated fashion (similar to human motherese), and while doing so mothers place themselves directly in front of the infant, often lowering themselves to infants' eye-level and engaging in bouts of head bobbing [79].

It is interesting to note, however, that very few reports have investigated the natural occurrence of neonatal imitation [81-83]. From these few studies it seems that human neonates themselves only rarely spontaneously imitate during interactions with parents. This observation is not surprising considering that newborns spend most of their time sleeping and, when awake, face-to-face interaction episodes are brief. We should also consider that, during interpersonal exchanges, imitation represents only one of many ways newborns can express themselves (e.g., [74]). Thus, it is not imitation by the neonate *per se* that is critical for communication and social understanding, but a more fundamental capacity that infants' occasional imitation reveals: that is, the capacity to connect one's own and another's actions and experience [83].

Why some laboratories have not found neonatal imitation at the population level

Neonatal imitation is a difficult behavior to observe in the laboratory, as evidenced by some inconsistent findings (e.g., [84-86]); consequently, the phenomenon is not unanimously accepted. Experimental tests of neonatal imitation in humans have used a variety of procedures, modeled actions, inclusion criteria, and operational definitions of imitation (see reviews [32,43,87-88]) and, it is not, therefore, surprising that results have varied across studies. Although methodological differences may account for different results [51], there has been only one previous systematic report, to our knowledge, comparing successful and unsuccessful methods, specifically focused on TP imitation [43]. Numerous factors influence imitation, including the position of the infant [43], the length of response period [29], and infants' age [43]. Out of 29 published studies of imitation in the first month of life (Table 1), 7 failed to find evidence of imitation (from 5 laboratories), and 21 found evidence of imitation (from 11 laboratories). It is instructive to consider the differences between studies that found evidence of imitation and those that did not.

One common feature of several studies reporting null results for facial gesture imitation is that infants were prevented from gesturing concurrently with the adult model through the use of a pacifier [46,48]. Pacifiers were used to block infants' immediate facial mimicry to test delayed imitation [28], to rule out perceptual-motor resonance as an explanation for imitation [89-90], or to prevent the model from unintentionally imitating the infant [28,49]. In fact, concurrent interaction synchrony plays an important role in early parent-infant interactions (e.g., [91]), and infants who do not experience these synchronous interactions—such as when prevented with pacifiers—may be less likely to match facial gestures during still face (i.e., response) periods. Actual imitation rates may also be underestimated due to a related issue: that is, in some studies, researchers did not measure infants' gestures produced during the gesture/dynamic stimulus period (e.g., [49]). We think this omission may have limited infant opportunities for imitation, given that much of infants' matching behavior may occur during this dynamic period.

A second feature common among studies reporting null results is a low statistical power resulting from small sample sizes (average number of usable participants: 12; range: 6-16 participants), relative to those reporting positive results (average number of usable participants: 43; range 6-121 participants), a point highlighted by others (e.g., [29,43]). Of those studies with sample sizes larger than 26 infants (determined to be a necessary sample size, based on an *a priori* power analysis, reported below), the vast majority found positive results, while studies including 26 or fewer infants contribute the most to the "failures to replicate," illustrated in Figure 1. Thus, among the studies reported in Table 1, over 85% of the behaviors examined in those with large sample sizes (*n*s ≥ 26) revealed positive results (i.e., evidence of neonatal imitation), while in studies with smaller sample sizes (*n*s < 26), 69% of behaviors tested failed to show any evidence of imitation. This result may explain why previous reviews, which did not consider sample size as a factor contributing to the reliability of a study's findings' (e.g., see Table 1 in [87]; see Figure 2 in [92]; see Table 1 in [93]), have drawn different conclusions concerning the phenomenon of neonatal imitation. Below we discuss effect sizes found in neonatal imitation studies and suggest the sample sizes necessary to detect those effects.

Core questions and misunderstandings about neonatal imitation

Is neonatal imitation a reflex? It has been suggested that neonatal imitation is not actually imitation, but instead may be an automatic and involuntary reflex-like phenomenon, driven by subcortical mechanisms, a fixed action pattern, or an innate releasing mechanism (e.g., [39,46,48,50,94-95]). According to this view, matching should occur for only a few evolutionarily privileged gestures, that is, gestures that are, putatively, fixed and stereotypic, and produce a matching response that is time-locked to the modeled "trigger" action [96]. This prediction, however, has been tested and has not been supported: infants produce a range of gestures which are not stereotyped, actions which have never been seen before are matched, corrections are made to initial attempts, and responses are not time-locked to modeled actions [31-32,40]. In addition, infants produce gestures without prompt after a delay, suggesting they are initiating social interaction rather than simply copying actions [97]. In humans, so-called deferred imitation is present (after a 24- hour delay) from at least 6 weeks of life [31,98], and in some macaque infants it is present (after a 60 sec delay) in the first week of life [53], which indicates that these gestures are communicative and under voluntary control rather than reflexive fixed action patterns.

Is neonatal imitation due to arousal? Infants might be aroused when they view facial gestures and consequently increase their activity (e.g., produce more facial gestures themselves [99-100]). However, even if this point is accepted, infants' capacity to match specific gestures goes beyond this general arousal response, reflecting additional neurophysiological and cognitive mechanisms. Numerous neonatal imitation tests have measured infants' imitation of more than one action, and in these cases, arousal alone cannot account for infants' imitation of specific actions [28,40]. Nagy and colleagues [43] also recently performed a thorough review of neonatal imitation of TP gestures (the gesture most commonly assumed to be produced by arousal) by assessing the specificity of the imitative response and measuring infants' states [101] as well as other indicators of arousal, and concluded that TP imitation is not simply an arousal effect. In addition, newborns' heart rates accelerate when imitating gestures and decelerate when performing unprompted gestures [97], suggesting that different mechanisms underlie imitative and exploratory spontaneous behaviors.

Does imitation decline after the first month of life? Given reports that imitation appears strong in the first month of life, but then declines in the following months (e.g., [27,49] [35,44,94]), it has been suggested that early imitation may be a phenomenon quite distinct from imitation occurring later (e.g., [58]). Neonatal imitation has been proposed to be a "transient ontogenetic adaptation," important for survival in early infancy but then disappearing when no longer necessary [102, p.89]. While it is true that the form and characteristics of imitation undergo changes throughout infancy, this particular characterization is misleading. Instead, careful testing has revealed that imitation does not decline after the first month of life, but depends on the type of action being presented. For example, facial imitation (e.g., tongue protrusion, mouth opening, emotional facial expressions) largely disappears by 3 months of age [49,94-95,103], whereas other actions (e.g., sounds, vocalizations, hand and finger movements) increase in frequency and accuracy [104-105], in line with the infants' wider development (e.g., improvements in vision at a distance and manipulation skills). Interestingly, behaviors reliably imitated earlier in development can also be elicited later on if the social context is altered, for example, if presented in the context of games or playful interactions, or if the actions form part of a sequence requiring novel combinations [106]. Apparent declines in imitation in the laboratory setting may be due, therefore, to these wider changes in infants' expectations and motivations during social interactions [98,107].

Does neonatal imitation depend on learning? Infants may learn to associate their own movements with those of others, and thus acquire the capacity to imitate through a process of associative learning (e.g., [87,108]). While experience, including associative processes, undoubtedly plays a role in developing the corpus of behaviors that infants imitate (see below in sections on plasticity and cultural differences), an associative learning account of the fundamental capacity to imitate is incompatible with the evidence on two fronts. First, only minutes to hours after birth, human infants imitate opening and closing of eyes [30,35], head movements [40], the /a/ sound [30,35], index finger protrusion [33,34], facial gestures (e.g., mouth opening, tongue protrusion; [29,40]), and emotional facial expressions (e.g., happiness, sadness, surprise [38]) prior to having opportunities to form strong associative links between action observation and imitative responses. Similarly, macaque infants reared in a nursery from birth imitate before they have experienced any contingent facial interactions with caregivers [18,53,109], and they additionally show specific electroencephalogram changes (i.e., mu suppression), evidence of a functioning MNS, on the day of birth [17,110]. These results fail to support an associative learning account of neonatal imitation [111-112].

Even setting aside such evidence, the associative learning account is problematic on a second front, since, for the proposed learned associations to be forged it would require the neonate to experience high levels of contingent responses from social partners that are almost exclusively imitative. In fact, while parents do indeed provide imitative feedback during social interactions with their infants, the rate is typically quite low (e.g., 1 per 2-3 minutes ([62]) and, moreover, such feedback occurs in the context of a wealth of parental behaviors that are non-imitative (e.g., affirmative marking, or even negating of infant expressions [113]). On a rigorous calculation of contingency [114], parents' imitative responses are, therefore, relatively non-salient for the infant. According to the associative learning account, this situation then leaves infants with the challenge of identifying which particular adult gestures or expressions among this plethora match their own, a task that may be cognitively equivalent to that of the production of imitative acts themselves. In short, an associative learning account does not so much solve the problem of imitation, as raise a set of further questions concerning the basis of infant capacities for identifying the equivalence between their own and others' actions.

Methodological differences across neonatal imitation studies

Standardizing the methodology for neonatal imitation tests would allow experimenters to more easily compare imitation across groups (e.g., species, cultures, special populations). We therefore propose a set of "best practices" for testing neonatal imitation, which serves to facilitate the elicitation of the phenomenon.

1. Sensitivity to infants' states. Sensitivity to infants' states is critical for maximizing the likelihood of neonatal imitation. Ideally, the test room should be quiet with few distractions (such as sounds or bright visual displays). Very young newborns or infants waking after sleeping may need time to adjust to the lighting of the room. Infants should be adequately fed and relatively awake before testing commences. In addition, infants should be seated or laying, and may need to be adjusted to maximize their comfort [30]. Infants should be attentive (i.e., looking at the model) for at least part of the time the model is performing the gestures. Infants who insist on sucking their thumbs may be excluded when facial gestures are modeled, or, ideally, thumb sucking could be coded and included in the analysis to determine whether it confounds or moderates imitation. If the attention criterion is not met, infants should be excluded from data analysis, although, obviously, the number of infants and reason for exclusion should be clearly reported.

2. Appropriately modeled actions. For standardization purposes, models should be unfamiliar to the infant (unless specific effects of the mother or caretaker are being investigated; e.g., [51,61,115]) and should avoid interacting with the infant before testing [29]. Models should be positioned at an appropriate distance, taking into account newborns' reduced visual acuity, and should make continuous eye contact with infants for the duration of the test. Nonverbal cues such as eye contact set up an expectation of a social exchange, and may direct infants' attention towards the adults' modeled actions [116]. There is disagreement about what constitutes adequate speed, rhythm, and repetition of action presentation, so these aspects should be clearly documented. One critical aspect of the procedure is the length of time the gesture is modeled. In a review of TP studies, modeling the gesture for 60 sec or longer resulted in evidence of imitation in all reported studies, whereas modeling the gesture for 40 sec or less resulted in only 31% of studies finding evidence of imitation [84]. Therefore, we recommend a minimum of 60 sec of presenting modeled gestures. Modeled behaviors should be age-appropriate, prominent in the infant's expressive repertoire, and structured at a predetermined frequency and speed so all infants view the same actions. We also recommend modeling actions in a "burst-pause" procedure, whereby the model alternates between static and dynamic periods, as this procedure—compared to modeling only dynamic actions—results in higher frequencies of imitation [29].

3. Time frame for recording responses. At times, infants will imitate quickly [39], or even concurrently with the models' actions [117], and these instances of imitation should be recorded as such. On other occasions, imitation may be delayed, and thus, after the modeled actions, the model should be still and wait for a predetermined period, allowing the infant to produce or finish producing a response. A microanalysis of infants' imitation revealed that infants can take some time before they start to respond (e.g., 20-60 seconds [45]), and they may gradually refine and correct their responses (e.g., during a 2-and-a-half minute response period

[31]), so sufficient time must be provided for infants to initiate, refine, and complete their response. In addition, it is important that the length of this response period be predetermined and not based on infants' behaviors (e.g., [35]), as this may introduce a bias for gestures produced spontaneously [48].

4. More than one action to show specificity of response. More than one behavior should be presented in order to show that the imitative response is not due to an infant's preference for a certain action (e.g., facial gesture) or a more general response to a moving social stimulus, and to decrease the probability of false positives. The frequency of matched actions produced in the matching action condition should be higher than those in the non-matching (i.e., social control) action condition. For example, the frequency of infants' TP when TP is modeled should be higher than the frequency of infants' TP when MO is modeled, and *vice versa* [28]. Because some studies have suggested that infants may associate specific individuals with specific facial gestures [31], ideally, each action should be modeled by a different individual, and each action's test session should be separated by a break period in order to avoid carry-over effects across sessions.

5. Testing for individual differences. For certain purposes it may be useful to categorize infants based on whether or not they consistently and successfully imitate. In such cases, the definition of imitator should include consideration of imitation across test sessions. Ideally, infants should be tested multiple times within the same day (in different test sessions to avoid carry-over effects) or across days with the same gestures; infants should consistently imitate (i.e., imitate in the majority of sessions) to be defined as imitators.

6. Sufficient power. We calculated effect sizes for neonatal imitation studies that have given sufficient detail necessary for such calculations [29-30,35-36,40,41-42,51], and found that among those actions analyzed with parametric tests (10 actions), Cohen's d ranged from .34 (small) to .58 (medium), with a median of .40, and for studies that used non-parametric tests for analysis (9 actions), effect sizes (r) ranged from .37 (medium) to 3.75 (large), with a median of .64 (large). Using the most conservative estimate of effect size ($d = .34$), we carried out an *a priori* power analysis to determine the sample size necessary for power = .80 ($f = .40$; $\alpha = .05$) to detect this effect and determined a sample size of 26 is needed [118]. Thus, like any study with infants, a relatively large sample is required to allow for small to medium effect sizes and potentially high dropout rates. Although it may be unnecessary for infants to complete all trials to be included, we think, at the very least, the number or proportion of unusable trials should be reported, along with reasons for excluding trials.

7. Optional additional control conditions (static nonsocial baseline period and nonsocial comparison). Infants' actions produced after seeing the modeled gestures can additionally be compared to both a no-stimulation or static social baseline period (e.g., still face) and a nonsocial static and dynamic control condition (e.g., disk with both still and rotating periods), to guard against the possibility that the action in question may happen by chance or as a result of non-specific arousal. The nonsocial control stimulus should be matched to the social stimulus in its static and dynamic nature. To be classified as imitation, the model behavior should increase in frequency relative to the baseline level, and should be more frequent in the test condition than in the nonsocial control condition. For example, in one study with 5- to 8-week-old infants, TP and MO gestures were produced only when a social model (human face) produced the gestures, but not when inanimate objects produced similar movement patterns [119]. It is worth noting that the vast majority of studies fail to include this condition. Although its inclusion is not a necessary requirement for demonstrating neonatal imitation, it can increase the sensitivity of the test by allowing a subtraction of baseline rates across a more diverse collection of control conditions. This can be particularly useful for studies examining individual differences in imitative skills, as it offers a more sensitive test of imitation-specific action reproduction.

Neonatal imitation as a predictor of later developmental outcomes

A number of possibilities have been suggested for why some neonates imitate and others do not. Variability in recorded imitative performance may be due to error variance, methodological differences (as we described), or, perhaps most intriguingly, it may reflect genuine individual differences among infants. As we explain below, we think it may be useful to consider the extent to which these individual differences predict, or are related to, other behavioral outcomes. In particular, if some infants imitate because they possess a more responsive facial MNS, then other abilities that also rely on mirror neuron circuits (e.g., reaching-grasping, understanding goal-directed actions, emotion recognition) may be systematically related to early imitation. Indeed, many researchers argue that it is important to examine whether neonatal imitation is predictive of later social and cognitive development [44-45,58,104,120-121] because it could be an early marker of later deficits in social skills [57]. Previous studies suggest that in both humans and macaque monkeys, only about 50% of neonates consistently engage in imitation of facial gestures [53-54,122]. Only one study has examined neonatal imitation predictively in human infants: imitation at three ages—2-3 days, 3 weeks, and 3 months of age—predicts visual attention at 3 months of age. In particular, neonatal imitators had fewer looks away during a face-to-face interaction at 3 months of age compared to non-imitators [44-45]. In another recent study, female infants were found to imitate finger movements more than male infants [34], consistent with adult studies that demonstrate females have greater mu suppression when viewing actions (e.g., [123-124]).

Though correlational evidence should clearly be interpreted with caution, we have evidence that neonatal imitation skills in macaques are related to behaviors both within and outside of the neonatal imitation task. During neonatal imitation, macaque LPS imitators show increased visual attention to the faces of human social partners [109], are better at recognizing human social partners [59], and are better at remembering gestures and initiating social interactions after a delay (i.e., deferred imitation [53]). We also found that individual differences in neonatal imitation in macaques are positively correlated with later motor and social development. Specifically, infants who consistently imitate in the first week of life, compared to those who do not, show superior reaching-grasping abilities [54] and greater visual attention to the eyes between 10-28 days of age [57], suggesting links between neonatal imitation, intentional movements, and general social attention capacities. In contrast, other individual characteristics of nursery macaques do not appear to be related to imitative skills, including infants' body weight, gross motor maturity (e.g., muscle tone, response speed), the capacity to attend to visual stimuli, or emotionality [54]. Together, these lines of evidence suggest that imitators may be advantaged in their voluntary motor and social-cognitive skills, compared to their non-imitative peers.

With regard to the wider implications of individual differences in imitation, although much can be learned from studying typically developing populations, as described above, the study of neonatal imitation in special populations may be particularly informative, especially in those with conditions associated with social deficits. For example, studies with human children have shown that imitation is impaired in children with autism spectrum disorders (ASD), including oral-facial imitation [125-126] as well as immediate and deferred imitation of a variety of other actions [127-128]. We know of no work that has examined infants at high-risk for social deficits, such as siblings of children with ASD (who are therefore at higher risk for developing ASD), to see if they exhibit neonatal imitation at the same levels as low-risk infants, or if failure to show neonatal imitation is associated with higher risk of a future diagnosis of ASD. We think that such high-risk infants, including siblings of children with an ASD diagnosis, would be particularly useful to study in this context because it has been suggested that MNS dysfunction may be implicated in ASD [129], and information about the developmental emergence of this disorder could provide valuable insights. Notably, there is some work that suggests that these high-risk infants display lower levels of coherence in measures of mother-infant synchrony compared to low-risk infants at 4 months of age [130], which may be indicative of decreased social sensitivity and responsiveness at an early age prior to a clinical diagnosis.

Plasticity of neonatal imitation

Even though postnatal experience is not necessary for facial gesture imitation, neonatal imitation may nonetheless be influenced by experiences in the first weeks of life. Here we describe studies that provide evidence of environmental influences on neonatal imitation, with nursery-reared and mother-reared newborn macaques, and discuss how, in humans, unique cultural influences may influence the types and frequencies of imitation.

To determine the influence of early face-to-face interactions on imitation, we randomly assigned nursery-reared macaque newborns to either receive exposure to facial gestures ($n = 12$), extra handling ($n = 12$), or standard rearing ($n = 15$). The exposure to facial gestures consisted of human caregivers engaging in face-to-face communicative exchanges using LPS gestures directed at infants in 5-min-long sessions, four times a day, starting from the first day of life. In each session, a human caregiver directed LPS gestures at the infant for 5 sec, followed by 10 sec of eye contact, then a 15 sec break period. This sequence was repeated 10 times in the 5-min session. Infants in the extra-handling group were held at the same times and for the same durations as the exposure group, but did not receive the face-to-face interactions (caretakers' faces were covered so infants could not see them). Infants in the standard rearing group did not see facial gestures and did not receive any handling beyond basic care and other (non-related) experimental procedures. On day 7 or 8 infants were tested for neonatal imitation with two gestures—lipsmacking (LPS) and tongue protrusion (TP)—that were compared to a nonsocial control condition, a rotating disk with orthogonal stripes (for methodological details, see [53-54]). We found that only infants who were exposed to facial gestures showed increased LPS in the LPS condition (baseline: $M = 2.00$, $SD = 2.41$; stimulus: $M = 9.83$, $SD = 8.09$), $t(11) = 4.03$, $p = .002$, but not in the other two conditions (TP or Control disk), ps > .05, which suggests that early social experience—such as being held, mutual gaze, and/or early communicative exchanges—may improve imitation. In addition, our results with macaques are consistent with a number of findings in human infants concerning the role of experience. For example, infants improve their matching precision across days [29,31] and across trials [33,131], and human infants exposed to TP every day from 6 to 14 weeks of life show stronger TP imitation at 14 weeks [95]. Though speculative, we think evidence of plasticity in neonatal imitation, as documented here, suggests plasticity of action-perception mechanisms, likely mediated by the mirror neuron system. Further tests employing measures of mu rhythm as a function of experiences in the first weeks of life are necessary to more directly measure changes in the mirror neuron system.

In addition to controlled manipulations of infants' early experiences, some work has examined imitation in relation to the cultural variability in newborns' environments. Despite the universality of key features of parent-infant interactions, there is also notable variation in the extent and manner of parental responsiveness to infant behaviors. This variation is particularly apparent when comparing cultures that differ in the conditions and value systems accompanying child care [132]. Some, like the U.S. and many North European countries, place great value on infant individuation and independence; and parents tend to use high levels of facial and vocal expressiveness to respond to, as well as imitate, infant signals in face-to-face play. In turn, this style of responsiveness predicts earlier emergence of infant self-awareness (i.e., mirror recognition) [133]. Others cultures (e.g., Japanese, and certain rural African societies) place more value on infant affiliation and compliance, and on sharing and cohesiveness within the society. These parents, although similarly responsive to their infants, pick up on different infant cues, and are more likely to use close physical contact to respond to their infants (e.g., kissing, or rhythmical patting), and parents show far less vocal and facial imitation [134-135]. Correspondingly, infant behavior during interactions in these diverse cultures develops in different ways. Thus, a study comparing Nso mothers and infants (a rural society in the Cameroon) with those in Germany found most German infants to increasingly imitate maternal smiles during face-to-face interactions over the first three months, a pattern that did not occur in Nso infants [135]. Such findings indicate that, based on infants' fundamental capacities to identify correspondences between their own and others' actions, particular forms of infant expressive behaviors emerge in the development of different cultural styles of social communication. We believe that cross-cultural examination of neonatal imitation and its developmental consequences would be a particularly fruitful direction for future research.

Conclusion

We believe the study of neonatal behavior and its plasticity are critical for understanding the developmental emergence of the MNS, and the development of action-perception more generally. Despite some reviews that conclude that neonatal imitation is not a genuine phenomenon (e.g., [87,100, 108]), when full account is taken of procedural factors and considerations of statistical power, the evidence that imitation is present from birth is compelling.

The formation of an action-perception mechanism has been debated in the recent literature and, some scholars propose that it is unlikely that a rudimentary mechanism that matches observed facial gestures with the internal motor representation could be operative from birth. Instead, it is proposed that general sensorimotor connections link temporal regions that visually code for others' actions with parietal regions that are involved in executing actions. Further, in this account, these connections are refined through Hebbian learning processes, and become tuned so that visual and motor information become matched in the course of development [92]. The evidence on neonatal imitation reviewed here, however, does not support this proposal, as it clearly shows that, prior to any experience, there is a link between seeing facial gestures and the motor programs activating the same motor representations. Nevertheless, learning is not irrelevant to this process; indeed, it is likely to play an important role in shaping and refining such connections and, based on the surrounding social input, regulate the development of brain regions involved in early facial motor control and sensorimotor matching. Recent work utilizing EEG to measure brain responses to facial gestures in newborn monkeys shows that despite their limited social experience (i.e., monkeys have been reared in a nursery from the day of birth), there is specific cortical desynchronization within the alpha band, i.e., mu rhythm, during the observation and imitation of facial gestures [17]. The mu rhythm has been hypothesized to be an important indirect index of the mirror mechanism [110]. The existence of the mu rhythm in newborn macaques responding during observed and executed facial gestures supports the hypothesis that a mirror mechanism operates at birth and it may sustain early imitative responses. Variation in neonatal imitation may reflect individual differences in the MNS, aiding in the early detection of social deficits [57]. Together, these findings highlight the value of neonatal imitation as a behavioral measure of the MNS, providing a window into the early development of the action-perception system.

Acknowledgements

This research was supported by the Division of Intramural Research, NICHD, and NICHD P01HD064653. We thank Peter Cooper and Krisztina Varga Jakobsen for helpful comments on an earlier draft of this manuscript.

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Study	Sample size	Age	Actions	Demonstration	Response Period	Rounds	Results
Kugiumutzakis, 1998, Studies I-III [30]	121 (NR)	10-45 min	TP, MO □	3-19 sec	10 sec	5	+
Kugiumutzakis, 1998, Study IV [30] (same data in [35])	49 (NR)	14-42 min	TP, MO, Eyes open/close □	3-19 sec	10 sec	5	+
Reissland, 1988 [36]	12 (0)	< 1 hr	Lips widening, Lip pursing □	35-155 sec	None	4-14	+
Meltzoff & Moore, 1983 [29]	40 (67)	*M* = 32 hrs	MO, TP □	20 sec	20 sec	12	+
Field et al., 1983 [37]	96 (NR)	35-42 hrs	Happiness, Sadness, Surprise □	ID habituation	None	≥ 1 (ID)	+
Field et al., 1982 [38]	74 (NR)	*M* = 36 hrs	Happiness, Sadness, Surprise □	ID habituation	None	≥ 1 (ID)	+
Kaitz et al., 1988 [39]	26 (58)	10-51 hrs	TP, Happiness, Sadness, Surprise	ID habituation	None	1	+ for TP
Meltzoff & Moore, 1989 [40]	40 (53)	13-67 hrs	TP, Head movement □	20 sec	20 sec	2	+
Nagy et al., 2005, 2007 [33,34]	39 (4)	3-96 hrs	IFP	Length NR	*M* = 50 sec	25	+
Anisfeld et al., 2001 [41]	83 (103)	40 hrs	TP, MO	20 sec	20 sec	4	+ for TP
Vinter, 1986, Study I [42]	16 (NR)	2-5 days	TP, Hand opening/closing □	15 sec	25 sec	4	+
Nagy et al., 2012 [43]	115 (6)	1-5 days	TP	Length NR	ID; Approx 50 sec	ID	+
Heimann et al., 1989, Study I [44-45]	23 (9)	2-3 days	TP, MO, LPS	ID; *M* = 38 sec	60 sec	1	+ for TP
Koepke et al., 1983, Study I [46]	6 (5)	14-16 days	TP, Lip protrusion, MO, SFM	15 sec	20 sec	1	-
Koepke et al., 1983, Study II [46]	14 (9)	17-21 days	TP, MO	15 sec	150 sec	1	-
Lewis & Sullivan, 1985 [47]	14 (6)	2 wks	MO, TP, Arm wave, SFM	10 sec	10 sec	3	-
Hayes & Watson, 1981, Study I [48]	11 (32)	17-20 days	TP, MO	15 sec	150 sec	1	-
Hayes & Watson, 1981, Study II [48]	16 (39)	17-22 days	TP, MO	≥ 15 sec	150 sec	1	-
Fontaine, 1984 [49]	12 (NR)	21-33 days	TP, MO, Cheeks swelling, Eyes open/close, Hand open/close, IFP	20 sec	30 sec	2	-
Heimann et al., 1989, Study II [44-45]	23 (9)	3 wks	TP, MO	ID; *M* = 38 sec	60 sec	1	+ for TP
McKenzi & Over, 1983 [50]	14 (NR)	9-30 days	MO, TP, Hand to face, Hand to midline	15 sec	20 sec	1	-
Meltzoff & Moore, 1977, Study I [28]	6 (NR)	12-17 days	TP, MO, Lip protrusion, SFM □	15 sec	20 sec	≤ 3	+
Meltzoff & Moore, 1977, Study II [28]	12 (NR)	16-21 days	TP, MO □	15 sec	150 sec	1	+
Heimann & Schallller, 1985 [51]	11 (17)	14-21 days	Mother modeled: MO, TP	15-20 sec	60 sec	1	+ for TP
Bard, 2007, Study I [52]**	5 (0)	7-15 days	TP, MO	20 sec	20 sec	6	+ for MO
Ferrari et al., 2006 [18]*	21 (0)	1-14 days	MO, LPS, TP, Hand open/close, Eyes open/close □	20 sec	20 sec	1	+ for LPS & TP
Paukner et al., 2011 [53]* (includes some [54] data)	60 (0)	1-8 days	LPS, TP	20 sec	20 sec	3	+ for LPS
Ferrari et al., 2009 [54] (includes [18] data)*	41 (NR)	1-8 days	LPS, TP	20 sec	20 sec	3	+

Table 1. Criteria for inclusion: Tested primate infants under 28 days of age, used a structured paradigm (predetermined demonstration/response frequency/length), dynamic actions were visually demonstrated with a live model (sound imitation and imitation from videos were excluded), study is published in English (or an English translation is available), and the test was carried out with at least 5 infants (no case studies). Species is human unless otherwise indicated (* = chimpanzee, ** = macaque). Sample size refers to the number of infants who produced usable data for one or more conditions, and the number of infants excluded is in parentheses. NR = not reported (not reported for this specific age group). Actions modeled by unfamiliar individuals, unless otherwise indicated. □ indicates action-specificity, in which positive results indicate greater imitation in the modeled action relative to non-

modeled/control action(s). TP = tongue protrusion, MO = mouth opening, LPS = lipsmacking, SFM = sequential finger movement, IFP = index finger protrusion. ID = infant-determined (length varied across individuals). Rounds = the number of times the demonstration period was presented. Results are as interpreted by the authors of each study: +/- = positive/ negative results. Studies are arranged by infant age (with younger infants at the top of the table) and species (humans listed first).

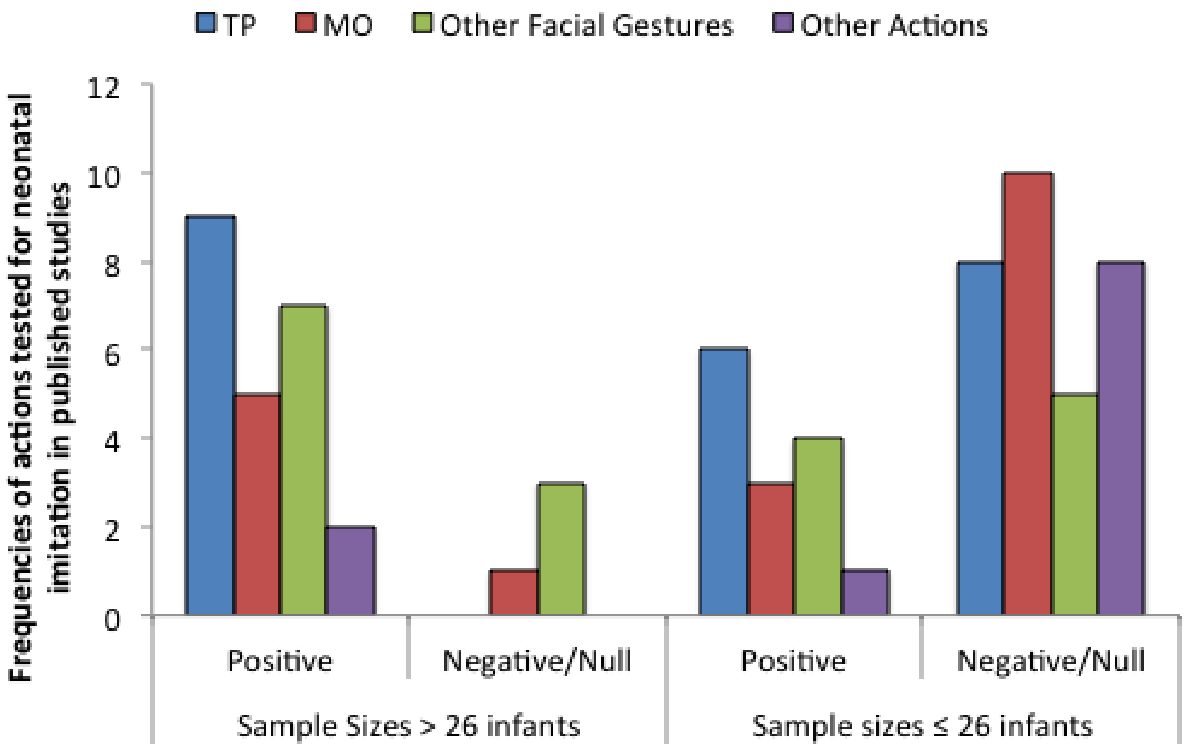

Figure 1. Among published studies of neonatal imitation in humans, across a variety of facial and other actions (shown here: tongue protrusion (TP), mouth opening (MO), other facial gestures, or other actions), sample size is a good predictor of whether the study found positive results (i.e., evidence of imitation) or negative/null results. We carried out an *a priori* power analysis to determine the sample size necessary for power = .80 (f = .40; α = .05) to detect this effect and determined a sample size of 26 is needed. The "frequencies of actions" axis label refers to the number of modeled actions that were tested, both within and between studies. For example, 9 studies with samples sizes > 26 tested TP and found positive results, while 6 studies tested MO and, of these, 5 found positive results.