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# Imitation promotes affiliation in infant macaques at risk for impaired social behaviors

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## Abstract

Parental responsiveness and synchronization during early face-to-face interactions between mother and infant have been theorized to affect a broad spectrum of positive developmental outcomes in social and cognitive infant growth and to facilitate the development of a sense of self in the baby. Here we show that being imitated can significantly affect the behavior of nursery-reared infant monkeys, which are at an increased risk for developing aberrant social behaviors. Infants look longer and lipsmack more at an experimenter both during imitation and after being imitated. These results demonstrate that from early in life imitation might be used as a privileged form of communication by adults to enhance infants' visual engagement and their social communication. Imitation may therefore be useful to counteract the negative effects of early social adversities.

### Keywords

imitation; social development; early communication; synchronization

During early face-to-face interactions, mothers often imitate infants' facial gestures and mirror the infants' level of arousal and emotions (Meltzoff & Moore, 1989; Stern, 1985). By providing turn-taking exchanges and contingent responses to infant signals, caregivers enable infants to match and share their own feelings and affects with those of another human being (Feldman, 2007; Henning & Striano, 2011; Stern, 1985, 2000; Tarabulsy, Tessier, & Kappas, 1996). From early on, infants are able to detect this social contingency between their own actions and external responses (Gergerly & Watson, 1996; Meltzoff & Moore, 1977, 1989, 1994; Stern, 1974; Trevarthen, 1979; Tronick & Brazelton, 1977) and are particularly sensitive to the imitative quality of the behavior of the responding partner (Striano, Reid, & Hoehl, 2006; Tarabulsy et al., 1996).

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Indeed, the quality of such interactions has been theorized to be a crucial developmental landmark for early forms of communication, facilitating social, emotional, and cognitive growth and influencing infants' subsequent sensitivity and responsiveness to social and non-social stimuli (Heimann, 1998; Stern, 2000). Several studies in which face-to-face exchanges between mothers and infants have been manipulated by using the still-face paradigm demonstrated that infants are sensitive not only to the contingency structure of face-to-face interactions, but also to disruptions in the contingent behavior of the social partner (Tronick, Als, Adamson, Wise, & Brazelton, 1978; Tronick & Cohn, 1989). If the mother is physically or emotionally unavailable, infant are more likely to experience a behavioral and physiological disorganization, due to either temporal or chronic loss of an important source of stimulation and affect modulation (Field, 1994; Tronick & Reck, 2009). In humans, a lack of or disturbances to this early interaction experience, such as in institutionalized children (Nelson, Fox, & Zeanah, 2013; Wismer Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005) or in infants of mothers who have experienced postnatal depression, might act as a mediator of poor and adverse child developmental outcomes, including language and cognitive problems (Wismer Fries et al., 2005; Murray, Cooper, Wilson, & Romaniuk, 2003; Murray, Fiori-Cowley, Hooper, & Cooper), impaired attachment relationships (Lyons-Ruth, Connel, Grunebaum, & Botein, 1990) and behavioral problems(Kouzakova, van Baaren, & Knippenberg, 2010).

In nonhuman primates, the effects of early adverse experiences have been studied by comparing animals reared by their mothers to those maternally separated at birth and reared in a nursery in a relative impoverished social environment, where infants' medical and nutritional needs were met, but their social and psychological needs were not met. Interestingly, many of the behavioral and socio-emotional characteristics of nursery-reared monkeys parallel features of the affective disorders showed by human infants with early adverse experiences, such as poor emotional/cognitive development and impaired socialization (Corcoran et al., 2011; Gilmer & McKinney, 2003; Machado & Bachevalier, 2003). Nursery-reared macaques therefore represent an optimal model to test the possible effects of early face-to-face exchanges on social-affective development.

Being imitated has been shown to increase gaze engagement between mothers and their infants (Field, 1977) and positively impact social interactions in children with impaired social competence, such as children affected by autistic syndrome disorders (Nadel et al., 2000). Moreover, theoretical accounts and recent empirical work have demonstrated positive effects of matching and synchronization of behaviors on social relationships and prosocial behaviors in adult human and non-human primates (Heyes, 2009; Hurley, 2008; Gallese, 2003; Paukner, Suomi, Visalberghi, & Ferrari, 2009). However, the effect of imitation on social interactions has not been thoroughly explored in infancy and therefore a non-human primate model to investigate this phenomenon might shed light on the psychological processes that underlie these positive effects of imitation. Such explorations may lead to the development of potential behavioral interventions in early development aimed at ameliorating social behaviors in infants with compromised social skills (e.g., Escalona, Field, Nadel, & Lundy, 2002).

Here we tested the hypothesis that in infancy being in synchrony with a caregiver can impact social interactions, thus promoting newborn visual engagement and affiliation. More specifically, we expected that imitating infants' facial gestures would increase their interest and frequency of affiliative behaviors towards a human model. Infants' engagement and affiliation toward the experimenter was assessed in term of frequency of lipsmacking, a core affiliative gesture in macaques involving rapid opening and closing of the mouth and lips. This facial gesture is present in all macaque species and communicates an intention to engage in affiliative interactions (Maestripieri, 1997). Moreover, recent work reported that lipsmacking is typically displayed by macaque mothers towards their own infants during face-to-face interactions in combination with mutual gaze, resembling the ritualized "motherese" between human mothers and infants (Ferrari, Paukner, Ionica, & Suomi, 2009).

Moreover, we hypothesized that the model's high levels of responsiveness would facilitate infants' understanding that they are effective agents in the world, and therefore we predicted this would stimulate infants to further explore the environment and to assess the consequences of their actions on it. We therefore investigated whether being imitated could affect infants' motor behavior, promoting oral and manual exploration of the surrounding physical environment.

## Methods

### Animals and Housing

Subjects were 32 infant rhesus macaques (*Macaca mulatta*), 16 males and 16 females aged from 7 to 30 days. All infants were separated from their mother on day 1 post-partum and reared in a nursery facility according to procedures described by Shannon, Champoux, and Suomi (1998). Infants were individually housed in plastic incubators (51 × 38 × 43 cm) for the first two weeks of life and in metal cages (65 × 73 × 83 cm) from the third week onward. Both housing arrangements contained an inanimate surrogate mother as well as loose pieces of fleece fabric and various rubber toys. During the first week of life, the surrogate mother was composed of 16.5-cm circumference polypropylene cylinder, wrapped in fleece fabric and attached by a flexible metal component to an 11.5-cm-wide circular metal base. From the second week onward, infants were provided with a hanging surrogate mother (see also Dettmer, Ruggiero, Novak, Meyer, & Suomi, 2008) consisting of a plastic cylinder core (20-cm-high and 19-cm circumference) with a wide soft cloth cover (20 × 25 cm). For the first month of life, infants could see and hear, but not physically contact, other infants of similar age.

Testing was conducted in accordance with regulations governing the care and use of laboratory animals. The Animal Care and Use Committee of the National Institutes of Health approved this study.

### Procedure

All infant monkeys were tested individually in their incubators/home cages. Two experimenters were involved in the data collection. One experimenter served as the source of the stimuli and was seated in front of the infant attempting to acquire infant's attention.

When eye contact with the infant was established, the model informed a second experimenter to start timing the onset and offset of the different phases of each session. For the entire test, the first experimenter attempted to maintain eye contact with the infant.

Infants were tested in two experimental conditions: imitation and control. Each trial started with a manipulative period in which one experimenter presented a stimulus for 2 minutes. In the *imitation* condition, the experimenter imitated all mouth openings, lipsmackings and tongue protrusions performed by the monkey, whereas in the *control* condition she simply performed a repetitive gesture, opening her mouth 5 times every 10 seconds. Although both of these conditions could be considered responsive, in the *imitation* condition there was structural and temporal matching, whereas in the *control* condition the experimenter simply performed a repetitive response. Thus, the *imitation* condition differs from the *control* condition in that the behavior of the model was more contingent, more variable in forms and temporal pattern, and, most importantly, closely resembled the topography of the behaviors exhibited by the infants. Each manipulative phase was followed by a still face period (2 min), in which the experimenter looked at the monkey with a neutral facial expression. Total testing time was 4 min per trial.

Each monkey was tested twice a day, once in the imitation condition and once in the control condition, in random order, between day 7 and day 30, for a minimum of two sessions to a maximum of five sessions. Infants were usually tested once in the morning between 10am and 12am, and once in the afternoon between 3pm and 5pm, and only when awake and calm. If infants were sleepy or distressed, we waited for a few minutes until they were awake or calm enough to be tested.

## Behavioral Analysis

Test sessions were videotaped using a Sony Digital Video camcorder ZR600. Tapes were analyzed off-line, frame by frame (30 frames per second), using The Observer XT coding software (Noldus Inc.). In each condition and each phase, the following behaviors were recorded:

1. infant visual attention, calculated as the looking time at the experimenter;
2. frequency of all infant lipsmackings (LPS) at the experimenter;
3. frequency of all infant tongue protrusions (TP; see Ferrari et al., 2006, for further details on the behaviors definitions);
4. objects exploration, calculated as the time spent by the infants in touching, grasping and manipulating the objects with the hands or interacting with them by using their mouth;
5. percentage of time spent by the infants in proximity to the experimenter. Infants were considered to be in proximity of the experimenter when they were within 13 cm from the front of the incubator or within 20 cm from the front of the cage;
6. scratching behavior as an index of stress (Maestripieri, Schino, Aureli, & Troisi, 1992).

Two independent coders, blind to the experimental condition, scored all the occurrences of infant's gestures and visual attention to the experimenter. Observers were researchers working with infant macaques and, therefore, familiar with their behaviours. Inter-observer reliability was calculated for 20% of infants (N = 6). Cohen's kappa coefficient was used to calculate the average observer agreement for all the behaviours analyzed (visual attention: $\kappa = .81$, $p < .001$; LPS: $\kappa = .85$, $p < .001$; TP: $\kappa = .81$, $p < .001$; objects' exploration: $\kappa = .85$, $p < .001$; proximity: $\kappa = .80$, $p < .001$; scratching: $\kappa = .89$, $p < .001$).

### Statistical Analysis

To test the effects of our experimental manipulation on infant affiliative and explorative behaviors, we applied a two-way repeated measures ANOVA with condition (imitation or control) and time period (stimulus or still face) as within-subject factors. Moreover, to assess whether infant behaviours were affected by the infant's sex, we applied a 2 × 2 × 2 mixed-design ANOVA with condition (imitation or control) and time period (stimulus or still face) as within factors, and sex (male, female) as a between factor. To determine whether infant behaviors changed over time from the second to the fourth week of life, we performed a 2 × 2 × 3 repeated measures ANOVA with condition (imitation or control), time period (stimulus or still face) and age (week 2, week 3, week 4) as within-subjects factors. Finally, to assess whether the number of sessions performed on each infant affected their behaviours, we performed a 2 × 2 × 4 repeated measures ANOVA with condition (imitation or control) and time period (stimulus or still face) as within-subjects factors, and number of sessions performed (2, 3, 4, 5) as a between-subject factor.

The Kolmorogov-Smirnov test revealed that our data violated the normality assumption required for running parametric statistics, therefore all data were square root transformed prior to analysis. To adjust the chance of finding significant results due to multiple comparisons, we performed post-hoc comparisons with Bonferroni corrections.

## Results

Analysis of visual attention as a measure of infants' interest (see Figure 1a) showed a significant main effect for condition, $F$ (1,30) = 21.18 $p < .001$ $\eta^2_p = .41$, and time period, $F$ (1,30) = 42.55 $p < .001$, $\eta^2_p = .60$, as well as an interaction between condition and period, $F$ (1,30) = 9.28, $p = .005$, $\eta^2_p = .23$, showing that infants looked at the experimenter more in the imitation condition ($M$ = 17.40, $SD$ = 7.49) than in the control condition ($M$ = 10.89, $SD$ = 4.10, $p < .001$), and more in the manipulation phase ($M$ = 17.27, $SD$ = 4.65) than in the still face period ($M$ = 11.02, $SD$ = 5.20, $p < .001$); levels of visual attention were also higher in the stimulus phase during imitation ($M$ = 19.59, $SD$ = 8.23) than during control, ($M$ = 14.94, $SD$ = 6.05, $p = .035$), and in the still face period during imitation ($M$ = 15.20, $SD$ = 8.82) than during control ($M$ = 6.83, $SD$ = 3.71, $p < .001$). We did not find any significant effect of sex, $F$ (1, 30) = .205, $p > .05$, $\eta^2_p = .007$, age, $F$ (1,18) = 1.552, $p > .05$, $\eta^2_p = .079$, or number of sessions performed, $F$ (3, 28) = 2.479, $p > .05$, $\eta^2_p = .210$. However, we found an interaction between condition and number of sessions performed, $F$ (3, 28) = 7.710, $p = .001$, $\eta^2_p = .452$, suggesting that in the imitation condition infants tested on 5 different sessions ($M$ = 24.35, $SD$ = 10.49) looked at the experimenter more than infants tested only in 2 ($M$ = 13.89, $SD$ = 10.49, $p$ = .003) or 3 sessions ($M$ = 13.55, $SD$ = 11.73, $p$ = .004), whereas no difference between infants tested on 5 sessions and infants tested on 4 sessions was found (M = 16.47, $SD$ = 16.58, $p$ > .05). Further, when infants were exposed to 4 or 5 experimental sessions, frequency of visual attention was higher in the imitation condition (4 sessions, $M$ = 16.47, $SD$ = 16.58; 5 sessions, $M$ = 24.35, $SD$ = 10.49) than in the control condition (4 sessions, $M$ = 9.95, $SD$ = 11.30, $p$ = .034; 5 sessions, $M$ = 9.46, $SD$ = 7.14, $p$ < .001).

Analysis of infant lipsmacking (LPS) as an indicator of infants' affiliative social responses (see Figure 1b) showed a main effect for condition, $F(1,30) = 16.557$, $p < .001$, $\eta^2_p = .35$, and time period, $F(1,30) = 23.48$, $p < .001$, $\eta^2_p = .43$, indicating that infants lipsmacked more in the imitation condition ($M$ = 6.46, $SD$ = 3.75) than in the control condition ($M$ = 3.97, $SD$ = 3.09, $p$ < .001), and more during the manipulative phase ($M$ = 6.68, $SD$ = .42) than during the still face period ($M$ = 3.76, $SD$ = 2.22, $p$ < .001). Contrast analyses revealed that LPS frequencies during the manipulation were significantly higher in the imitation ($M$ = 8.33, $SD$ = 6.21) than in the control condition ($M$ = 5.03, $SD$ = 4.39, $p$ = .003), and, similarly, that LPS during the still face period was higher in the imitation ($M$ = 4.60, $SD$ = 2.90) than in the control condition ($M$ = 2.92, $SD$ = 2.65, $p$ = .004). No significant effect of sex, $F(1, 30) = .001$, $p > .05$, $\eta^2_p = .00$, age, $F(1, 18) = .341$, $p > .05$, $\eta^2_p = .019$, or number of sessions performed, $F(3, 28) = 2.927$, $p > .05$, $\eta^2_p = .24$, was found.

In order to evaluate whether being imitated might also have affected the infants' motivation to explore the environment, we analyzed time spent in objects' manipulation (see Figure 1c), which revealed a main effect for time period, $F(1,30) = 5.22$, $p = .029$, $\eta^2_p = .14$, showing that in the imitation condition infants explored objects more during the still face period ($M$ = 27.13, $SD$ = 3.22) than during the imitation period ($M$ = 18.87, $SD$ = 2.38, $p$ = .026). No main effects for condition, $F(1,30) = 3.02$, $p > .05$, $\eta^2_p = .09$ and no interaction between condition and time period, $F(1,30) = .043$, $p > .05$, $\eta^2_p = .001$, were found. Moreover, we did not find any significant effect for sex, $F(1, 30) = .032$, $p > .05$, $\eta^2_p = .001$, age, $F(1, 18) = .341$, $p > .05$, $\eta^2_p = .019$, or number of sessions performed, $F(3, 28) = .736$, $p > .05$, $\eta^2_p = .073$. However, we found an interaction between condition and age, $F(2, 18) = 3.44$, $p = .043$, $\eta^2_p = .161$, and a three-way interaction between condition, time period and age, $F(2, 18) = 5.014$, $p = .012$, $\eta^2_p = .218$, which showed that the frequency of object manipulation in the imitation condition, and more specifically during the still face period, increased from week 2 ($M$ = 10.78, $SD$ = 2.41) to week 3 ($M$ = 40.15, $SD$ = 7.46, $p$ = .002) and from week 2 ($M$ = 10.78, $SD$ = 2.41) to week 4 ($M$ = 30.44, $SD$ = 6.13, $p$ = .019).

No other mouth gestures or other behaviors were affected by our social manipulation (see Supplementary Results and Supplementary Table S1).

## Discussion

This experiment demonstrates that, similar to other adult primates and children (Haun & Call, 2008; Meltzoff & Prinz, 2002; Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005), infant macaques reared in a nursery are sensitive to matched and synchronous behaviors and are more responsive to the condition with the higher level of contingent responsiveness. Although in the control condition infants were exposed to a higher number of mouth gestures (35 gestures per min) than in the imitation condition (12.90 ±1.01 gestures per min), the repetitive gesture alone made by the experimenter was less effective in soliciting responses from infants than imitative responses. In contrast, after experiencing a period of imitation, infants showed a significant increase in social interest, looking more at the caregiver and also displaying more affiliative gestures toward her. It could be argued that, in the imitation condition, the higher frequency of temporally contingent behaviors between the model and the infants, rather than the behavioral matching, was the critical factor in producing the prosocial effect. Although in our experimental design we did not specifically test this potential variable, we believe that this hypothesis is unlikely. In fact, previous studies demonstrated in adult monkeys that imitation rather than contingent behaviors elicits increased attention towards the model (Paukner et al. 2005) and that temporally contingent behaviors alone do not have any effect on prosocial behaviors towards a human experimenter (Paukner et al., 2009). Moreover, other studies demonstrated that human infants look and smile preferentially toward a mimicking rather than a contingent adult, suggesting infants possess an early capacity for detecting matching behaviors (Agnetta & Rochat, 2004).

Attention to others plays a significant role in human social and emotional exchanges and the level of eye-to-eye contact is a good indicator of the quality of the emerging relationship between the mother and her child (Berger & Cunnigham, 1981; Field, 1977). Several studies highlight the benefits of imitation on increasing children's communicative behaviors not only for typically developing infants (Field, 1977), but also for children with autism (Field, Sanders, & Nadel, 2001; Heiman, Laberg, & Nordøen, 2006; Sanefuji & Ohgami, 2011). Imitative behaviors seem also to facilitate infants' affective connection with the caregiver. Recent studies have shown that both in human and monkeys, being imitated enhances prosocial attitudes, acting as a social glue (Chartrand & Bargh, 1999) and making individuals more likely to interact with others (Gallese, 2003; Heyes, 2009; Hurley, 2008; Paukner et al., 2009). During imitation, when self and other-produced movements are highly aligned in both form and time, infants have the opportunity to make a connection between the visible world of others and their own internal states (Georgieff & Jeannerod, 1998). So, when infants observe others behaving like them, they are provided with a special channel of communication, in which both partners recognize they are in a relationship with each other. These findings seem therefore in line with theoretical accounts proposing that a reciprocal interaction prompts infants to elaborate a sense of self, others and the relation between the two (Meltzoff, 2007; Tiegerman & Primavera, 1984), thus promoting affiliation and social cohesion (Chartrand & Bargh, 1999; Gallese, 2003; Hove & Risen, 2009; Hurley, 2008).

An interesting finding emerging from this study is that the increased social interest in the imitation condition is more robust when infants were exposed to a higher number of experimental sessions. Thus, what appears critical for an effective positive outcome is the timing of exposure to such social experience. Interestingly, behavioral intervention studies on children with autism have shown that the intensity of the treatment is critical for a positive outcome in ameliorating social functioning (Roger & Vismara, 2008; Granpeesheh, Dixon, Tarbox, Kaplan, & Wilke, 2009). Even though our experimental protocol was not aimed at testing the efficacy of the intensity of the intervention, our findings seem consistent with previous studies demonstrating the benefits of intensive treatments in children with social impairments. Thus, our results could have important implications in designing possible interventions to improve social skills in infants at risk of impaired social and cognitive development, as they suggest that not only the quality of social interaction, but also the frequency and timing of exposure, might affect the positive outcomes.

Moreover, adult imitation might facilitate infants' social attention and enhance their social communication not only during imitation but also just after imitation. Infants are clearly sensitive to alterations within the dyadic interaction. When the caregiver shifted from active face-to-face interaction to silent and expressionless, infant monkeys responded with changes in behavior, exhibiting reduced attention and less affiliative behaviors, similar to human infants (Murray & Trevarthen, 1985; Nagy, 2008; Rochat, Striano & Blatt, 2002). Consistent with previous studies on human infants (Murray & Trevarthen, 1985; Nagy, 2008; Rochat et al., 2002), after being imitated our monkeys seemed to actively attempt to re-engage the experimenter and re-establish a pattern of communication, showing the ability to detect and respond to alterations within the dyadic interaction, which was observed to a much lesser degree in the *control* condition. According to these results, infants seem to understand their active role in instigating social interactions and their response to the still face procedure can be interpreted as evidence for their adaptive social competences from the very first weeks of life. Furthermore, this early developing ability to behave as active social participants seems to be extended also to the physical environment (Rochat & Striano, 2000). Indeed, our data indicate that imitation increased infants' levels of object exploration, suggesting that the positive effects of this social manipulation is not exclusive to the social domain, but it might also promote infants' motivation to explore their surrounding physical world. This effect, although stronger with age, was found only in the imitation condition, and therefore cannot be explained in terms of general improvements in motor development. Conversely, our experimental manipulation might have had a stronger influence on infants' interest towards objects at a stage when they become more sensitive to the surrounding environment and start acting on it, thus promoting and supporting the emergence and the development of their exploratory behaviors.

In conclusion, the results of this study suggest that imitation might be an effective vehicle for increasing infant's social interest and facilitating pro-social behaviors. Imitation might be used as an important tool for promoting positive social exchanges among infants at risk for poor developmental outcomes. Although some previous work reported positive effects of imitation on children with impaired social skills, such as in autism (Escalona et al., 2002; Field et el., 2001; Heiman et al., 2006; Sanefuji & Ohgami, 2011), surprisingly few experimental studies and programs focused on imitation as an interaction strategy for modifying the effects of early social adversities (van Ijzendoorn, Bard, Bakermans-Kranenburg, & Ivan, 2009). Our findings therefore could lead to the development of an early behavioral intervention for human infants who experienced early social deprivation, aimed at increasing their motivation to participate in social interactions and promoting more generalized improvements in their social abilities.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.


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## Research Highlights

- A population of nursery-reared infant monkeys was used as a model to test the effect of being imitated on early social interactions.
- Being imitated increased infants' visual engagement and affiliative behaviours.
- Imitation might be used as an early behavioural intervention for promoting positive social exchanges among infants at risk for poor developmental outcomes.

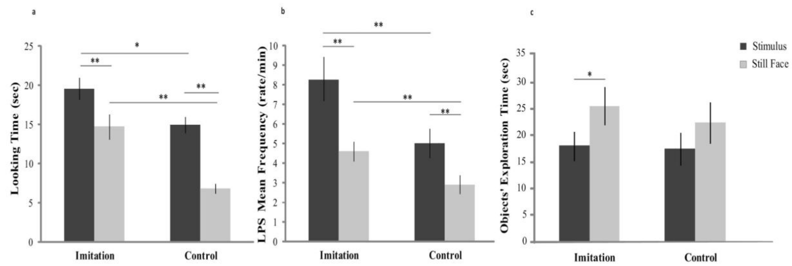


**Figure 1.**

Effects of imitation on infant monkeys affiliative and exploratory behaviors in the two different experimental conditions

Mean scores of (a) infant looking time to experimenter, (b) infant LPS and (c) infant’s exploration time. Infant monkeys looked at and lipsmacked to the experimenter more in the stimulus phase than in the still face period both during imitation and control condition. Moreover, after being imitated infants explored objects more than during the imitation period. Error bars show the S.E. *$p < 0.05$, **$p < 0.01$.