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

Article

Accepted Version

www.reading.ac.uk/centaur

CentAUR

Central Archive at the University of Reading

Reading's research outputs online

1
2
3
4
5   The mirror neuron system as revealed through neonatal imitation: Presence from birth, predictive
6   power, and evidence of plasticity
7
8   Elizabeth A. Simpson
9   Department of Neuroscience, University of Parma, Italy
10
11   Lynne Murray
12   School of Psychology and Clinical Language Sciences, University of Reading, UK, and
13   Department of Psychology, Stellenbosch University, South Africa
14
15   Annika Paukner
16   *Eunice Kennedy Shriver* National Institute of Child Health and Human Development,
17   Poolesville, Maryland, USA
18
19   Pier F. Ferrari
20   Department of Neuroscience, University of Parma, Italy
21
22
23   Author note
24   Corresponding author: Elizabeth A. Simpson, email: simpsonea@mail.nih.gov.

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

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 $= .80$ ($f = .40$; $α = .05$) 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.

515   References

516   1. Rizzolatti, G. & Craighero, L. 2004 The mirror-neuron system. *Annual Review of*
517   *Neuroscience* **27**, 169-192. (DOI 10.1146/annurev.neuro.27.070203.144230)
518   2. Ferrari, P. F., Bonini, L. & Fogassi, L. 2009 From monkey mirror neurons to primate
519   behaviours: possible 'direct'and 'indirect'pathways. *Philosophical Transactions of the*
520   *Royal Society B: Biological Sciences* **364**(1528), 2311-2323. (DOI
521   10.1098/rstb.2009.0062)
522   3. Rizzolatti, G. & Luppino, G. 2001 The cortical motor system. *Neuron* **31**(6), 889-901. (DOI
523   10.1016/S0896-6273(01)00423-8)
524   4. Rizzolatti, G., Fogassi, L. & Gallese, V. 2001 Neurophysiological mechanisms underlying the
525   understanding and imitation of action. *Nature Reviews Neuroscience* **2**(9), 661-670. (DOI
526   10.1038/35090060)
527   5. Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. Annual review of psychology,
528   60, 653-670. (DOI 10.1146/annurev.psych.60.110707.163604)
529   6. Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. & Rizzolatti, G. 1999
530   Cortical mechanisms of human imitation. *Science* **286**(5449), 2526-2528. (DOI
531   10.1126/science.286.5449.2526)
532   7. Buccino, G., Vogt, S., Ritzl, A., Fink, G. R., Zilles, K., Freund, H. J. & Rizzolatti, G. 2004
533   Neural circuits underlying imitation learning of hand actions: an event-related fMRI
534   study. *Neuron* **42**(2), 323-334. (DOI 10.1016/S0896-6273(04)00181-3)
535   8. Jackson, P. L., Meltzoff, A. N., & Decety, J. 2006 Neural circuits involved in imitation and
536   perspective-taking. *Neuroimage* **31**(1), 429-439. (DOI
537   10.1016/j.neuroimage.2005.11.026)
538   9. Kessler, K., Biermann-Ruben, K., Jonas, M., Roman Siebner, H., Bäumer, T., Münchau, A. &
539   Schnitzler, A. 2006 Investigating the human mirror neuron system by means of cortical
540   synchronization during the imitation of biological movements. *Neuroimage* **33**(1), 227-
541   238. (DOI 10.1016/j.neuroimage.2006.06.014)
542   10. Lepage, J. F. & Théoret, H. 2006 EEG evidence for the presence of an action observation–
543   execution matching system in children. *European Journal of Neuroscience* **23**(9), 2505-
544   2510. (DOI 10.1111/j.1460-9568.2006.04769.x)
545   11. Muthukumaraswamy, S. D., & Johnson, B. W. 2004 Changes in rolandic mu rhythm
546   during observation of a precision grip. *Psychophysiology* **41**(1), 152-156. (DOI
547   10.1046/j.1469-8986.2003.00129.x)
548   12. Muthukumaraswamy, S. D. & Johnson, B. W. 2004 Primary motor cortex activation during
549   action observation revealed by wavelet analysis of the EEG. *Clinical Neurophysiology*
550   **115**(8), 1760-1766. (DOI 10.1016/j.clinph.2004.03.004)
551   13. Marshall, P. J., Young, T. & Meltzoff, A. N. 2011 Neural correlates of action observation
552   and execution in 14-month-old infants: an event-related EEG desynchronization study.
553   *Developmental Science* **14**(3), 474-480. (DOI 10.1111/j.1467-7687.2010.00991.x)
554   14. Saby, J. N., Marshall, P. J. & Meltzoff, A. N. 2012 Neural correlates of being imitated: An
555   EEG study in preverbal infants. *Social Neuroscience* **7**(6), 650-661. (DOI
556   10.1080/17470919.2012.691429)
557   15. Marshall, P. J. & Meltzoff, A. N. 2011 Neural mirroring systems: Exploring the EEG mu
558   rhythm in human infancy. *Developmental Cognitive Neuroscience* **1**(2), 110-123. (DOI
559   10.1016/j.dcn.2010.09.001)
560   16. Arnstein, D., Cui, F., Keysers, C., Maurits, N. M. & Gazzola, V. 2011 μ-suppression during

561   action observation and execution correlates with BOLD in dorsal premotor, inferior
562   parietal, and SI cortices, *Journal of Neuroscience* **31**, 14243–14249. (DOI 10.1523/
563   JNEUROSCI.0963-11.2011)
564   17. Ferrari, P. F., Vanderwert, R. E., Paukner, A., Bower, S., Suomi, S. J. & Fox, N. A. 2012
565   Distinct EEG amplitude suppression to facial gestures as evidence for a mirror
566   mechanism in newborn monkeys. *Journal of Cognitive Neuroscience* **24**, 1165–72. (DOI
567   10.1162/jocn_a_00198)
568   18. Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A. & Suomi, S. J. 2006
569   Neonatal imitation in rhesus macaques. *PLoS Biology* **4**, e302. (DOI
570   10.1371/journal.pbio.0040302)
571   19. Casile, A., Caggiano, V. & Ferrari, P. F. 2011 The mirror neuron system: A fresh view.
572   *Neuroscientist* **17**, 524–538. (DOI 10.1177/1073858410392239)
573   20. Lepage, J. F. & Théoret, H. 2007 The mirror neuron system: Grasping others' actions from
574   birth? *Developmental Science* **10**, 513-523. (DOI 10.1111/j.1467-7687.2007.00631.x)
575   21. Guillaume, P. 1926/1971 *L'imitation chez l'enfant*. Paris Libr. Felix Alcan (1926); Engl.
576   transl *Imitation in Children.* Chicago: University of Chicago Press (1971).
577   22. Valentine, C. W. 1930 The psychology of imitation with special reference to early childhood.
578   *British Journal of Psychology. General Section* **21**, 105-132. (DOI: 10.1111/j.2044-
579   8295.1930.tb00580.x)
580   23. Piaget, J. 1935 Les théories de l'imitation. *Cahiers de pédagogie expérimentale et de
581   psychologie de l'enfant* **6***, 1-13.
582   24. Gardner, J. & Gardner, H. 1970 A note on selective imitation by a six-week-old infant. *Child
583   Development* **41**, 1209-1213.
584   25. Zazzo, R. 1957 Le problème de l'imitation chez le nouveau-né. *Enfance* **10**, 135–142. (DOI
585   10.3406/enfan.1957.1350)
586   26. Maratos, O. 1973 The origin and development of imitation in the first six months of life.
587   Paper presented at the *Annual Meeting of the British Psychological Society*, Liverpool.
588   27. Maratos, O. 1982 Trends in the development of imitation in the first six months of life. In
589   *Intersubjective communication and emotion in ontogeny* (ed. T. G. Bever), pp. 81-101.
590   Hillsdale, New Jersey: Lawrence Erlbaum Associates.
591   28. Meltzoff, A. N. & Moore, M. K. 1977 Imitation of facial and manual gestures by human
592   neonates. *Science* **198**, 75–78. (DOI 10.1126/science.198.4312.75)
593   29. Meltzoff, A. N. & Moore, M. K. 1983 Newborn infants imitate adult facial gestures. *Child
594   Development* **54**, 702–709. (DOI 10.2307/1130058)
595   30. Kugiumutzakis, G. 1998 Neonatal imitation in the intersubjective companion space. In
596   *Intersubjective communication and emotion in early ontogeny* (ed. S. Braten), pp. 63-88.
597   Cambridge: Cambridge University Press.
598   31. Meltzoff, A. N. & Moore, M. K. 1994 Imitation, memory, and the representation of
599   persons. *Infant behavior and development* **17**, 83-99. (DOI 10.1016/0163-
600   6383(94)90024-8)
601   32. Meltzoff, A. N. & Moore, M. K. 1997 Explaining facial imitation: A theoretical model. *Early
602   Development and Parenting* **6**, 179-192. (DOI 10.1002/(SICI)1099-
603   0917(199709/12)6:3/4<179::AID-EDP157>3.0.CO;2-R)
604   33. Nagy, E., Kompagne, H., Orvos, H., Pal, A., Molnar, P., Janszky, I., . . . Bardos, G. 2005

Index finger movement imitation by human neonates: Motivation, learning, and left-hand preference. *Pediatric Research* **58**, 749–753. (DOI 10.1203/01.PDR.0000180570.28111.D9)

34. Nagy, E., Kompagne, H., Orvos, H. & Pal, A. 2007 Gender-related differences in neonatal imitation. *Infant and Child Development* **16**, 267–276. (DOI 10.1002/icd.497)

35. Kugiumutzakis, J. 1999 Genesis and development of early infant mimesis to facial and vocal models. In *Imitation in infancy* (eds. J. Nadel & G. Butterworth), pp. 36-59. Cambridge: Cambridge University Press.

36. Reissland, N. 1988 Neonatal imitation in the first hour of life: Observation in rural Nepal. *Developmental Psychology* **24**, 464–469. (DOI 10.1037/0012-1649.24.4.464)

37. Field, T. M., Woodson, R., Cohen, D., Greenberg, R., Garcia, R. & Collins, K. 1983 Discrimination and imitation of facial expressions by term and preterm neonates. *Infant Behavior & Development* **6**, 485–489. (DOI 10.1016/S0163-6383(83)90316-8)

38. Field, T. M., Woodson, R., Greenberg, R. & Cohen, D. 1982 Discrimination and imitation of facial expressions by neonates. *Science* **418**, 179-181. (DOI 10.1126/science.7123230)

39. Kaitz, M., Meschulach-Sarfaty, O., Auerbach, J. & Eidelman, A. 1988 A reexamination of newborns' ability to imitate facial expressions. *Developmental Psychology* **24**, 3–7. (DOI 10.1037/0012-1649.24.1.3)

40. Meltzoff, A. N. & Moore, K. M. 1989 Imitation in newborn infants: Exploring the range of gestures imitated and the underlying mechanisms. *Developmental Psychology* **25**, 954–962. (DOI 10.1037/0012-1649.25.6.954)

41. Anisfeld, M., Turkewitz, G., Rose, S. A., Rosenberg, F. R., Sheiber, F. J., Couturier-Fagan, D. A. & Sommer, I. 2001 No compelling evidence that newborns imitate oral gestures. *Infancy* **2**, 111–122. (DOI 10.1207/S15327078IN0201_7)

42. Vinter, A. 1986 The role of movement in eliciting early imitations. *Child Development* **57**, 66–71. (DOI 10.2307/1130638)

43. Nagy, E., Pilling, K., Orvos, H. & Molnar, P. 2012 Imitation of tongue protrusion in human neonates: Specificity of the response in a large sample. Advanced online publication. *Developmental Psychology*. (DOI 10.1037/a0031127)

44. Heimann, M., Nelson, K. E. & Schaller, J. 1989 Neonatal imitation of tongue protrusion and mouth opening: Methodological aspects and evidence of early individual differences. *Scandinavian Journal of Psychology* **30**, 90–101. (DOI 10.1111/j.1467-9450.1989.tb01072.x)

45. Heimann, M. 1989 Neonatal imitation, gaze aversion, and mother-infant interaction. *Infant Behavior and Development* **12**, 493-503. (DOI 10.1016/0163-6383(89)90029-5)

46. Koepke, J. E., Hamm, M., Legerstee, M. & Russell, M. 1983 Neonatal imitation: Two failures to replicate. *Infant Behavior & Development* **6**, 97–102. (DOI 10.1016/S0163-6383(83)80012-5)

47. Lewis, M. & Sullivan, M. W. 1985 Imitation in the first six months of life. *Merrill-Palmer Quarterly*, **31**, 315–333.

48. Hayes, L. A. & Watson, J. S. 1981 Neonatal imitation: Fact or artifact? *Developmental Psychology* **17**, 655–660. (DOI 10.1037/0012-1649.17.5.655)

49. Fontaine, R. 1984 Imitative skills between birth and six months. *Infant Behavior and Development* **7**, 323-333. (DOI 10.1016/S0163-6383(84)80047-8)

50. McKenzie, B. E. & Over, R. 1983 Young infants fail to imitate facial and manual gestures. *Infant Behavior & Development* **6**, 85–95. (DOI 10.1016/S0163-6383(83)80011-3)

651   51. Heimann, M. & Schaller, J. 1985 Imitative reactions among 14–21 day old infants. *Infant*
652   *Mental Health Journal* **6**, 31–39. (DOI 10.1002/1097-0355(198521)6:1<31::AID-
653   IMHJ2280060106>3.0.CO;2-M)
654   52. Bard, K. A. 2007 Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two
655   paradigms. *Animal Cognition* **10**, 233-242. (DOI 10.1007/s10071-006-0062-3)
656   53. Paukner, A., Ferrari, P. F. & Suomi, S. J. 2011 Delayed imitation of lipsmacking gestures by
657   infant rhesus macaques (*Macaca mulatta*). *PLoS ONE* **6**, e28848. (DOI
658   10.1371/journal.pone.0028848)
659   54. Ferrari, P. F., Paukner, A., Ruggiero, A., Darcey, L., Unbehagen, S. & Suomi, S. J. 2009
660   Interindividual differences in neonatal imitation and the development of action chains in
661   rhesus macaques. *Child development* **80**, 1057-1068. (DOI 10.1111/j.1467-
662   8624.2009.01316.x)
663   55. Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M. & Matsuzawa, T. 2004 Imitation in
664   neonatal chimpanzees (*Pan troglodytes*). *Developmental Science* **7**, 437-442. (DOI
665   10.1111/j.1467-7687.2004.00364.x)
666   56. Paukner, A., Ferrari, P. F. & Suomi, S. J. 2013 A comparison of neonatal imitation abilities
667   in human and macaque infants. In *Navigating the social world: What infants, children,*
668   *and other species can teach us* (eds. M. R. Banaji, & S. A. Gelman), New York: Oxford
669   University Press.
670   57. Paukner, A., Simpson, E. A., Ferrari, P., Mrozek, T. & Suomi, S. J. revision in preparation
671   Neonatal imitation predicts how infants engage with faces. *Developmental Science.*
672   58. Suddendorf, T., Oostenbroek, J., Nielsen, M. & Slaughter, V. 2012 Is newborn imitation
673   developmentally homologous to later social-cognitive skills? *Developmental*
674   *Psychobiology* **55**, 54-58. (DOI 10.1002/dev.21005)
675   59. Simpson, E. A., Paukner, A., Sclafani, V., Suomi, S. J. & Ferrari, P. F. in press Person
676   recognition during neonatal imitation in rhesus macaques. *PLoS ONE.*
677   60. Sclafani, V., Paukner, A., Suomi, S. J., Ferrari, P. F. under review Imitation promotes
678   affiliation in infant macaques at risk for impaired social behaviors.
679   61. Ullstadius, E. 1998 Neonatal imitation in a mother–infant setting. *Early Development and*
680   *Parenting* **7**(1), 1-8. (DOI 10.1002/(SICI)1099-0917(199803)7:1<1::AID-
681   EDP158>3.0.CO;2-J)
682   62. Pawlby, S. F. 1977 Imitative interaction. In *Studies in mother-infant interaction* (ed. H. R.
683   Schaffer), pp. 203-224. New York: Academic Press.
684   63. Stern, D. N. 1985 *The interpersonal world of the infant: A view from psychoanalysis and*
685   *developmental psychology*. New York: Basic Books.
686   64. Trevarthen, C. & Aitken, K. J. 2001 Infant intersubjectivity: research, theory, and clinical
687   applications. *Journal of Child Psychology and Psychiatry* **42**, 3-48. (DOI 10.1111/1469-
688   7610.00701)
689   65. Tronick, E. Z. 1989 Emotions and emotional communication in infants. *American*
690   *Psychologist* **44**, 112-119. (DOI 10.1037/0003-066X.44.2.112)
691   66. Trevarthen, C. 1974 Conversation with a two-month-old. *New Scientist* **2**, 230–235.
692   67. Kringelbach, M. L., Lehtonen, A., Squire, S., Harvey, A. G., Craske, M. G., Holliday, I. E.,
693   ... & Stein, A. 2008 A specific and rapid neural signature for parental instinct. *PLoS One*
694   **3**(2), e1664. (DOI 10.1371/journal.pone.0001664)
695   68. Caria, A., de Falco, S., Venuti, P., Lee, S., Esposito, G., Rigo, P., ... & Bornstein, M. H. 2012

696   Species-specific response to human infant faces in the premotor cortex. *NeuroImage*
697   **60**(2), 884-893. (DOI 10.1016/j.neuroimage.2011.12.068)
698   69. Swain, J. E. 2008 Baby stimuli and the parent brain: functional neuroimaging of the neural
699   substrates of parent-infant attachment. *Psychiatry* **5**(8), 28-36.
700   70. Goren, C. C., Sarty, M., & Wu, P. Y. 1975 Visual following and pattern discrimination of
701   face-like stimuli by newborn infants. *Pediatrics* **56**(4), 544-549.
702   71. Johnson, M. H. & Morton, J. 1991 *Biology and cognitive development: The case of face*
703   *recognition*. Oxford: Blackwell Publishing.
704   72. Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J. & Ahluwalia, J. 2000 Is there an
705   innate gaze module? Evidence from human neonates. *Infant Behavior and Development*
706   **23**(2), 223-229. (DOI 10.1016/S0163-6383(01)00037-6)
707   73. Farroni, T., Csibra, G., Simion, F. & Johnson, M. H. 2002 Eye contact detection in humans
708   from birth. *Proceedings of the National Academy of Sciences* **99**(14), 9602-9605. (DOI
709   10.1073/pnas.152159999)
710   74. Trevarthen, C. 1979 Communication and cooperation in early infancy: A description of
711   primary intersubjectivity. In *Before Speech* (ed. M. Bullowa), Cambridge, Cambridge
712   University Press. pp. 321-347.
713   75. Feldman, R. & Eidelman, A. I. 2007 Maternal postpartum behavior and the emergence of
714   infant–mother and infant–father synchrony in preterm and full-term infants: The role of
715   neonatal vagal tone. *Developmental Psychobiology* **49**(3), 290-302. (DOI
716   10.1002/dev.20220)
717   76. MacFarlane, A. 1977 *The Psychology of Childbirth.* London: Fontana.
718   77. Papoušek, H. & Papoušek, M. 1977 Mothering and the cognitive head-start:
719   Psychobiological considerations. In *Studies in Mother-Infant Interaction* (ed. H. R.
720   Shaffer), London: Academic Press.
721   78. Trevarthen, C. 1977 Descriptive studies in infant behavior. In *Studies in Mother-Infant*
722   *Interaction* (ed. H. R. Schaffer), London: Academic Press.
723   79. Ferrari, P. F., Paukner, A., Ionica, C. & Suomi, S. J. 2009 Reciprocal face-to-face
724   communication between rhesus macaque mothers and their newborn infants. *Current*
725   *Biology* **19**(20), 1768-1772. (DOI 10.1016/j.cub.2009.08.055)
726   80. Mancini, G., Ferrari, P. F. & Palagi, E. 2013 Rapid facial mimicry in geladas. *Scientific*
727   *Reports* **3**, 1527. (DOI 10.1038/srep01527)
728   81. Lavelli, M. & Fogel, A. 2002 Developmental changes in mother-infant face-to-face
729   communication: Birth to 3 months. *Developmental Psychology* **38**(2), 288-305. (DOI
730   10.1037/0012-1649.38.2.288)
731   82. Legerstee, M., Pomerleau, A., Malcuit, G. & Feider, H. 1987 The development of infants'
732   responses to people and a doll: Implications for research in communication. *Infant*
733   *Behavior and Development* **10**(1), 81-95. (DOI 10.1016/0163-6383(87)90008-7)
734   83. Murray, L. in press The Psychology of babies: How relationships support development from
735   birth to two. Constable & Robinson, London.
736   84. Anisfeld, M. 1991 Neonatal imitation. *Developmental Review*, **11**, 60-97. (DOI
737   10.1016/0273-2297(91)90003-7)
738   85. Meltzoff, A. N. & Gopnik, A. 1993 The role of imitation in understanding persons and
739   developing a theory of mind. In *Understanding other people's minds* (eds. S. Baron-
740   Cohen, H. Tager-Flushberg, & D. J. Cohen), pp. 335-366. Oxford, UK: University Press.
741   86. Uzgiris, I. C. 1991 The social context of infant imitation. In *Social influences and*

742   *socialization in infancy.* (eds. M. Lewis & S. Feinman), pp. 215-251. New York: Plenum
743   Press.
744   87. Ray, E. & Heyes, C. 2011 Imitation in infancy: the wealth of the stimulus. *Developmental*
745   *Science* **14**, 92-105. (DOI 10.1111/j.1467-7687.2010.00961.x)
746   88. Oostenbroek, J., Slaughter, V., Nielsen, M. & Suddendorf, T. 2013 Why the confusion
747   around neonatal imitation? A review. *Journal of Reproductive and Infant Psychology.*
748   Advance Online Publication. doi: 10.1080/02646838.2013.832180
749   89. Gibson, J. J. 1966 *The senses considered as perceptual systems*. Boston, MA: Houghton
750   Mifflin.
751   90. Gibson, J. J. 1979 *The ecological approach to visual perception*. Boston, MA: Houghton
752   Mifflin.
753   91. Feldman, R. 2007 Parent–infant synchrony and the construction of shared timing;
754   physiological precursors, developmental outcomes, and risk conditions. *Journal of Child*
755   *Psychology and Psychiatry* **48**(3-4), 329-354. (DOI 10.1111/j.1469-7610.2006.01701.x)
756   92. Cook, R., Bird, G., Catmur, C., Press, C. & Heyes, C. (in press) Mirror neurons: From origin
757   to function. *Behavioral and Brain Sciences*.
758   93. Oostenbroek, J., Slaughter, V., Nielsen, M., & Suddendorf, T. 2013 Why the confusion
759   around neonatal imitation? A review. *Journal of Reproductive and Infant Psychology*
760   **31**(4), 328-341. (DOI 10.1080/02646838.2013.832180)
761   94. Abravanel, E. & Sigafoos, A. D. 1984 Exploring the presence of imitation during early
762   infancy. *Child Development* **55**, 381-392.
763   95. Jacobson, S. W. 1979 Matching behavior in the young infant. *Child Development* **50**, 425-
764   430.
765   96. Meltzoff, A. N. & Moore, M. K. 1999 Resolving the debate about early imitation. In *The*
766   *Blackwell reader in developmental psychology* (ed. A. Slater & D. Muir), pp. 151-155.
767   Oxford: Blackwell.
768   97. Nagy, E. & Molnar, P. 2004 Homo imitans or homo provocans? Human imprinting model of
769   neonatal imitation. *Infant Behavior & Development* **27**, 54–63. (DOI
770   10.1016/j.infbeh.2003.06.004)
771   98. Meltzoff, A. N. & Moore, M. K. 1992 Early imitation within a functional framework: The
772   importance of person identity, movement, and development. *Infant Behavior and*
773   *Development* **15**, 479-505. (DOI 10.1016/0163-6383(92)80015-M)
774   99. Jones, S. S. 2006 Exploration or imitation? The effect of music on 4-week-old infants'
775   tongue protrusions. *Infant Behavior and Development* **29**(1), 126-130. (DOI
776   10.1016/j.infbeh.2005.08.004)
777   100. Jones, S. S. 1996 Imitation or exploration? Young infants' matching of adults' oral gestures.
778   *Child Development* **67**(5), 1952-1969. (DOI 10.1111/j.1467-8624.1996.tb01837.x)
779   101. Prechtl, H. F. R. 1974. The behavioural states of the newborn infant. *Brain Research* **76**,
780   185–212. (DOI 10.1016/0006-8993(74)90454-5)
781   102. Bjorklund, D. F. 1987 A note on neonatal imitation. *Developmental Review* **7**, 86-92. (DOI
782   10.1016/0273-2297(87)90006-2)
783   103. Field, T., Goldstein, S., Vega-Lahr, N. & Porter, K. 1986 Changes in imitative behavior
784   during early infancy. *Infant Behavior and Development* **9**, 415-421. (DOI 10.1016/0163-
785   6383(86)90015-9)
786   104. Maratos, O. 1998 Neonatal, early and later imitation: Same order phenomena? In *The*

787   *development of sensory, motor and cognitive capacities in early infancy: From*
788   *perception to cognition* (ed. F. Simion & G. Butterworth), p. 145-160. East Sussex, UK:
789   Psychology Press Ltd.
790   105. Kuhl, P. K. & Meltzoff, A. N. 1996 Infant vocalizations in response to speech: Vocal
791   imitation and developmental change. *The Journal of the Acoustical Society of America*
792   **100**(4), 2425. (DOI 10.1121/1.417951)
793   106. Hanna, E. & Meltzoff, A. 1993 Peer imitation by toddlers in laboratory, home and day-care
794   contexts: Implications for social learning and memory. *Developmental Psychology* **29**
795   701-710.
796   107. Kaplan, F. & Oudeyer, P. Y. 2007 The progress-drive hypothesis: An interpretation of early
797   imitation. In *Models and mechanisms of imitation and social learning: Behavioural,*
798   *social and communication dimensions* (eds. K. Dautenhahn & C. Nehaniv), pp. 361-377.
799   Cambridge: Cambridge University Press.
800   108. Heyes, C. 2001 Causes and consequences of imitation. *Trends in Cognitive Sciences* **5**, 253-
801   261. (DOI 10.1016/S1364-6613(00)01661-2)
802   109. Simpson, E. A., Paukner, A., Sclafani, V., Suomi, S. J. & Ferrari, P. F. in press Visual
803   attention during neonatal imitation in newborn macaque monkeys. *Developmental*
804   *Psychobiology*.
805   110. Vanderwert, R. E., Fox, N. A. & Ferrari, P. F. 2012 The mirror mechanism and mu rhythm
806   in social development. *Neuroscience Letters* **540**, 15-20. (DOI
807   10.1016/j.neulet.2012.10.006)
808   111. Ferrari, P. F., Tramacere, A., Simpson, E. A. & Iriki, A. 2013 Mirror neurons through
809   the lens of epigenetics. *Trends in Cognitive Sciences* **17**(9), 450-457. (DOI
810   10.1016/j.tics.2013.07.003)
811   112. Simpson, E. A., Fox, N. A., Tramacere, A. & Ferrari, P. F. in press Neonatal imitation and
812   an epigenetic account of mirror neuron development. *Behavioral and Brain Sciences*.
813   113. Murray, L., Fiori-Cowley, A., Hooper, R. & Cooper, P.J. 1996 The impact of postnatal
814   depression and associated adversity on early mother-infant interactions and later infant
815   outcome. *Child Development* **67**, 2512-2526.
816   114. Watson, J. S. 1979 Perception of contingency as a determinant of social responsiveness. In
817   *Origins of the infant's social responsiveness*. (ed. E. B. Thoman) Hillsdale, NJ: Erlbaum.
818   115. Ullstadius, E. 2000 Variability in judgment of neonatal imitation. *Journal of Reproductive*
819   *and Infant Psychology* **18**, 239–247. (DOI 10.1080/713683038)
820   116. Csibra, G. & Gergely, G. 2006 Social learning and social cognition: The case for
821   pedagogy. In *Processes of change in brain and cognitive development: Attention and*
822   *performance XXI* (eds. Y. Munakata & M. H. Johnson), pp. 249-274. New York: Oxford
823   University Press.
824   117. Nagy, E. 2006 From imitation to conversation: The first dialogues with human neonates.
825   *Infant and Child Development* **15**(3), 223-232. (DOI 10.1002/icd.460)
826   118. Cohen, J. 1988 Statistical power analysis for the behavioral sciences. Hillsdale, NJ:
827   Lawrence Erlbaum Associates.
828   119. Legerstee, M. 1991 The role of person and object in eliciting early imitation. *Journal of*
829   *Experimental Child Psychology* **51**(3), 423-433. (DOI 10.1016/0022-0965(91)90086-8)
830   120. Heimann, M. 2001 Neonatal imitation: A fuzzy phenomenon? In *Emerging cognitive*
831   *abilities in early infancy* (eds. F. Lacerda, C. von Hofsten, & M. Heimann), pp. 231-246.
832   London, England: Erlbaum.

833   121. Siller, M. & Sigman, M. 2004 From neonatal imitation to social cognition: Social and
834   cognitive pathways to developmental continuity. In *Social and moral development:*
835   *Emerging evidence on the toddler years* (eds. L. A. Leavitt & D. M. B. Hall) pp. 143-164.
836   New Brunswick, NJ: Johnson & Johnson Pediatric Institute.
837   122. Heimann, M. 2002 Notes on individual differences and the assumed elusiveness of neonatal
838   imitation. In *The imitative mind: development, evolution, and brain bases*. (A.N. Meltzoff
839   & W. Prinz eds.), Cambridge: Cambridge University Press, pp. 74-84.
840   123. Cheng, Y., Chou, K. H., Decety, J., Chen, I. Y., Hung, D., Tzeng, O. L. & Lin, C. P. 2009
841   Sex differences in the neuroanatomy of human mirror-neuron system: A voxel-based
842   morphometric investigation. *Neuroscience* **158**(2), 713-720. (DOI
843   10.1016/j.neuroscience.2008.10.026)
844   124. Silas, J., Levy, J. P., Nielsen, M. K., Slade, L. & Holmes, A. 2010 Sex and individual
845   differences in induced and evoked EEG measures of action observation.
846   *Neuropsychologia* **48**(9), 2417-2426. (DOI 10.1016/j.neuropsychologia.2010.03.004)
847   125. Page, J. & Boucher, J. 1998 Motor impairments in children with autistic disorder. *Child
848   Language Teaching and Therapy* **14**(3), 233-259. (DOI 10.1177/026565909801400301)
849   126. Rogers, S. J., Hepburn, S. L., Stackhouse, T. & Wehner, E. 2003 Imitation performance in
850   toddlers with autism and those with other developmental disorders. *Journal of Child
851   Psychology and Psychiatry* **44**(5), 763-781. (DOI 10.1111/1469-7610.00162)
852   127. Dawson, G., Meltzoff, A. N., Osterling, J. & Rinaldi, J. 1998 Neuropsychological
853   correlates of early symptoms of autism. *Child Development* **69**(5), 1276-1285. (DOI
854   10.1111/j.1467-8624.1998.tb06211.x)
855   128. Munson, J., Faja, S., Meltzoff, A., Abbott, R. & Dawson, G. 2008 Neurocognitive
856   predictors of social and communicative developmental trajectories in preschoolers with
857   autism spectrum disorders. *Journal of the International Neuropsychological Society*
858   **14**(6), 956. (DOI 10.10170S1355617708081393)
859   129. Williams, J. H., Whiten, A., Suddendorf, T. & Perrett, D. I. 2001 Imitation, mirror neurons
860   and autism. *Neuroscience & Biobehavioral Reviews* **25**(4), 287-295. (DOI
861   10.1016/S0149-7634(01)00014-8)
862   130. Yirmiya, N., Gamliel, I., Pilowsky, T., Feldman, R., Baron-Cohen, S. & Sigman, M. 2006
863   The development of siblings of children with autism at 4 and 14 months: Social
864   engagement, communication, and cognition. *Journal of Child Psychology and Psychiatry*
865   **47**(5), 511-523. (DOI 10.1111/j.1469-7610.2005.01528.x)
866   131. Soussignan, R., Courtial, A., Canet, P., Danon-Apter, G. & Nadel, J. 2011 Human newborns
867   match tongue protrusion of disembodied human and robotic mouths. *Developmental
868   Science* **14**, 385–394. (DOI 0.1111/j.1467-7687.2010.00984.x)
869   132. Tronick, E. 2007 *The neurobehavioral and social-emotional development of infants and
870   children*. New York, Norton.
871   133. Keller, H., Kärtner, J., Borke, J., Yovsi, R. & Kleis, A. 2005 Parenting styles and the
872   development of the categorical self: A longitudinal study on mirror self-recognition in
873   Cameroonian Nso and German families. *International Journal of Behavioral
874   Development* **29**(6), 496-504. (DOI 10.1080/01650250500147485)
875   134. Fogel, A., Toda, S. & Kawai, M. 1988 Mother-infant face-to-face interaction in Japan and
876   the United States: A laboratory comparison using 3-month-old infants. *Developmental
877   Psychology* **24**(3), 398-406. (DOI 10.1037/0012-1649.24.3.398)
878   135. Kärtner, J., Keller, H. & Yovsi, R. D. 2010 Mother–infant interaction during the first 3

879   months: The emergence of culture‑specific contingency patterns. *Child Development*

880   **81**(2), 540-554. (DOI 10.1111/j.1467-8624.2009.01414.x)

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).
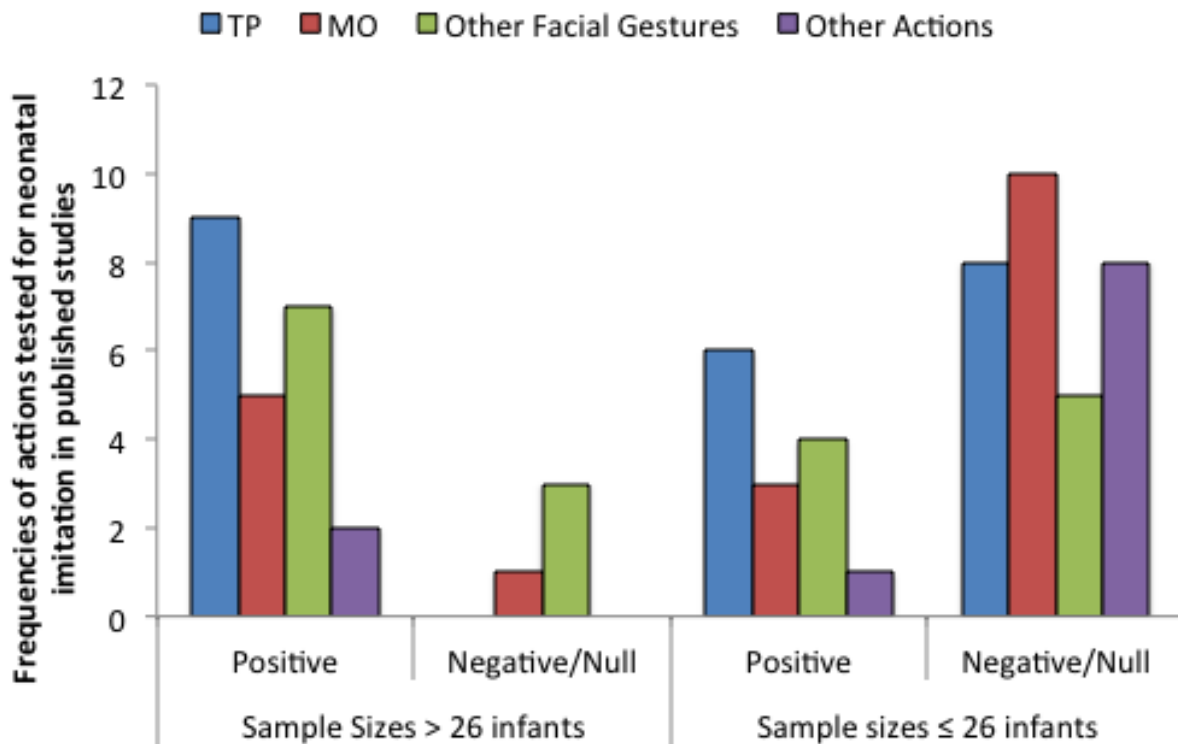
892
893 *Figure 1*. Among published studies of neonatal imitation in humans, across a variety of facial
894 and other actions (shown here: tongue protrusion (TP), mouth opening (MO), other facial
895 gestures, or other actions), sample size is a good predictor of whether the study found positive
896 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