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

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### 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

## 44 **Introduction**

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

61         These issues have also been explored in infant development using less invasive  
62 techniques, such as electroencephalography (EEG). EEG studies reveal that during the execution  
63 and observation of actions, specific frequency bands within the alpha range (9-13 Hz in the adult  
64 and 5-9Hz in infants) desynchronize in newborns [9-12] and older infants [13-15]. This  
65 suppression, termed the mu rhythm, is associated with the activation of mirror neurons areas  
66 (i.e., inferior frontal gyrus, ventral premotor cortex, posterior parietal lobe) [16] and thus may be  
67 considered a marker for mirror neuron activity.

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

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

89 experience (e.g., culture) influence infants' imitation and whether individual differences in  
90 imitation are related to later developmental outcomes.

91

### 92 **Historical and recent observations of neonatal imitation**

93 Human infant imitation has been studied for almost a century [21-23]. Early reports were  
94 primarily anecdotal or uncontrolled observations [22,24-25]. Maratos found that 1-month-olds  
95 imitated tongue protrusion (TP), mouth opening (MO), and head shaking [26-27]. Imitation in  
96 newborns was subsequently confirmed by Meltzoff and Moore [28-29], in their seminal, well-  
97 controlled experiments, and thereafter found in infants as young as 45 minutes after birth [29-  
98 30]. Importantly, Meltzoff and colleagues demonstrated that infants could identify the particular  
99 body part producing the modeled action, as well as the particular action pattern of that body part  
100 [28,31-32]. In addition to facial imitation, neonates only 3- to 96-hours old also appear to imitate  
101 finger movements (e.g., [33], [34]). These studies, and others (Table 1), provide strong evidence  
102 that neonatal imitation is present from birth. This evidence suggests newborns are capable of  
103 perceptual-motor coordination and cross-modal matching (i.e., matching the visual perception of  
104 the model with the proprioceptive experience of performing the action themselves), as well as  
105 demonstrating that newborns already possess complex social and cognitive skills.

106 Neonatal imitation has also been observed in nonhuman primates, including chimpanzees  
107 [52,55], and rhesus macaques [18]. In fact, the phenomenon appears very similar in humans and  
108 macaques [56]. In both species, neonatal imitation of facial gestures is elicited in the laboratory  
109 most easily in the first few weeks after birth (compared to later in development) and mothers  
110 imitate facial gestures of infants more than infants imitate mothers. Additionally, in both species  
111 there are large individual differences in imitative skills; that is, some infants consistently imitate  
112 while others do not, which may be a reflection of infants' social predispositions (e.g., [57-59]).  
113 Though not yet tested in humans, recent work demonstrates that macaque newborns recognize  
114 when others imitate them [60], suggesting action observation and execution are intricately  
115 linked.

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

129 Human mothers engage in complex, emotional, two-way face-to-face exchanges with  
130 their newborns, including mutual gaze and body contact (e.g., hand-body contact, kisses), and  
131 exaggerated maternal facial and vocal expressions [63,65-66]. There is a fundamental motivation  
132 on the part of both the parents and newborns to be in social engagement with each other,  
133 reflected in their preferential responses to faces and eye contact [67-73]. Even neonates show  
134 myriad facial expressions and gestures when in face-to-face contact. These include different

135 facial expressions of emotion, lip and tongue movements, and active shaping of the mouth,  
136 which are unconnected to clearly internal ‘biological’ events (e.g., digestion; [74]). This  
137 expressiveness provides a rich corpus of behaviors that helps adults understand the nature of  
138 infant needs and experience. Mothers are sensitive to neonates’ rare moments of alertness, and  
139 although such times are infrequent (15-20% of time observed), mothers choose them to socially  
140 engage with infants, otherwise providing relatively little social stimulation [75]. Human mothers  
141 initiate active engagements with clear ‘greeting’ and ‘marking’ behaviors, and also imitate  
142 infants’ expressions, including vocal and facial expressions, immediately after birth and in the  
143 first months of life (e.g., [76-78]). Similar mother-infant interactions also occur in rhesus  
144 macaques [79] and gelada baboons [80]. For example, macaque mothers direct lipsmacking  
145 (LPS)—an affiliative facial gesture—at their infants, often in an exaggerated fashion (similar to  
146 human motherese), and while doing so mothers place themselves directly in front of the infant,  
147 often lowering themselves to infants’ eye-level and engaging in bouts of head bobbing [79].

148 It is interesting to note, however, that very few reports have investigated the natural  
149 occurrence of neonatal imitation [81-83]. From these few studies it seems that human neonates  
150 themselves only rarely spontaneously imitate during interactions with parents. This observation  
151 is not surprising considering that newborns spend most of their time sleeping and, when awake,  
152 face-to-face interaction episodes are brief. We should also consider that, during interpersonal  
153 exchanges, imitation represents only one of many ways newborns can express themselves (e.g.,  
154 [74]). Thus, it is not imitation by the neonate *per se* that is critical for communication and social  
155 understanding, but a more fundamental capacity that infants’ occasional imitation reveals: that is,  
156 the capacity to connect one’s own and another’s actions and experience [83].

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

158 Neonatal imitation is a difficult behavior to observe in the laboratory, as evidenced by  
159 some inconsistent findings (e.g., [84-86]); consequently, the phenomenon is not unanimously  
160 accepted. Experimental tests of neonatal imitation in humans have used a variety of procedures,  
161 modeled actions, inclusion criteria, and operational definitions of imitation (see reviews  
162 [32,43,87-88]) and, it is not, therefore, surprising that results have varied across studies.  
163 Although methodological differences may account for different results [51], there has been only  
164 one previous systematic report, to our knowledge, comparing successful and unsuccessful  
165 methods, specifically focused on TP imitation [43]. Numerous factors influence imitation,  
166 including the position of the infant [43], the length of response period [29], and infants’ age [43].  
167 Out of 29 published studies of imitation in the first month of life (Table 1), 7 failed to find  
168 evidence of imitation (from 5 laboratories), and 21 found evidence of imitation (from 11  
169 laboratories). It is instructive to consider the differences between studies that found evidence of  
170 imitation and those that did not.

171 One common feature of several studies reporting null results for facial gesture imitation  
172 is that infants were prevented from gesturing concurrently with the adult model through the use  
173 of a pacifier [46,48]. Pacifiers were used to block infants’ immediate facial mimicry to test  
174 delayed imitation [28], to rule out perceptual-motor resonance as an explanation for imitation  
175 [89-90], or to prevent the model from unintentionally imitating the infant [28,49]. In fact,  
176 concurrent interaction synchrony plays an important role in early parent-infant interactions (e.g.,  
177 [91]), and infants who do not experience these synchronous interactions—such as when  
178 prevented with pacifiers—may be less likely to match facial gestures during still face (i.e.,  
179 response) periods. Actual imitation rates may also be underestimated due to a related issue: that  
180 is, in some studies, researchers did not measure infants’ gestures produced during the

181 gesture/dynamic stimulus period (e.g., [49]). We think this omission may have limited infant  
182 opportunities for imitation, given that much of infants' matching behavior may occur during this  
183 dynamic period.

184 A second feature common among studies reporting null results is a low statistical power  
185 resulting from small sample sizes (average number of usable participants: 12; range: 6-16  
186 participants), relative to those reporting positive results (average number of usable participants:  
187 43; range 6-121 participants), a point highlighted by others (e.g., [29,43]). Of those studies with  
188 sample sizes larger than 26 infants (determined to be a necessary sample size, based on an *a*  
189 *priori* power analysis, reported below), the vast majority found positive results, while studies  
190 including 26 or fewer infants contribute the most to the "failures to replicate," illustrated in  
191 Figure 1. Thus, among the studies reported in Table 1, over 85% of the behaviors examined in  
192 those with large sample sizes ( $ns \geq 26$ ) revealed positive results (i.e., evidence of neonatal  
193 imitation), while in studies with smaller sample sizes ( $ns < 26$ ), 69% of behaviors tested failed to  
194 show any evidence of imitation. This result may explain why previous reviews, which did not  
195 consider sample size as a factor contributing to the reliability of a study's findings' (e.g., see  
196 Table 1 in [87]; see Figure 2 in [92]; see Table 1 in [93]), have drawn different conclusions  
197 concerning the phenomenon of neonatal imitation. Below we discuss effect sizes found in  
198 neonatal imitation studies and suggest the sample sizes necessary to detect those effects.  
199

## 200 **Core questions and misunderstandings about neonatal imitation**

201 **Is neonatal imitation a reflex?** It has been suggested that neonatal imitation is not  
202 actually imitation, but instead may be an automatic and involuntary reflex-like phenomenon,  
203 driven by subcortical mechanisms, a fixed action pattern, or an innate releasing mechanism (e.g.,  
204 [39,46,48,50,94-95]). According to this view, matching should occur for only a few  
205 evolutionarily privileged gestures, that is, gestures that are, putatively, fixed and stereotypic, and  
206 produce a matching response that is time-locked to the modeled "trigger" action [96]. This  
207 prediction, however, has been tested and has not been supported: infants produce a range of  
208 gestures which are not stereotyped, actions which have never been seen before are matched,  
209 corrections are made to initial attempts, and responses are not time-locked to modeled actions  
210 [31-32,40]. In addition, infants produce gestures without prompt after a delay, suggesting they  
211 are initiating social interaction rather than simply copying actions [97]. In humans, so-called  
212 deferred imitation is present (after a 24- hour delay) from at least 6 weeks of life [31,98], and in  
213 some macaque infants it is present (after a 60 sec delay) in the first week of life [53], which  
214 indicates that these gestures are communicative and under voluntary control rather than reflexive  
215 fixed action patterns.

216 **Is neonatal imitation due to arousal?** Infants might be aroused when they view facial  
217 gestures and consequently increase their activity (e.g., produce more facial gestures themselves  
218 [99-100]). However, even if this point is accepted, infants' capacity to match specific gestures  
219 goes beyond this general arousal response, reflecting additional neurophysiological and cognitive  
220 mechanisms. Numerous neonatal imitation tests have measured infants' imitation of more than  
221 one action, and in these cases, arousal alone cannot account for infants' imitation of specific  
222 actions [28,40]. Nagy and colleagues [43] also recently performed a thorough review of neonatal  
223 imitation of TP gestures (the gesture most commonly assumed to be produced by arousal) by  
224 assessing the specificity of the imitative response and measuring infants' states [101] as well as  
225 other indicators of arousal, and concluded that TP imitation is not simply an arousal effect. In  
226 addition, newborns' heart rates accelerate when imitating gestures and decelerate when



227 performing unprompted gestures [97], suggesting that different mechanisms underlie imitative  
228 and exploratory spontaneous behaviors.

229 **Does imitation decline after the first month of life?** Given reports that imitation  
230 appears strong in the first month of life, but then declines in the following months (e.g., [27,49]  
231 [35,44,94]), it has been suggested that early imitation may be a phenomenon quite distinct from  
232 imitation occurring later (e.g., [58]). Neonatal imitation has been proposed to be a “transient  
233 ontogenetic adaptation,” important for survival in early infancy but then disappearing when no  
234 longer necessary [102, p.89]. While it is true that the form and characteristics of imitation  
235 undergo changes throughout infancy, this particular characterization is misleading. Instead,  
236 careful testing has revealed that imitation does not decline after the first month of life, but  
237 depends on the type of action being presented. For example, facial imitation (e.g., tongue  
238 protrusion, mouth opening, emotional facial expressions) largely disappears by 3 months of age  
239 [49,94-95,103], whereas other actions (e.g., sounds, vocalizations, hand and finger movements)  
240 increase in frequency and accuracy [104-105], in line with the infants’ wider development (e.g.,  
241 improvements in vision at a distance and manipulation skills). Interestingly, behaviors reliably  
242 imitated earlier in development can also be elicited later on if the social context is altered, for  
243 example, if presented in the context of games or playful interactions, or if the actions form part  
244 of a sequence requiring novel combinations [106]. Apparent declines in imitation in the  
245 laboratory setting may be due, therefore, to these wider changes in infants’ expectations and  
246 motivations during social interactions [98,107].

247 **Does neonatal imitation depend on learning?** Infants may learn to associate their own  
248 movements with those of others, and thus acquire the capacity to imitate through a process of  
249 associative learning (e.g., [87,108]). While experience, including associative processes,  
250 undoubtedly plays a role in developing the corpus of behaviors that infants imitate (see below in  
251 sections on plasticity and cultural differences), an associative learning account of the  
252 fundamental capacity to imitate is incompatible with the evidence on two fronts. First, only  
253 minutes to hours after birth, human infants imitate opening and closing of eyes [30,35], head  
254 movements [40], the /a/ sound [30,35], index finger protrusion [33,34], facial gestures (e.g.,  
255 mouth opening, tongue protrusion; [29,40]), and emotional facial expressions (e.g., happiness,  
256 sadness, surprise [38]) prior to having opportunities to form strong associative links between  
257 action observation and imitative responses. Similarly, macaque infants reared in a nursery from  
258 birth imitate before they have experienced any contingent facial interactions with caregivers  
259 [18,53,109], and they additionally show specific electroencephalogram changes (i.e., mu  
260 suppression), evidence of a functioning MNS, on the day of birth [17,110]. These results fail to  
261 support an associative learning account of neonatal imitation [111-112].

262 Even setting aside such evidence, the associative learning account is problematic on a  
263 second front, since, for the proposed learned associations to be forged it would require the  
264 neonate to experience high levels of contingent responses from social partners that are almost  
265 exclusively imitative. In fact, while parents do indeed provide imitative feedback during social  
266 interactions with their infants, the rate is typically quite low (e.g., 1 per 2-3 minutes ([62]) and,  
267 moreover, such feedback occurs in the context of a wealth of parental behaviors that are non-  
268 imitative (e.g., affirmative marking, or even negating of infant expressions [113]). On a rigorous  
269 calculation of contingency [114], parents’ imitative responses are, therefore, relatively non-  
270 salient for the infant. According to the associative learning account, this situation then leaves  
271 infants with the challenge of identifying which particular adult gestures or expressions among  
272 this plethora match their own, a task that may be cognitively equivalent to that of the production

273 of imitative acts themselves. In short, an associative learning account does not so much solve the  
274 problem of imitation, as raise a set of further questions concerning the basis of infant capacities  
275 for identifying the equivalence between their own and others' actions.  
276

### 277 **Methodological differences across neonatal imitation studies**

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

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

294 **2. Appropriately modeled actions.** For standardization purposes, models should be  
295 unfamiliar to the infant (unless specific effects of the mother or caretaker are being investigated;  
296 e.g., [51,61,115]) and should avoid interacting with the infant before testing [29]. Models should  
297 be positioned at an appropriate distance, taking into account newborns' reduced visual acuity,  
298 and should make continuous eye contact with infants for the duration of the test. Nonverbal cues  
299 such as eye contact set up an expectation of a social exchange, and may direct infants' attention  
300 towards the adults' modeled actions [116]. There is disagreement about what constitutes  
301 adequate speed, rhythm, and repetition of action presentation, so these aspects should be clearly  
302 documented. One critical aspect of the procedure is the length of time the gesture is modeled. In  
303 a review of TP studies, modeling the gesture for 60 sec or longer resulted in evidence of  
304 imitation in all reported studies, whereas modeling the gesture for 40 sec or less resulted in only  
305 31% of studies finding evidence of imitation [84]. Therefore, we recommend a minimum of 60  
306 sec of presenting modeled gestures. Modeled behaviors should be age-appropriate, prominent in  
307 the infant's expressive repertoire, and structured at a predetermined frequency and speed so all  
308 infants view the same actions. We also recommend modeling actions in a “burst-pause”  
309 procedure, whereby the model alternates between static and dynamic periods, as this  
310 procedure—compared to modeling only dynamic actions—results in higher frequencies of  
311 imitation [29].

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

319 [31]), so sufficient time must be provided for infants to initiate, refine, and complete their  
320 response. In addition, it is important that the length of this response period be predetermined and  
321 not based on infants' behaviors (e.g., [35]), as this may introduce a bias for gestures produced  
322 spontaneously [48].

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

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

340 **6. Sufficient power.** We calculated effect sizes for neonatal imitation studies that have  
341 given sufficient detail necessary for such calculations [29-30,35-36,40,41-42,51], and found that  
342 among those actions analyzed with parametric tests (10 actions), Cohen's *d* ranged from .34  
343 (small) to .58 (medium), with a median of .40, and for studies that used non-parametric tests for  
344 analysis (9 actions), effect sizes (*r*) ranged from .37 (medium) to 3.75 (large), with a median of  
345 .64 (large). Using the most conservative estimate of effect size ( $d = .34$ ), we carried out an *a*  
346 *priori* power analysis to determine the sample size necessary for power = .80 ( $f = .40$ ;  $\alpha = .05$ ) to  
347 detect this effect and determined a sample size of 26 is needed [118]. Thus, like any study with  
348 infants, a relatively large sample is required to allow for small to medium effect sizes and  
349 potentially high dropout rates. Although it may be unnecessary for infants to complete all trials  
350 to be included, we think, at the very least, the number or proportion of unusable trials should be  
351 reported, along with reasons for excluding trials.

352 **7. Optional additional control conditions (static nonsocial baseline period and**  
353 **nonsocial comparison).** Infants' actions produced after seeing the modeled gestures can  
354 additionally be compared to both a no-stimulation or static social baseline period (e.g., still face)  
355 and a nonsocial static and dynamic control condition (e.g., disk with both still and rotating  
356 periods), to guard against the possibility that the action in question may happen by chance or as a  
357 result of non-specific arousal. The nonsocial control stimulus should be matched to the social  
358 stimulus in its static and dynamic nature. To be classified as imitation, the model behavior  
359 should increase in frequency relative to the baseline level, and should be more frequent in the  
360 test condition than in the nonsocial control condition. For example, in one study with 5- to 8-  
361 week-old infants, TP and MO gestures were produced only when a social model (human face)  
362 produced the gestures, but not when inanimate objects produced similar movement patterns  
363 [119]. It is worth noting that the vast majority of studies fail to include this condition. Although  
364 its inclusion is not a necessary requirement for demonstrating neonatal imitation, it can increase

365 the sensitivity of the test by allowing a subtraction of baseline rates across a more diverse  
366 collection of control conditions. This can be particularly useful for studies examining individual  
367 differences in imitative skills, as it offers a more sensitive test of imitation-specific action  
368 reproduction.

369

### 370 **Neonatal imitation as a predictor of later developmental outcomes**

371 A number of possibilities have been suggested for why some neonates imitate and others  
372 do not. Variability in recorded imitative performance may be due to error variance,  
373 methodological differences (as we described), or, perhaps most intriguingly, it may reflect  
374 genuine individual differences among infants. As we explain below, we think it may be useful to  
375 consider the extent to which these individual differences predict, or are related to, other  
376 behavioral outcomes. In particular, if some infants imitate because they possess a more  
377 responsive facial MNS, then other abilities that also rely on mirror neuron circuits (e.g.,  
378 reaching-grasping, understanding goal-directed actions, emotion recognition) may be  
379 systematically related to early imitation. Indeed, many researchers argue that it is important to  
380 examine whether neonatal imitation is predictive of later social and cognitive development [44-  
381 45,58,104,120-121] because it could be an early marker of later deficits in social skills [57].  
382 Previous studies suggest that in both humans and macaque monkeys, only about 50% of neonates  
383 consistently engage in imitation of facial gestures [53-54,122]. Only one study has examined  
384 neonatal imitation predictively in human infants: imitation at three ages—2-3 days, 3 weeks, and  
385 3 months of age—predicts visual attention at 3 months of age. In particular, neonatal imitators  
386 had fewer looks away during a face-to-face interaction at 3 months of age compared to non-  
387 imitators [44-45]. In another recent study, female infants were found to imitate finger  
388 movements more than male infants [34], consistent with adult studies that demonstrate females  
389 have greater mu suppression when viewing actions (e.g., [123-124]).

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

405 With regard to the wider implications of individual differences in imitation, although  
406 much can be learned from studying typically developing populations, as described above, the  
407 study of neonatal imitation in special populations may be particularly informative, especially in  
408 those with conditions associated with social deficits. For example, studies with human children  
409 have shown that imitation is impaired in children with autism spectrum disorders (ASD),  
410 including oral-facial imitation [125-126] as well as immediate and deferred imitation of a variety

411 of other actions [127-128]. We know of no work that has examined infants at high-risk for social  
412 deficits, such as siblings of children with ASD (who are therefore at higher risk for developing  
413 ASD), to see if they exhibit neonatal imitation at the same levels as low-risk infants, or if failure  
414 to show neonatal imitation is associated with higher risk of a future diagnosis of ASD. We think  
415 that such high-risk infants, including siblings of children with an ASD diagnosis, would be  
416 particularly useful to study in this context because it has been suggested that MNS dysfunction  
417 may be implicated in ASD [129], and information about the developmental emergence of this  
418 disorder could provide valuable insights. Notably, there is some work that suggests that these  
419 high-risk infants display lower levels of coherence in measures of mother-infant synchrony  
420 compared to low-risk infants at 4 months of age [130], which may be indicative of decreased  
421 social sensitivity and responsiveness at an early age prior to a clinical diagnosis.

422

### 423 **Plasticity of neonatal imitation**

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

429 To determine the influence of early face-to-face interactions on imitation, we randomly  
430 assigned nursery-reared macaque newborns to either receive exposure to facial gestures ( $n = 12$ ),  
431 extra handling ( $n = 12$ ), or standard rearing ( $n = 15$ ). The exposure to facial gestures consisted of  
432 human caregivers engaging in face-to-face communicative exchanges using LPS gestures  
433 directed at infants in 5-min-long sessions, four times a day, starting from the first day of life. In  
434 each session, a human caregiver directed LPS gestures at the infant for 5 sec, followed by 10 sec  
435 of eye contact, then a 15 sec break period. This sequence was repeated 10 times in the 5-min  
436 session. Infants in the extra-handling group were held at the same times and for the same  
437 durations as the exposure group, but did not receive the face-to-face interactions (caretakers'  
438 faces were covered so infants could not see them). Infants in the standard rearing group did not  
439 see facial gestures and did not receive any handling beyond basic care and other (non-related)  
440 experimental procedures. On day 7 or 8 infants were tested for neonatal imitation with two  
441 gestures—lipsmacking (LPS) and tongue protrusion (TP)—that were compared to a nonsocial  
442 control condition, a rotating disk with orthogonal stripes (for methodological details, see [53-  
443 54]). We found that only infants who were exposed to facial gestures showed increased LPS in  
444 the LPS condition (baseline:  $M = 2.00$ ,  $SD = 2.41$ ; stimulus:  $M = 9.83$ ,  $SD = 8.09$ ),  $t(11) = 4.03$ ,  
445  $p = .002$ , but not in the other two conditions (TP or Control disk),  $ps > .05$ , which suggests that  
446 early social experience—such as being held, mutual gaze, and/or early communicative  
447 exchanges—may improve imitation. In addition, our results with macaques are consistent with a  
448 number of findings in human infants concerning the role of experience. For example, infants  
449 improve their matching precision across days [29,31] and across trials [33,131], and human  
450 infants exposed to TP every day from 6 to 14 weeks of life show stronger TP imitation at 14  
451 weeks [95]. Though speculative, we think evidence of plasticity in neonatal imitation, as  
452 documented here, suggests plasticity of action-perception mechanisms, likely mediated by the  
453 mirror neuron system. Further tests employing measures of mu rhythm as a function of  
454 experiences in the first weeks of life are necessary to more directly measure changes in the  
455 mirror neuron system.

456 In addition to controlled manipulations of infants' early experiences, some work has  
457 examined imitation in relation to the cultural variability in newborns' environments. Despite the  
458 universality of key features of parent-infant interactions, there is also notable variation in the  
459 extent and manner of parental responsiveness to infant behaviors. This variation is particularly  
460 apparent when comparing cultures that differ in the conditions and value systems accompanying  
461 child care [132]. Some, like the U.S. and many North European countries, place great value on  
462 infant individuation and independence; and parents tend to use high levels of facial and vocal  
463 expressiveness to respond to, as well as imitate, infant signals in face-to-face play. In turn, this  
464 style of responsiveness predicts earlier emergence of infant self-awareness (i.e., mirror  
465 recognition) [133]. Others cultures (e.g., Japanese, and certain rural African societies) place  
466 more value on infant affiliation and compliance, and on sharing and cohesiveness within the  
467 society. These parents, although similarly responsive to their infants, pick up on different infant  
468 cues, and are more likely to use close physical contact to respond to their infants (e.g., kissing, or  
469 rhythmical patting), and parents show far less vocal and facial imitation [134-135].  
470 Correspondingly, infant behavior during interactions in these diverse cultures develops in  
471 different ways. Thus, a study comparing Nso mothers and infants (a rural society in the  
472 Cameroon) with those in Germany found most German infants to increasingly imitate maternal  
473 smiles during face-to-face interactions over the first three months, a pattern that did not occur in  
474 Nso infants [135]. Such findings indicate that, based on infants' fundamental capacities to  
475 identify correspondences between their own and others' actions, particular forms of infant  
476 expressive behaviors emerge in the development of different cultural styles of social  
477 communication. We believe that cross-cultural examination of neonatal imitation and its  
478 developmental consequences would be a particularly fruitful direction for future research.  
479

### 480 **Conclusion**

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

487 The formation of an action-perception mechanism has been debated in the recent  
488 literature and, some scholars propose that it is unlikely that a rudimentary mechanism that  
489 matches observed facial gestures with the internal motor representation could be operative from  
490 birth. Instead, it is proposed that general sensorimotor connections link temporal regions that  
491 visually code for others' actions with parietal regions that are involved in executing actions.  
492 Further, in this account, these connections are refined through Hebbian learning processes, and  
493 become tuned so that visual and motor information become matched in the course of  
494 development [92]. The evidence on neonatal imitation reviewed here, however, does not support  
495 this proposal, as it clearly shows that, prior to any experience, there is a link between seeing  
496 facial gestures and the motor programs activating the same motor representations. Nevertheless,  
497 learning is not irrelevant to this process; indeed, it is likely to play an important role in shaping  
498 and refining such connections and, based on the surrounding social input, regulate the  
499 development of brain regions involved in early facial motor control and sensorimotor matching.  
500 Recent work utilizing EEG to measure brain responses to facial gestures in newborn monkeys  
501 shows that despite their limited social experience (i.e., monkeys have been reared in a nursery

502 from the day of birth), there is specific cortical desynchronization within the alpha band, i.e., mu  
503 rhythm, during the observation and imitation of facial gestures [17]. The mu rhythm has been  
504 hypothesized to be an important indirect index of the mirror mechanism [110]. The existence of  
505 the mu rhythm in newborn macaques responding during observed and executed facial gestures  
506 supports the hypothesis that a mirror mechanism operates at birth and it may sustain early  
507 imitative responses. Variation in neonatal imitation may reflect individual differences in the  
508 MNS, aiding in the early detection of social deficits [57]. Together, these findings highlight the  
509 value of neonatal imitation as a behavioral measure of the MNS, providing a window into the  
510 early development of the action-perception system.

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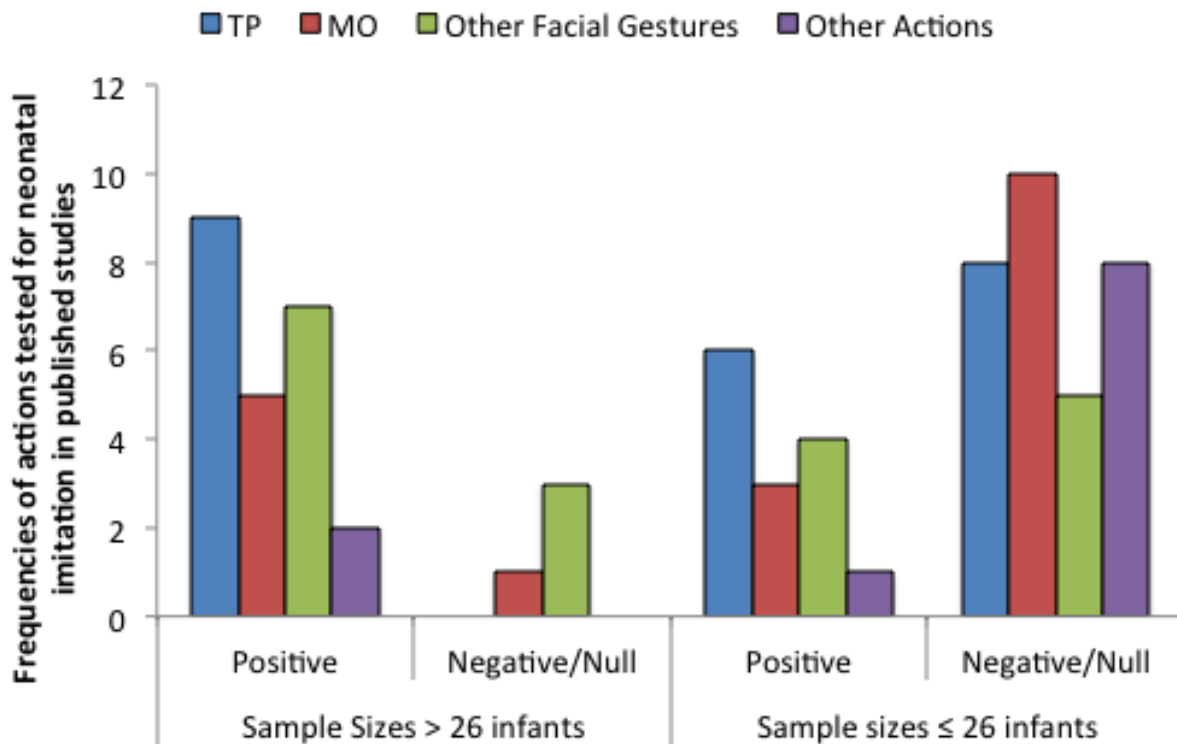


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Study	Sample size	Age	Actions	Demonstration	Response Period	Rounds	Results
Kugiumutzakis, 1998, Studies I-III [30]	121 (NR)	10-45 min	TP, MO □	3-19 sec	10 sec	5	+
Kugiumutzakis, 1998, Study IV [30] (same data in [35])	49 (NR)	14-42 min	TP, MO, Eyes 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)	<i>M</i> = 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)	<i>M</i> = 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	<i>M</i> = 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; <i>M</i> = 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; <i>M</i> = 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 & Schaller, 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	+

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

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



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*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 ( $f = .40$ ;  $\alpha = .05$ ) 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.