



Published in final edited form as:

Dev Psychobiol. 2014 May ; 56(4): 864–870. doi:10.1002/dev.21146.

Visual attention during neonatal imitation in newborn macaque monkeys

Elizabeth A. Simpson^{1,2}, Annika Paukner¹, Stephen J. Suomi¹, and Pier F. Ferrari^{1,2}

¹Eunice Kennedy Shriver National Institute of Child Health and Human Development, Laboratory of Comparative Ethology, Poolesville, Maryland ²Dipartimento di Neuroscienze, Università di Parma, Parma, Italy

Abstract

Previous studies suggest that about 50% of rhesus macaque infants engage in neonatal imitation of facial gestures. Here we measured whether individual differences in newborn macaques' ($n = 49$) visual attention may explain why some infants imitate lipsmacking (LPS) and tongue protrusion (TP) gestures. LPS imitators, but not TP imitators, looked more to a human experimenter's face and to a control stimulus compared to non-imitators ($p = .017$). LPS imitation was equally accurate when infants were looking at faces and when they were looking away ($p = .221$); TP imitation was more accurate when infants were looking at faces ($p = .001$). Potentially, less attention is necessary for LPS imitation compared to TP imitation, as LPS is part of macaques' natural communicative repertoire. These findings suggest that facial gestures may differentially engage imitators and non-imitators, and infants' visual attention during neonatal assessments may uncover the conditions that support this skill.

Keywords

Rhesus Macaque; Infant; Visual Attention; Neonatal Imitation; Monkey; Newborn; Social behavior; Communication; Facial gestures; Mother-infant interaction; Mirror neuron system

Facial communication is common in mammalian species, and especially in primates (Brecht & Freiwald, 2012). Rhesus macaque (*Macaca mulatta*) mother-infant pairs, like humans, exhibit complex socioemotional interactions, including facial gesturing and sustained mutual gaze (Ferrari, Paukner, Ionica, & Suomi, 2009a; Ferrari, Visalberghi, Paukner, Fogassi, Ruggiero, & Suomi, 2006). In the first week of life, macaque infants imitate facial gestures of adults (Ferrari et al., 2009a), suggesting a functioning action-perception mechanism from birth (Ferrari, Vanderwert, Paukner, Bower, Suomi, & Fox, 2012). Importantly, imitation is gesture-specific, and recent work has shown that it cannot be explained as a consequence of general arousal (Ferrari et al., 2006; Nagy, Pilling, Orvos, & Molnar, 2012; Paukner, Ferrari, & Suomi, 2011). In addition, neonatal imitation is not a simple reflex, but rather a response with characteristics that suggest a voluntary nature and complex modulation based on self-

Correspondence to: Elizabeth A. Simpson.

Author Contributions Statement

PFF is the Principal Investigator of the study and was responsible for obtaining funding and supervising data collection. SJS is the Senior Research Associate who supervised the study. EAS and AP collected and coded the data. EAS analyzed the data and prepared the figure. PF, AP, and EAS interpreted the data and wrote the manuscript. All authors reviewed the manuscript.

Competing financial interests

The authors declare no competing financial interests.

other tuning. In fact, infants remember a gesture after a delay and initiate social interactions with that gesture, revealing sophisticated and flexible affective communication (Paukner et al., 2011). Neonatal imitation occurs in a variety of primates, including humans (Meltzoff & Moore, 1977, 1983), chimpanzees (Bard, 2005, 2007; Bard & Russell, 1999; Myowa, 1996; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004), and rhesus macaques (Ferrari et al., 2009), suggesting it may be a shared behavioral adaptation.

Within each species there is great variability in imitative ability: some infants consistently imitate, some imitate only sometimes, and others show no evidence of imitation (Ferrari, Paukner, Ruggiero, Darcey, Unbehagen, & Suomi, 2009b; Heimann, 2002); however, these individual differences are rarely addressed (Heimann, 1989). Understanding individual differences in neonatal imitation may explain why some research groups have been unable to replicate neonatal imitation in humans. In addition, examining factors potentially related to individual differences in imitative ability, such as visual or motor maturity, could help us to more fully understand the phenomenon. However, a recent study on newborn macaques (Ferrari et al., 2009b) showed that gross measurements of motor maturity or visual tracking of objects do not differ between imitators and non-imitators, suggesting that more subtle factors related to basic capacities of attending to social stimuli may account for the differences found in infant imitative behaviors at birth.

In fact, little is known about infants' visual attention during neonatal assessments, as only a small number of studies to date have directly examined visual attention in relation to neonatal imitative ability. One study found that infant rhesus macaques are more visually attentive during neonatal imitation assessments when stimuli are dynamic, compared to static, but found no differences in visual attention related to imitative skills (Ferrari et al., 2006). Three-month-old human infants' habituation speed to visual stimuli—which is believed to reflect information processing speed—fails to predict deferred imitation performance at 8- to 12-months of age (Courage, Howe, & Squires, 2004). Only one study in humans has directly linked individual differences in visual attention to neonatal imitative skills (Heimann, 1989). In this study, imitation in human infants—at 2- to 3-days of age, 3 weeks of age, and 3 months of age—predicted visual attention at 3 months of age: imitators had fewer looks away during a face-to-face interaction at 3 months of age, compared to non-imitators (Heimann, 1989). However, visual attention during the neonatal imitation assessment was not reported, so it remains unknown whether newborns' visual attention differs as a function of imitative ability.

We predicted that macaque infants who are imitators might simply be paying more attention to facial gestures than non-imitators; therefore, imitators may be more likely to see the gestures and copy them correctly. If this is the case, all infants may be capable of neonatal imitation, but some fail to demonstrate their ability due to inattention. We also predicted that imitators might be more attentive to dynamic social stimuli (facial gestures), compared to a dynamic nonsocial stimulus (rotating disk). Finally, we predicted that all infants might produce more matching gestures when attentive, compared to when inattentive. To test these predictions, we measured infant macaques' visual attention and gestures in the first week of life in a face-to-face interaction task with a human experimenter, who provided facial gestures to elicit infants' imitative responses. Infants were videotaped every-other day, while they viewed one of three stimuli (experimenter producing one of two gestures or presenting a disk), for 3 minutes, while the stimulus alternated between static (still-face or still-disk) and dynamic (two facial gestures, rotating disk) periods. This design is ideal for testing a large sample of infants to determine whether visual attention can account for differences in neonatal imitative responses.

Methods

Subjects

The National Institute of Child Health and Human Development Animal Care and Use Committee approved this study. We tested 49 infant rhesus macaque monkeys (*Macaca mulatta*), 21 females and 28 males, and 27 LPS imitators and 22 non-imitators. Two infants were born via caesarean section; all infants were full-term, of normal birth weights, and born without complications. On the day of birth, infants were separated from their mothers and were reared by humans in a nursery facility. Infants were individually housed in incubators (51cm × 63.8cm × 64.3cm), containing inanimate surrogate mothers covered with fleece fabric as well as loose pieces of fleece fabric and various rubber and plush toys. Infants could see and hear other infants, but could not touch them. Further details on rearing methodologies have been published elsewhere (Ferrari et al., 2006; Shannon, Champoux, & Suomi, 1998).

Procedure

Infants were tested three times a day, every other day, in the first week of life (days 1–2, 3–4, 5–6, and 7–8), for up to four days. Before testing and during coding, we assessed infants' states (Prechtl, 1974; Nagy et al., 2012). In order to be included, infants had to have their eyes open and had to show signs of active orientation towards stimuli appearing in their visual field (e.g., the experimenter approaching the incubator). Infants were tested within an hour of feeding to ensure they were not fussy due to hunger. During transportation to the testing room, infants clung to the arm of the experimenter, and had to show signs of body reactivity towards changes in posture and support instability. Individual test sessions were excluded from analysis if infants were excessively fussy or sleepy, or if they did not show the signs of reactivity to stimuli required to demonstrate a sufficient state of alertness. We additionally assessed infants' states during testing by measuring yawning, but found no differences between LPS imitators' and non-imitators' yawn frequencies, $p > .10$. This assessment of infants' state resulted in 43 infants contributing data on days 1–2, 47 infants on days 3–4, 46 infants on days 5–6, and 44 infants on days 7–8.

Testing typically took place at 9:30am, 12:30pm, and 2:30pm; there was at least an hour between each test session. The procedure was the same as detailed by Paukner et al. (2011). A demonstrator silently presented infants with three stimuli, one at a time, approximately 30 cm away, at eye-level with the infant: a lipsmacking gesture (LPS, rapid opening and closing of the mouth; ~100 openings/20s), a tongue protrusion gesture (TP, protrusion and retraction of the tongue; ~seven openings/20s), and a nonsocial control condition (CTRL; a white plastic disk with orthogonal stripes—which were either black and red or green and yellow—slowly rotated 180° clockwise and counter-clockwise). Each stimulus type was presented once a day to infants, one at each time of day; the order of stimulus presentations remained the same for each infant but was randomized between infants. In each test session, one experimenter held the infant, a second experimenter—the demonstrator—served as the source of the stimuli, and a third experimenter was the time-keeper who ensured stimuli were presented for appropriate lengths. All sessions were videotaped using a Sony Digital Video camcorder ZR600. Individual demonstrators were randomly assigned to be the models in the LPS and TP conditions, and whenever possible, remained consistent within each infant (e.g., the LPS model was always the same person for a given infant).

At the beginning of a trial, a 40 sec baseline was conducted, in which the demonstrator displayed a passive/neutral facial expression (or the still disk in CTRL). The demonstrator then displayed a facial gesture (LPS or TP, or rotating the disk in CTRL) for 20 seconds, followed by a passive/neutral facial expression (still disk in CTRL) period for 20 sec. This

gesture-neutral face sequence was repeated three times, with the final neutral expression period lasting 40 sec.

Coding Reliability and Analysis

All infants' eye movements were coded off-line, frame-by-frame (30 frames per second) from videotape, using the Noldus Observer XT; Leesburg, VA. Coders scored the durations of infants' look location (at stimulus or away from stimulus). Coders separately coded the frequency of infants' gesturing (LPS, TP), as well as other mouth-movements (e.g., yawns, thumb-in-mouth). Observers were blind to the stimulus type.

Infants were classified as LPS imitators and non-imitators, as defined previously (Ferrari et al., 2009b), based on whether they produced a greater increase in facial gestures matching the demonstrator (LPS) in the stimulus period, relative to the baseline period, in the LPS condition, compared to the increase in LPS gestures in the baseline and stimulus periods in the CTRL condition (i.e., difference score in LPS condition had to be greater than difference scores in CTRL condition to be classified as LPS imitator). Gestures were averaged across days, and infants who displayed a higher average frequency of matched gestures during the stimulus period than the baseline period, compared to the CTRL condition, were classified as LPS imitators. Infants who failed to match gestures with a higher average frequency in the stimulus period than in the baseline period, or who had an equal or higher frequency of matched gestures in the CTRL condition, were classified as non-imitators. Though not reported here, infants were also classified as TP imitators and non-imitators, using the same criteria as described above (Ferrari et al., 2009b); however, we found no effects of this TP imitator variable, so it was dropped from the analysis.

Inter-observer reliability was assessed between an anchor observer and one of two additional observers for a randomly selected 20% of test sessions. The average level of agreement among observers for the total look duration at the stimulus was high ($r = .91, p < .001, n = 110$), as was the level of agreement among observers for the frequencies of gestures for LPS ($r = .961, p < .001, n = 66$), and for TP ($r = .965, p < .001, n = 66$). For analysis, we averaged data from all test days and adjusted data of each phase to a common time frame (20 sec), to control for the different lengths of the trial phases.

Results

All *t* tests are two-tailed and include a least significant difference (LSD) adjustment for multiple comparisons, unless otherwise indicated. There were no main effects or interactions for infants' sex ($ps > .10$), so this factor is not reported in subsequent analyses. Examining the increase in gesturing from the baseline to the stimulus phase, we find that LPS imitators increased LPS in the LPS condition, on average, by 4.84 gestures ($SD = 4.13$, range = .25 to 20.75), and TP imitators increased TP in the TP condition, on average, by 7.26 gestures ($SD = 3.89$, range = 1.5 to 15).

Do imitators look more than non-imitators?

A mixed design $2 \times 3 \times 3$ analysis of variance (ANOVA) with the between subjects factor of LPS Imitator-Status (Imitator, Non-Imitator), and the within subjects factors of Condition (LPS, TP, CTRL), and Stimulus Period (Baseline 1, Stimulus, Baseline 2), revealed a main effect of LPS Imitator-Status ($F(1,47) = 6.73, p = .013, \eta^2 = .125$). Throughout all conditions and periods LPS imitators looked more to the stimulus ($M = 15.59$ sec, $SD = 5.95$) compared to non-imitators ($M = 11.38$, $SD = 5.95$), Figure 1A. There was a main effect of Stimulus Period ($F(2,94) = 8.46, p < .001, \eta_p^2 = .153$), in which there was more looking during the Baseline 1 and Stimulus periods ($M = 14.56$ sec, $SD = 6.69$, and $M =$

13.94 sec, $SD = 5.71$, respectively), compared to the Baseline 2 period ($M = 13.41$ sec, $SD = 6.65$), $ps < .05$. There was an interaction between LPS Imitator-Status and Stimulus Period ($F(2,94) = 4.40$, $p = .015$), in which non-imitators looked more during the Baseline 1 ($M = 11.74$ sec, $SD = 6.34$) and Stimulus ($M = 12.00$ sec, $SD = 5.98$) phases compared to the Baseline 2 ($M = 10.88$ sec, $SD = 6.38$) $ps < .05$, while LPS imitators looked the most during Baseline 1 ($M = 16.85$ sec, $SD = 6.17$), and less during the Stimulus ($M = 15.53$ sec, $SD = 5.06$) and Baseline 2 ($M = 15.48$ sec, $SD = 6.23$), $ps < .05$. There was no main effect of condition ($p = .161$), nor any other interactions ($ps > .05$).

Does looking increase imitation in the stimulus period?

In the first analysis, gesture and visual attention were coded separately (not concurrently), so we did not have precise timestamps for each gesture. Therefore, to explore whether there was an increase in imitation when infants were looking at the gesturing face, compared to when they were not looking, we coded gesturing and looking concurrently in a random subsample of infants ($n = 26$). To this end, a 2×2 ANOVA assessed the proportion of imitative gestures produced (the frequency of matching gestures divided by the total frequency of all LPS and TP gestures) during the stimulus period, across the within subjects variables of Visual Attention (Looking at Stimulus, Not Looking at Stimulus) and Condition (LPS, TP). There was an interaction between Visual Attention and Condition, ($F(1,24) = 11.27$, $p = .003$), Figure 1B. There were no other main effects or interactions ($ps > .05$). Follow up tests revealed that in the TP condition, infants produced a higher proportion of imitative gestures when looking at the face ($M = .57$, $SD = .14$), compared to when looking away ($M = .45$, $SD = .17$), $p = .001$, $d = .762$. In contrast, in the LPS condition, infants' proportion of imitative gestures was the same when looking at the face ($M = .42$, $SD = .21$) as when looking away ($M = .47$, $SD = .30$), $p = .221$. We also confirmed that there were no differences in the LPS and TP condition, in overall gesture (LPS and TP) frequencies produced in the stimulus period, when looking at the face ($M = 38.98$, $SD = 21.02$), or when looking away ($M = 16.90$, $SD = 15.56$), $ps > .05$.

Discussion

Neonatal imitation appears to be a behavior shared across numerous primate species (humans, chimpanzees, rhesus macaques), all of which exhibit individual differences in imitative abilities. It remains unknown why some infants imitate and some infants do not. In the present study, we found that in rhesus macaque infants, LPS imitators looked more at the stimuli than non-imitators, suggesting that perhaps imitators are better at matching gestures simply because they are more attentive than non-imitators. However, this explanation only applied to TP gestures; increased looking was associated with increased imitation for TP, but not for LPS. Potentially, LPS is a more natural communicative gesture, commonly observed between mothers and infants (e.g., Ferrari et al., 2009a), and therefore less visual attention is required for LPS imitation compared to TP imitation. Furthermore, while LPS involves a relatively simple pattern of behavior (i.e., alternation between mouth opening and closing), which probably relies on limited sensorimotor coordination, TP involves a more complex coordination between the mouth and the tongue. It is therefore possible that, from a perceptual viewpoint, in order to imitate TP, greater cognitive effort and increased attentional load may be required, compared to LPS imitation.

Consistent with previous work (Ferrari et al., 2006), we found macaque infants were more attentive during the dynamic stimulus, compared to the static stimulus baseline period that followed; however, we additionally found that attention across the stimulus phases differed for LPS imitators and non-imitators. Namely, while non-imitators showed greater attention during the first baseline and stimulus phases, LPS imitators showed the most attention in the

first baseline period, compared to the stimulus and second baseline periods. This finding suggests that there are differences in interest in social partners (i.e., human experimenter) between imitators and non-imitators, even prior to any communicative interaction, and this may reflect how their brains are differently tuned for processing social information and for responding to facial gestures. Previous work (Ferrari et al., 2006) only measured the frequencies of looking towards stimuli, whereas in the present study we measured the durations of looking, which may explain why previous work found no differences in visual attention between imitators and non-imitators.

It is also noteworthy that LPS imitators displayed greater amounts of visual attention, relative to non-imitators, across all stimulus conditions, including the non-social control (disk). In addition to being more interested in social partners, LPS imitators may also be more aware of or interested in interacting with objects in their environment. It is also possible that LPS imitators' visual system is more developed than non-imitators' and therefore imitators have a greater capacity to focus on objects in their environment. This latter hypothesis, however, seems unlikely since previous work demonstrated that imitators and non-imitators are equally capable of tracking objects moving in front of them (Ferrari et al., 2009b) and do not display other differences with respect to several indices of visual system functioning.

One unexpected result was that non-imitators looked more during the Baseline 1 and Stimulus phases compared to Baseline 2, while LPS imitators looked the most during Baseline 1 and less during the Stimulus and Baseline 2 phases. While it is not surprising that both groups of infants attend less to the stimuli over the course of the test session, we can only speculate as to why LPS imitators and non-imitators attended less at different points. Non-imitators demonstrated no differences in visual attention to the first static stimulus and the dynamic stimulus, perhaps reflecting their inability to efficiently process this visual information. In contrast, LPS imitators were the most attentive in the very first static stimulus period, and their visual attention dropped during the dynamic phase, perhaps due to the fact that they were concentrating on producing the gestures, and therefore spent less time watching the gestures.

Individual differences in visual attention show some stability across development: human infants between 4 and 24 weeks old display stable levels of visual attention towards social and nonsocial features of their environments (Messinger, Ekas, Ruvolo, & Fogel, 2012). Since increased visual attentiveness appears to increase TP imitation, this leads to the question of why some infants are more attentive than others, and the extent to which this increased visual attention is specific to social stimuli. Given that individual differences in visual attention to faces appear in human neonates only hours old, the cause is likely biological, rather than socio-cultural, perhaps due to individual differences in neurogenetic or neuroendocrine systems (Connellan, Baron-Cohen, Wheelwright, Batki, & Ahluwalia, 2000).

However, given that visual attention did not entirely explain imitative ability—at least for LPS gestures—it is necessary to consider other factors which may contribute to this individual difference, such as the infant's temperament (e.g., extraversion), cognitive ability (e.g., working memory, information processing speed), motor development, maturity of the mirror neuron system (a system which underlies action-perception), or inhibitory control (e.g., control over facial gestures). There appear to be no differences between infant macaque imitators and non-imitators, in terms of their weight, postural maturity, capacity to track visual stimuli, or emotional behavior (Ferrari et al., 2009b). However, individual differences in neonatal imitation are related to differences in the maturity of the motor system (Ferrari et al., 2009b), and as past studies have shown, observing facial gestures

activates parts of the mirror neuron system, which is found in the parietal and premotor areas (Ferrari et al., 2012). In fact, infant macaque imitators consistently outperform non-imitators in a standardized neobehavioral assessment scale—which measures reaching-grasping and fine hand motor control—administered during the first month of life (Ferrari et al., 2009b). Additionally, infants who consistently imitate appear to be better at remembering gestures and initiating social interactions after a delay (Paukner et al., 2011), and are better at recognizing human social partners (Simpson, Paukner, Sclafani, Suomi, & Ferrari, under review), suggesting imitators may be at a social advantage, compared to their less-imitative peers.

Longitudinal (Suddendorf, Oostenbroek, Nielsen, & Slaughter, 2012) and comparative (de Waal & Ferrari, 2010) studies would be particularly insightful for determining the causes of individual differences in neonatal imitation. A bottom-up approach to social cognition within a comparative perspective (de Waal & Ferrari, 2010) will provide unique insights into the development of early socioemotional exchanges, behaviors that are likely phylogenetically continuous (Hecht, Patterson, & Barbey, 2012). Though differences in visual attention cannot account for all individual differences in imitative abilities, visual attention during social interactions is critically important for ensuring that communicative exchanges are accurately conveyed and received. As Heimann (2002, p.80) describes, “Neonatal imitation is not a direct response, not even a certain response, but a response that emerges from the interplay between what the child sees (e.g., tongue movements), what the child wants (motivational state, alertness, and attention) and what the child selects to do (motor output).” Infants with greater interest in social partners likely gain more experiences viewing communicative interactions with adults than infants who do not show the same amount of social interest. Such early imitative exchanges may be crucially important for shaping infants’ early social relationships, particularly those between mothers and infants (Bjorklund, 1987; Trevarthen, 1998).

Acknowledgments

This research was supported by the Division of Intramural Research, NICHD, and NICHD P01HD064653. We thank Valentina Sclafani, Seth Bower, Michelle Miller, Judy Songrady, and Angela Ruggiero for help in collecting the data. Thanks to John Richards and Nathan Fox for data analysis suggestions.

References

- Bard, KA. Emotions in chimpanzee infants: The value of a comparative developmental approach to understand the evolutionary origins of emotions. In: Nadel, J.; Muir, D., editors. *Emotional Development*. Oxford University Press; 2005. p. 31-60.
- Bard KA. Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Animal Cognition*. 2007; 10:233–242.10.1007/s10071-006-0062-3 [PubMed: 17180698]
- Bard, KA.; Russell, CL. Evolutionary foundations of imitation: Social cognitive and developmental aspects of imitative processes in non-human primates. In: Nadel, J.; Butterworth, G., editors. *Imitation in infancy*. Cambridge University Press; 1999. p. 89-123.
- Bjorklund DF. A note on neonatal imitation. *Developmental Review*. 1987; 7:86–92.10.1016/0273-2297(87)90006-2
- Brecht M, Freiwald WA. The many facets of facial interactions in mammals. *Current Opinions in Neurobiology*. 2012; 22:259–266.10.1016/j.conb.2011.12.003
- Connellan J, Baron-Cohen S, Wheelwright S, Batki A, Ahluwalia J. Sex differences in human neonatal social perception. *Infant Behavior and Development*. 2000; 23:113–118.10.1016/S0163-6383(00)00032-1
- Courage ML, Howe ML, Squires SE. Individual differences in 3.5-month-olds’ visual attention: What do they predict at 1 year? *Infant Behavior and Development*. 2004; 27:19–30.10.1016/j.infbeh.2003.05.004

- de Waal FBM, Ferrari PF. Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*. 2010; 14:201–207.10.1016/j.tics.2010.03.003 [PubMed: 20363178]
- Ferrari PF, Visalberghi E, Paukner A, Fogassi L, Ruggiero A, Suomi SJ. Neonatal imitation in rhesus macaques. *PLoS Biology*. 2006; 4:e302.10.1371/journal.pbio.0040302 [PubMed: 16953662]
- Ferrari PF, Paukner A, Ionica C, Suomi SJ. Reciprocal face-to-face communication between rhesus macaque mothers and their newborn infants. *Current Biology*. 2009a; 19:1768–1772.10.1016/j.cub.2009.08.055 [PubMed: 19818617]
- Ferrari PF, Paukner A, Ruggiero A, Darcey L, Unbehagen S, Suomi SJ. Interindividual differences in neonatal imitation and the development of action chains in rhesus macaques. *Child Development*. 2009b; 80:1057–1068.10.1111/j.1467-8624.2009.01316.x [PubMed: 19630893]
- Ferrari PF, Vanderwert RE, Paukner A, Bower S, Suomi SJ, Fox NA. Distinct EEG amplitude suppression to facial gestures as evidence for a mirror mechanism in newborn monkeys. *Journal of Cognitive Neuroscience*. 2012; 24:1165–1172.10.1162/jocn_a_00198 [PubMed: 22288390]
- Hecht EE, Patterson R, Barbey AK. What can other animals tell us about human social cognition? An evolutionary perspective on reflective and reflexive processing. *Frontiers in Human Neuroscience*. 2012; 6:1–13.10.3389/fnhum.2012.00224 [PubMed: 22279433]
- Heimann M. Neonatal imitation, gaze aversion, and mother-infant interaction. *Infant Behavior and Development*. 1989; 12:495–505.10.1016/0163-6383(89)90029-5
- Heimann, M. Notes on individual differences and the assumed elusiveness of neonatal imitation. In: Meltzoff, AN.; Prinz, W., editors. *The imitative mind: Development, evolution, and brain bases*. Cambridge University Press; 2002. p. 74-84.
- Meltzoff AN, Moore MK. Imitation of facial and manual gestures by human neonates. *Science*. 1977; 198:75–78.10.1126/science.198.4312.75 [PubMed: 17741897]
- Meltzoff AN, Moore MK. Newborn infants imitate adult facial gestures. *Child Development*. 1983; 54:702–709.10.2307/1130058 [PubMed: 6851717]
- Messinger DS, Ekas NV, Ruvolo P, Fogel AD. “Are you interested, baby?” Young infants exhibit stable patterns of attention during interaction. *Infancy*. 2012; 17:233–244.10.1111/j.1532-7078.2011.00074.x [PubMed: 22523476]
- Myowa M. Imitation of facial gestures by an infant chimpanzee. *Primates*. 1996; 37:207–213.10.1007/BF02381408
- Myowa-Yamakoshi M, Tomonaga M, Tanaka M, Matsuzawa T. Imitation in neonatal chimpanzees (*Pan troglodytes*). *Developmental Science*. 2004; 7:437–442.10.1111/j.1467-7687.2004.00364.x [PubMed: 15484592]
- Nagy E, Pilling K, Orvos H, Molnar P. Imitation of tongue protrusion in human neonates: Specificity of the response in a large sample. *Developmental Psychology*. 2012 Advance online publication. 10.1037/a0031127
- Paukner A, Ferrari PF, Suomi SJ. Delayed imitation of lipsmacking gestures by infant rhesus macaques (*Macaca mulatta*). *PLoS ONE*. 2011; 6:e28848.10.1371/journal.pone.0028848 [PubMed: 22174913]
- Prechtl HFR. The behavioural states of the newborn infant (a review). *Brain Research*. 1974; 76:185–212.10.1016/0006-8993(74)90454-5 [PubMed: 4602352]
- Shannon C, Champoux M, Suomi SJ. Rearing condition and plasma cortisol in rhesus monkey infants. *American Journal of Primatology*. 1998; 46:311–321.10.1002/(SICI)1098-2345(1998)46:4<311::AID-AJP3>3.0.CO;2-L [PubMed: 9839904]
- Simpson EA, Paukner A, Sclafani V, Suomi SJ, Ferrari PF. Person recognition during neonatal imitation in rhesus macaques. *Psychological Science*. under review.
- Suddendorf T, Oostenbroek J, Nielsen M, Slaughter V. Is newborn imitation developmentally homologous to later social-cognitive skills? *Developmental Psychobiology*. 2012; 55:54–58.10.1002/dev.21005
- Trevarthen, C. The concept and foundations of infant intersubjectivity. In: Braten, S., editor. *Intersubjective communication and emotion in early ontogeny*. Cambridge University Press; 1998. p. 15-46.

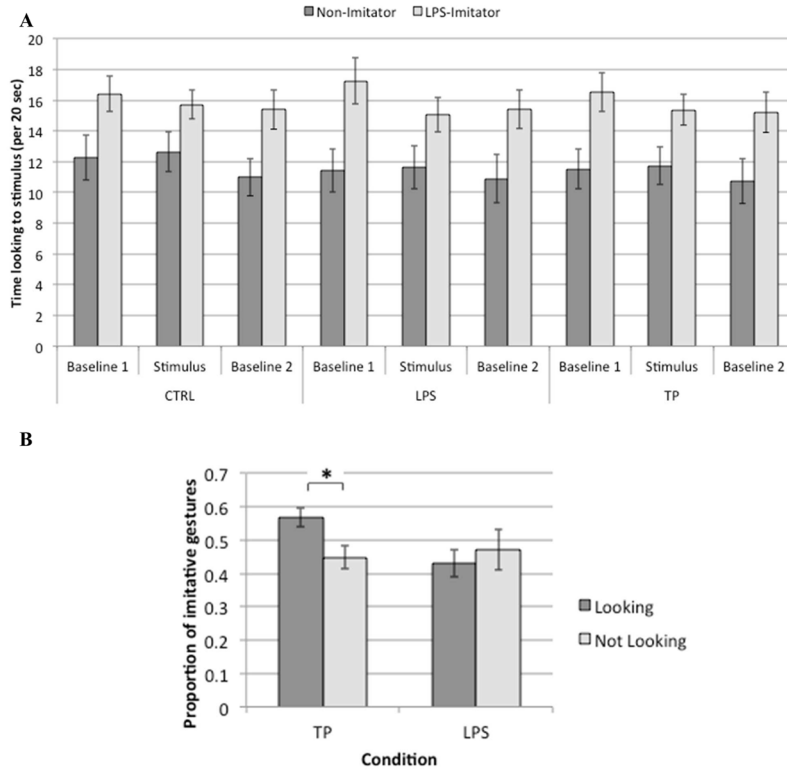


Figure 1. Imitation and visual attention. Graph A: Time (in seconds) looking at the stimulus across all three conditions—control (CTRL) disk, lipsmacking (LPS) gesture, and tongue protrusion (TP) gesture—during the three stimulus phases (static Baseline 1, dynamic Stimulus, and static Baseline 2). Dark grey bars represent infants who were LPS imitators, and light grey bars represent infants who were not LPS imitators. Graph B: Proportion of imitative gestures for TP and LPS conditions when infants were looking at the face (dark grey), compared to when looking away (light grey); $*p = .001$. In both graphs error bars reflect between subjects standard error of the mean.