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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: simpsona@mail.nih.gov.

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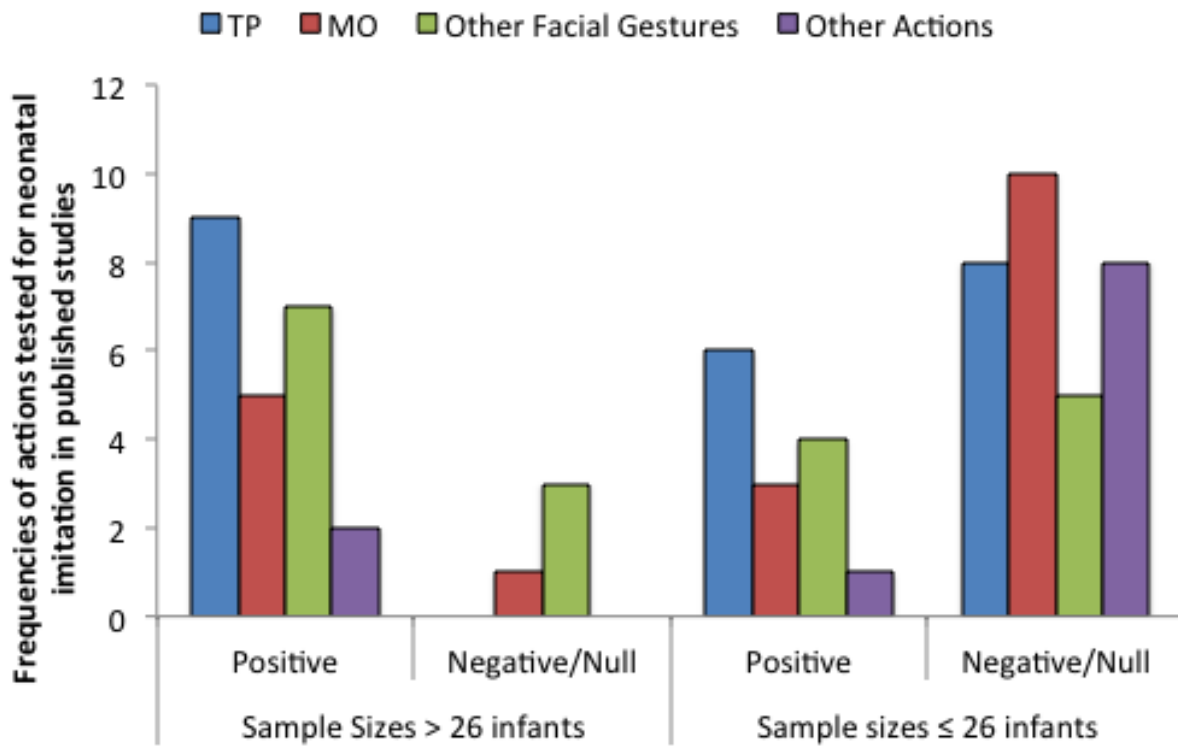
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Study	Sample size	Age	Actions	Demonstration	Response Period	Rounds	Results
Kugiumutzakis, 1998, Studies I-III [30]	121 (NR)	10-45 min	TP, MO □	3-19 sec	10 sec	5	+
Kugiumutzakis, 1998, Study IV [30] (same data in [35])	49 (NR)	14-42 min	TP, MO, Eyes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