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

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6                                    power, and evidence of plasticity
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25                                                      Abstract
26      There is strong evidence that neonates imitate previously unseen behaviors. These behaviors are
27      predominantly used in social interactions, demonstrating neonates' ability and motivation to
28      engage with others. Research on neonatal imitation can provide a wealth of information about
29      the early mirror neuron system (MNS): namely, its functional characteristics, its plasticity from
30      birth, and its relation to skills later in development. Though numerous studies document the
31      existence of neonatal imitation in the laboratory, little is known about its natural occurrence
32      during parent-infant interactions and its plasticity as a consequence of experience. We review
33      these critical aspects of imitation, which we argue are necessary for understanding the early
34      action-perception system. We address common criticisms and misunderstandings about neonatal
35      imitation and discuss methodological differences among studies. Recent work reveals that
36      individual differences in neonatal imitation positively correlate with later social, cognitive, and
37      motor development. We propose that such variation in neonatal imitation could reflect important
38      individual differences of the MNS. Although postnatal experience is not necessary for imitation,
39      we present evidence that neonatal imitation is influenced by experience in the first week of life.
40
41      *Keywords*: neonatal imitation, newborn, social development, mother-infant interaction, mu
42      suppression, sensorimotor
43

**Introduction**

44
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
**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.

**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), $p$s $> .05$, 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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| 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 & Schalller, 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).
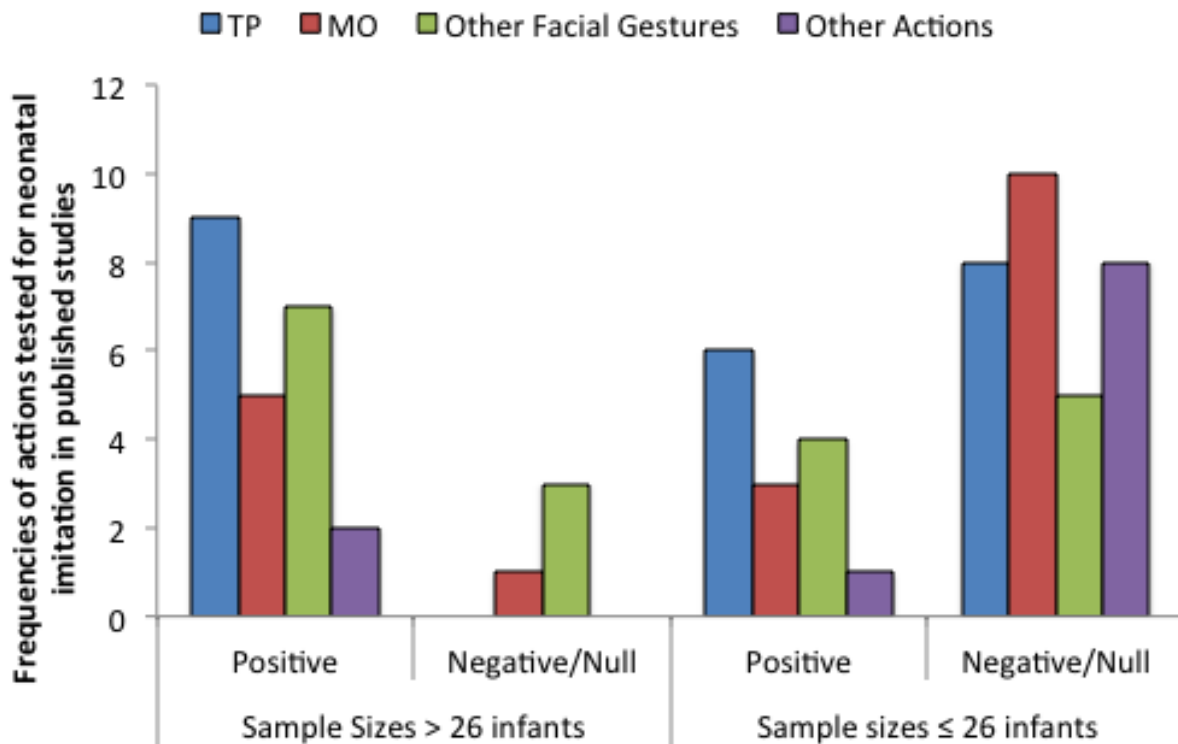
892
893    *Figure 1*. Among published studies of neonatal imitation in humans, across a variety of facial
894    and other actions (shown here: tongue protrusion (TP), mouth opening (MO), other facial
895    gestures, or other actions), sample size is a good predictor of whether the study found positive
896    results (i.e., evidence of imitation) or negative/null results.  We carried out an *a priori* power
897    analysis to determine the sample size necessary for power = .80 ($f$ = .40; α = .05) to detect this
898    effect and determined a sample size of 26 is needed.  The "frequencies of actions" axis label
899    refers to the number of modeled actions that were tested, both within and between studies.  For
900    example, 9 studies with samples sizes > 26 tested TP and found positive results, while 6 studies
901    tested MO and, of these, 5 found positive results.
902