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Effects of a Mechanical Response-Contingent Surrogate on the Development of Behaviors in Nursery-Reared Rhesus Macaques (*Macaca mulatta*)

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Nursery-reared infants have several behavioral and physiologic differences from their mother-reared counterparts. We investigated whether a response-contingent surrogate mitigated some of those differences by decreasing fearfulness and partner-clinging and increasing environmental exploration in nursery-reared infants continuously paired with a peer. Six nursery-reared infant rhesus macaques (in pairs) were given a mechanical responsive surrogate (RS), and 6 (in pairs) were given an identical but nonresponsive surrogate (NRS). The 2 treatment groups were compared and then combined into a single group of all 12 of surrogate-exposed animals (CS) that was compared with a nonsurrogate control group (NS) of 10 nursery-reared infants. Results showed significant differences between CS and NS infants but no significant differences between the RS and NRS infants. As compared with NS infants, CS infants showed less partner-clinging, less affiliation directed toward only partner, and more foraging and tactile–oral exploration of the environment. These advantageous effects support additional research to develop improved surrogate and the implementation of surrogate programs for nursery-reared infants.

Abbreviations: RS, responsive surrogate group; NRS, nonresponsive surrogate group; CS, combined nonresponsive and responsive surrogate group; NS, nonsurrogate control group.

The maintenance of a successful nursery-rearing program for rhesus macaques (*Macaca mulatta*) is an important goal of biomedical primate research facilities that require these animals for infant-specific research projects. Nursery rearing provides easier access to infants, consistency in rearing conditions such as diet and temperature, reduced exposure to pathogens that could affect research results, and an alternative for incompetent mothers that do not care for their infants.[6] Crucial to the long-term success of establishing and maintaining these nursery-reared animals and breeding groups is the creation and implementation of effective strategies for raising infant macaques in ways that minimize the emergence of behavioral pathologies due to being deprived of their mothers and that lead to the development of species-typical behaviors and social competence. Nursery-reared macaques develop different psychologic and physiologic responses than do their mother-reared counterparts, and these altered responses could interfere with and thus confound the studies to which these animals are assigned. Infants raised in nurseries, both singly housed and with a partner, would benefit from having improved health and developmental outcomes,[7,9,12,16,18,20,21,32,37,40,41] and decreased development of abnormal behaviors.[4,5,8,13,19,22,23,31,37,38,44]

Nursery-rearing strategies vary but often involve an early incubation period of approximately 1 mo during which the infant is singly housed to monitor food intake, dehydration, and thermoregulation and which is followed by continuous pairing with a single conspecific. Nursery-reared infants typically are handled only during daily weighing and cleaning of the incubator or cage, a practice that is dramatically different from the amount of handling and other sensory inputs received by mother-reared infants, such as kinesthetic stimulation from the mother's movement, tactile stimulation via maternal grooming and embracing, as well as vocal and visual stimulation received by hearing and observing their mother and other conspecifics in a social group.

Compared with mother-raised infants, those raised in the nursery without a mother show more emotional reactivity, startle more easily,[40] and are less flexible in habituating to new environments, resulting in increased reactivity to environmental change.[15,35] In addition, peer-only–reared monkeys show a higher frequency of aggressive and stereotypic behavior overall[46] and exhibit less environmental exploration[8,42] than do mother-reared infants raised in a social environment. During exposure to a novel environment, a social companion alone is not effective in buffering behavioral and physiologic responses for peer-only reared infants[46] compared with monkeys reared with their mothers in a social group. However, the most noticeable difference from mother-reared monkeys in a social group is a strong tendency for peer-only reared monkeys to show excessive mutual clinging for prolonged periods throughout development, such that the activities of one macaque are often restricted by an animal holding on to it. Because macaques do not break the clasp of their partners, they have less opportunity to develop appropriate exploratory and social behaviors despite having more social peer exposure. Juvenile peer-only–reared monkeys show less reciprocal social behavior[46] and are developmentally

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delayed[29,43] compared with mother-reared monkeys in social groups, perhaps due to the excessive clinging behavior.[8,30,36]

In addition, infant macaques that have a surrogate but are peer-reared only part-time are more likely to develop phobic behavior in response to a novel object,[32] and are more likely—as are peer-only–reared animals without a surrogate—to show digit-sucking as a self-calming technique.[41]

Early experience is especially important with regard to the perception that the environment is either controllable or independent of the organism's behavior.[14] Subjects that have experienced a nearly complete lack of control over environmental events may enter a state of learned helplessness and show a dramatic decrease in the detection of new opportunities to affect their environment.[24] An organism can learn how to exert some control over its environment through the process of responding, receiving feedback from the environment, and then adjusting the response to optimize the environmental outcome.[45] Without such feedback, an infant may perceive that it has no control over its environment and may not develop correct species-typical behavior and normative responses to stimuli such as novel objects, fearful situations, and social cues. Infants that have experienced the opportunity for response-contingent stimulation show increased environmental exploration, confidence, and adaptability.[17,28,33]

In the current study, we sought to create and test a complex responsive surrogate that resembled some maternal characteristics such as warmth, movement, physical proximity and nestling, nursing, heartbeat, and vocalizations. Our hypothesis was that if elements of normal maternal inputs could be replicated and combined with the social interaction of a continuously paired peer, then the development of mother-deprived infants could be improved. We predicted that infants would be less clingy and fearful and more confident and exploratory. This study differs from previous studies in that the infants were not isolated (except for their first month in the incubator) nor were they peered-paired part-time in addition to having a surrogate. Instead the infants were maintained in a continuously paired rearing environment along with 2 complex surrogates (one per macaque). This design allowed us to observe the infants' responses to each other and the surrogate and to compare them with those of nonsurrogate control infants. We also compared the development of behaviors over time, to see whether a treatment×age interaction occurred due to the addition of a complex surrogate.

Materials and Methods

The study was conducted in the indoor nursery at the California National Primate Research Center (Davis, CA) from April through December 2010. This research was approved by the University of California–Davis IACUC (protocol no. 15814) and adhered to the requirements of Animal Welfare Act and US Department of Agriculture regulations.[2,3]

We used 12 infants, all of which were part of the facility's SPF breeding program. As infants arrived in the nursery within 1 d of birth, each was assigned to a pair. Each member in a pair was assigned to the same treatment group. Six of the infants were assigned to the responsive surrogates (RS) treatment group, and 6 were assigned to the nonresponsive surrogates (NRS) treatment group. Members of the pair differed in age by 4 to 15 d.

Two of the NRS treatment group pairs were female and one was mixed-sex, whereas 2 of the RS treatment group pairs were male and one was mixed-sex. Every attempt was made to assign equal numbers of male and female infants to each treatment group, but several factors contributed to unequal groups, including birth order, timing, and availability of correct surrogate types for the treatment group. Each infant was singly housed in an incubator (31 × 31 × 36 cm) for 4 wk with its surrogate (small version of either the RS or NRS), supplemental heat from a heating pad, soft cotton diapers for bedding, a pacifier, and free access to formula (Enfamil With Iron Liquid Formula, Mead Johnson, Evansville, IN) supplied from a plastic nursing bottle attached to the top of the surrogate. For the first 1 to 3 d, nursery staff directed the infants to the bottle, helping to prop them up against the surrogate until the infants were able to support themselves. After this period, handling was limited to daily weighing and cage cleaning. When the younger pair-mate was 28 d old, we began adapting the infants to 'quad cages' (24 × 18 × 27.5 in.); Carter$_2$Systems, Beaverton, OR) by transferring them to one side of the cage, initially for 2 h daily and then increasing the length of time each day. The quad cage included the larger version of the surrogate, soft cotton diapers for bedding, a pacifier, a chew toy, a shelf and a swing, and visibility with their pair-mate through a clear acrylic divider. When the younger infant of a pair was 35 d old, the divider between the cage sides was removed, and the pair-mates were allowed access to each other. They then were paired continuously, with access to both surrogates until age 120 d. Infants were weaned off the plastic nursing bottles at around age 56 d, at which time they were provided with 3 bottles (Lixit, Napa, CA) that were attached to the cage walls, one each containing infant formula, citrus-flavored beverage (Tang, Kraft Foods, Northfield, IL), and water. At 14 d old, the infants also received banana and were introduced to monkey chow to gnaw on. At 21 d, they received banana, apple, and soaked chow to eat. At approximately 2 mo, they received hard chow and fruit. When the younger pair-mate was 120 d old, the pairs gradually were weaned from their surrogates over a 20-d period, because of their increased strength and ability to destroy them and to prevent possible trauma to digits or ingestion of pieces of fabric or plastic. At the end of the weaning period, the infants were moved with their pair-mates to adult-size cages, at which time we discontinued observations. During the entire study, pairs had visual access to other infants in adjacent cages and across the room and auditory access to infants in other areas of the room. Nursery rooms were kept on a timed cycle of lights on at 0600 and off at 2200, with lights on again during overnight feedings at 0100 and 0400.

In addition to comparing the 2 types of surrogates, we compared the combined surrogate (CS) data with data taken from 10 nonsurrogate (NS) control infants that were raised by using the same rearing conditions but without the surrogate. Instead the infants were provided a small stuffed animal, and their plastic nursing bottle was attached to the side of the incubator or cage rather than to the top of the surrogate.

Surrogates. Surrogates were designed by the investigators and manufactured by a biomedical engineering graduate. The covers were designed and assembled by a textile seamstress. There were 4 versions: a large RS, a large NRS, and a small version of each.

Large RS (Figure 1)**.** The large RS was an acrylic cylinder (TAP Plastics, Sacramento, CA) that was 15 cm tall with a diameter of 15 cm and set on an acrylic base 28 cm in diameter. The entire surrogate was covered with a removable cover made of faux sheep wool for grasping and had a drawstring on the bottom to secure it in place. A movable faux sheep wool 'arm' that was 13 cm in length extended from each side. Running vertically down each side directly in front of the arms were handles of a softer fleece material, for texture variation and for easier grasping when held in the 'ventral-ventral' (chest to chest) position. On the front of the RS was a button that, when pushed, activated a vibrating heartbeat, which had been extracted and repurposed

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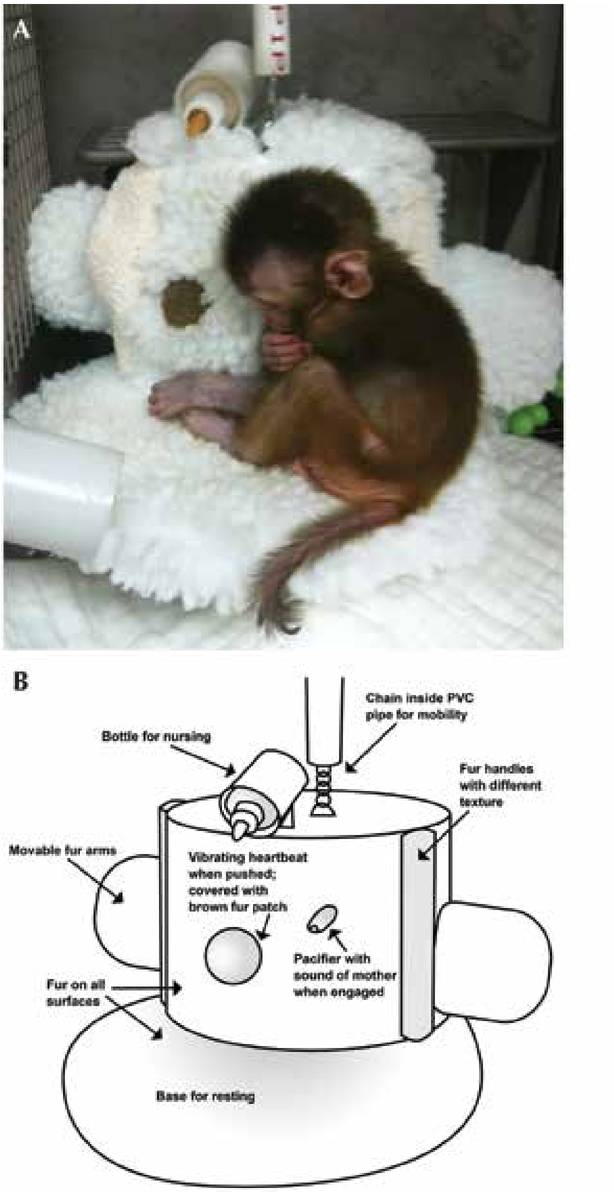

Figure 1. (A) Large surrogate. The infant shown is approximately 1.5 mo old. (B) Labeled diagram of large surrogate.

Figure 2. Small surrogate. The infant shown is approximately 1 wk old.

from a Polar Bear Cuddle Cub (Cloud B, Gardena, CA) and then covered with a half of a pingpong ball to increase the surface area of the button. The surrogate cover included a 5-cm circular brown piece of felt fabric directly over the 'heartbeat' to differentiate it from the rest of the cover and to give the infant a target to push. Also on the front was a pacifier nipple that, when compressed, engaged a copper-wire–activated sound that was an affiliative vocalization previously recorded from rhesus macaque dams at the facility. The heartbeat and sound were both battery-operated and accessible to caretakers by removing the top plate of the acrylic cylinder. On top of the RS, the plastic nursing bottle containing the infants' formula was braced at an angle to allow the infant to sit on the base in a ventral-ventral position and nurse on the bottle. The entire RS was suspended from the ceiling of the cage by using a PVC enclosed chain and secured underneath to the floor with another chain to allow movement but to prevent excessive swinging or spinning.

Small RS (Figure 2)**.** The small RS version was created specifically to fit in the incubator that housed the infants for the first 4 wk of life. Several modifications were made to adapt it to the smaller space. The size was decreased to 13 cm tall and 11 cm in diameter, and the small RS rested on the floor of the incubator, secured at the top with 2 hooks to prevent spinning or tipping. The base was removed, given that the small RS rested on the floor of the incubator, and the bottle remained on top to allow nursing while in a ventral-ventral position. The sound pacifier remained on the front, but the arms were removed.

Large and small NRS (controls). The large and small NRS looked exactly like the large and small RS, but no vibrating heartbeat was elicited when the brown felt circle was pushed, and no sound was emitted when the pacifier was engaged. In addition, the chain on the bottom was tightened to decrease movement.

Behavioral observations. To assess differences in behaviors and development of behaviors between treatment groups, each subject was observed in its home cage for 15-min periods, an average of 3 times per week over a 17- to 18-wk period (and an additional 3-wk weaning period), for a total of 21 wk (approximately 5 mo). During the 3-wk weaning process, we gradually removed the surrogate in stages. Behaviors were recorded by using focal one–zero sampling,[1] with 15-s intervals. Infants were allowed approximately 3 min of habituation time to the observer before the observations began. For the 10 NS control infants, all procedures were the same, with the exception of session duration, which was 5-min sessions due to time constraints. For the current study, we did not have the same constraints, so we observed our infants for 15-min sessions, which allowed us to have a longer time period in which to compare the RS and NRS groups. NS data were converted so that the score was comparable to RS and NRS data. Data were collected by using HanDBase 4 software (ddhsoftware.com) on PalmPilots (Palm Inc, Sunnyvale, CA), and transferred to an MS Access (Microsoft, Redmond, WA) database on a PC computer. The observer sat in front of the incubator or quad cage at a distance of approximately 3 to 4 feet from the front of the cage without making eye contact with the animal. Behaviors were scored according to the ethogram provided in Figure 3. We used 5 different observers, who were tested prior to the study for at least 85% reliability and were retested once during the study. One of the observers

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Behavior	Description
Contact surrogate	Ventral-ventral contact or other body contact with the surrogate (sitting, lying) for at least 3 s.
Contact partner	Sitting or lying in contact with partner for at least 3 s.
Cling partner	Full body contact with the partner and wrapping arms or legs around the partner. Clinging can be initiated, mutual, or received.
Groom partner	Picking, scraping, spreading, mouth picking, or licking of partner's hair or skin.
Affiliative behavior partner	Nonaggressive behavior directed toward or received from partner, such as sniff or oral, lip-smacking, present, mount, and play (nonaggressive chasing, bouncing, sitting or stepping on, grabbing, wrestling, soliciting, and mock biting of partner). Present: Exposing parts of the body in exaggerated ways, typically the rump, neck, ventrum, or back. Mount: One monkey grasps the hindlegs of another monkey, with the hind feet and placing his or her hands on the lower back (and sometimes the side or front) of the recipient.
Foraging	Searching for, manipulating, and ingesting food items such as monkey chow or fruit. Manipulating refers to prepping the food item to eat, not exploratory behavior.
Self-play	Nonsocial play for at least 3 s, including motion play such as swinging, jumping, or bouncing on swings or other parts of the cage; nonsurrogate object play such as throwing, jumping on, or kicking an object such as a toy, puzzleball, coconut, or chew toy.
Scratch	Vigorous strokes of own hair or skin by using the fingernails or toenails.
Self-orality	Sucking a part of the monkey's own body, including digits, tail, skin, and genitals, for at least 3 s
Tactile–oral exploration on surrogate only	Picking at, mouthing, or investigating the surrogate (excluding the oral pacifier) with the hands, feet, mouth, or tongue.
Tactile–oral exploration on non-surrogate areas	Picking at, mouthing, or investigating non-surrogate parts of the cage or nonfood items (caging, chew toy, mirror, etc.) by using the hands, feet, mouth, or tongue; investigating a food item with hands, feet, mouth, or tongue, other than eating the item.
Oral pacifier	Enclosing the nonnutritive–sound pacifier nipple with the mouth.

Figure 3. Behavior ethogram.

had also been assigned to the previous nonsurrogate study, and other observers on that study had an 85% or more reliability score with the one observer.

Statistical analysis. Using SAS 9.2,[39] we analyzed behavioral outcomes according to a Poisson generalized linear model with treatment and age as fixed effects and the individual within treatment as the random effect. We also compared longitudinal changes between groups by examining treatment×age interaction. An offset variable (logcount) was used to account for the fact that the number of focal periods in a given time period varied, due to animal unavailability or scheduling conflicts. Log transformations were applied when the data were not normally distributed. For treatment by age analyses, data were broken out by age into developmental 'periods' (period 0, birth to 2 wk old; period 1, 2 to 6 wk old; period 2, 6 to 10 wk old; period 3, 10 to 14 wk old; period 4, 14 to 18 wk old; period 5, 18 to 21 wk old). Behaviors that are reflective of partner interaction were analyzed starting at period 2 after the infants were paired. Behaviors that did not require partner interaction were analyzed from period 0.

Because sex was nonsignificant in preliminary analyses for the behaviors in our ethogram, male and female infants were combined for all subsequent analyses.

A P value of less than 0.05 was regarded as statistically significant, with a P value between 0.05 and 0.10 indicative of a trend.

Results

Results of treatment-group comparisons are summarized in Table 1. Results are presented as mean proportions of focal intervals in which the behavior occurred. We expected to see differences in behavior over time, but we were looking for interactions of treatment×age, so longitudinal graphs by developmental period are shown only when an interaction was found. All graphs show ±2 SE, reflecting a confidence interval of 95%.

There were no significant treatment differences or interactions in behaviors for the RS compared with NRS infants. We therefore combined NRS and RS infants into a single combined surrogate treatment group (CS) and compared it with the NS control group from the previous year. The analysis revealed that CS infants had higher rates of tactile–oral exploration of the environment including the surrogate ($\beta = 0.574$, $P < 0.0001$; Figure 4), tactile–oral exploration of the environment excluding the surrogate ($\beta = 0.273$, $P = 0.0082$; Figure 4), and foraging ($\beta = 1.324$, $P < 0.0001$; Figure 4) compared with NS infants. NS infants had higher rates of partner affiliation ($\beta = -0.525$, $P < 0.0001$; Figure 5) and partner clinging ($\beta = -0.589$, $P = 0.0468$; Figure 5) than did CS infants. There were no treatment differences in rates of initiation of and mutual partner clinging ($\beta = -0.242$, $P = 0.5245$), contact with partner ($\beta = -0.066$, $P = 0.5402$), self-orality (digit sucking; $\beta = -0.273$, $P = 0.4855$) or sleeping ($\beta = -0.016$, $P = 0.9451$).

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Table 1. Behaviors in CS compared with NS infants

Behavior	Group	Mean	95% CI		β	P
Tactile–oral exploration including the surrogate						
	NS	0.219	0.19–0.25	CS > NS	0.574	<0.0001
	CS	0.375	0.34–0.41			
Tactile–oral exploration excluding the surrogate						
	NS	0.219	0.19–0.25	CS > NS	0.273	0.0082
	CS	0.290	0.26–0.32			
Foraging						
	NS	0.034	0.02–0.04	CS > NS	1.324	<0.0001
	CS	0.114	0.10–0.13			
Partner affiliation						
	NS	0.185	0.15–0.22	NS > CS	–0.525	<0.0001
	CS	0.106	0.09–0.13			
Partner clinging						
	NS	0.111	0.08–0.14	NS > CS	–0.589	0.0468
	CS	0.056	0.04–0.07			
Partner clinging (initiate or mutual only)						
	NS	0.052	0.03–0.08	CS = NS	–0.242	0.5245
	CS	0.031	0.02–0.04			
Partner contact						
	NS	0.200	0.16–0.24	CS = NS	–0.066	0.5402
	CS	0.184	0.15–0.22			
Self-orality						
	NS	0.405	0.35–0.46	CS = NS	–0.273	0.4855
	CS	0.338	0.29–0.39			
Sleeping						
	NS	0.188	0.14–0.23	CS = NS	–0.016	0.9451
	CS	0.170	0.14–0.20			

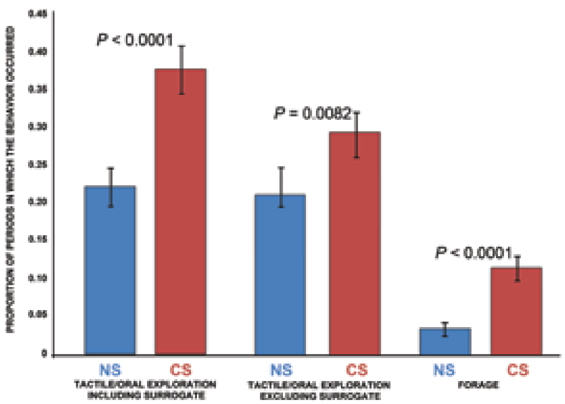

Figure 4. CS infants had significantly higher rates of tactile–oral exploration of the environment including the surrogate (β = 0.574, $P < 0.0001$), tactile–oral exploration of the environment excluding the surrogate (β = 0.273, $P = 0.0082$), and foraging (β = 1.324, $P < 0.0001$), compared with NS infants.

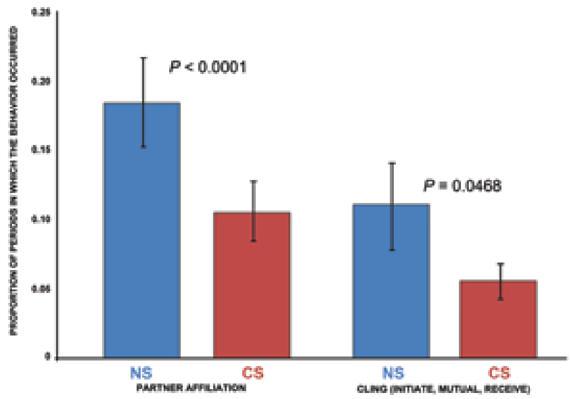

Figure 5. NS infants had significantly higher rates of partner affiliation (β = –0.525, $P < 0.0001$) and partner clinging (β = –0.589, $P = 0.0468$) than did CS infants.

In addition to comparing the CS and NS infant treatment groups with each other as a whole, we looked at differences over time and found significant or near-significant interactions in 3 of the behaviors. For partner affiliation and partner contact, the first data point on the *x* axis is period 2 (6 to 10 wk of age), after pairing has occurred. For self-orality, the first data point on the *x* axis is period 0 (birth to 2 wk of age).

Compared with CS macaques, NS infants had a higher rate of partner affiliative behaviors for periods 2 through 5. There was also a near-significant interaction ($P = 0.0827$) in partner affiliation, with an increase during periods 4 and 5 (which includes the surrogate weaning period) in CS infants but not NS infants (Figure 6).

When partner contact behavior was analyzed by treatment group, there was no significant difference between CS and NS infants, but there was a trend in the interaction ($P = 0.0827$), with the CS infants showing less partner contact in the first period and more partner contact in the fifth period, which is during the weaning process (Figure 7).

For self-orality behavior (that is, digit sucking), there was no significant difference between CS and NS infants overall, but there was a significant interaction ($P = 0.0159$), with CS infants

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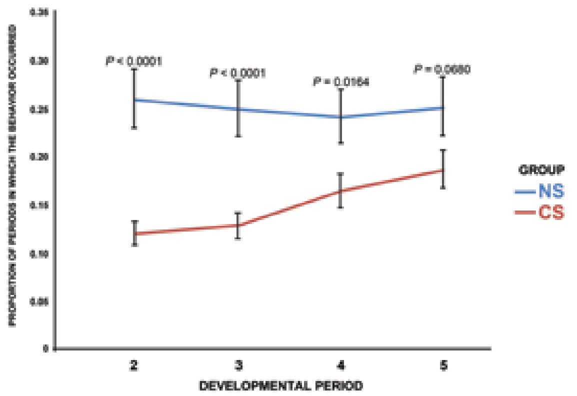

Figure 6. NS infants had a significantly higher rate than CS infants in partner-affiliative behaviors for periods 2 through 5. There was also a near-significant interaction ($P = 0.0827$) in partner affiliation, with an increase during periods 4 and 5 (which includes the surrogate weaning period) in CS infants but not NS infants.

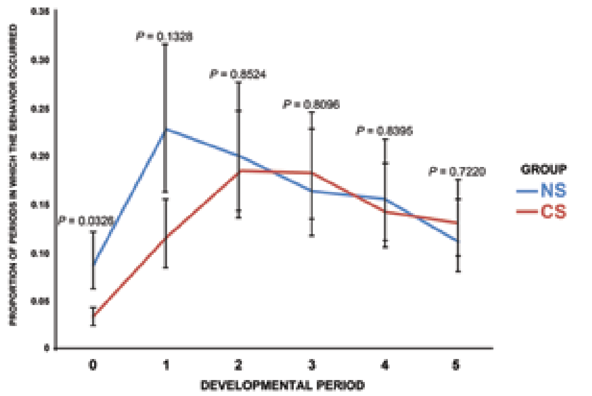

Figure 8. For self-orality behavior (that is, digit sucking), there was no significant difference between CS and NS infants overall, but there was a significant interaction ($P = 0.0159$), with CS infants having a significantly higher rate of behavior during period 0, a trend toward higher rate of behavior in period 1, and a decrease to the same level as NS infants after period 2.

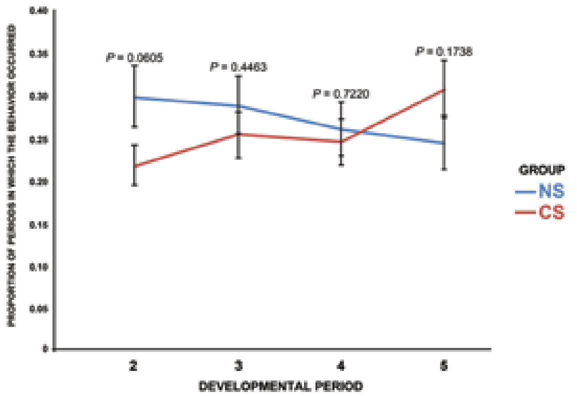

Figure 7. When partner-contact behavior was analyzed by treatment group, there was no significant difference between CS and NS infants, but there was a trend in the interaction ($P = 0.0827$), with the CS infants showing less partner contact in the first period and more partner contact in the fifth period, which is during the weaning process.

having a higher rate of the behavior in period 0, a trend toward a higher rate of the behavior in period 1, and then a decrease to the same level as that of NS infants after period 2 (Figure 8).

Discussion

There has been no shortage of surrogate research in the past several decades, beginning with several controversial studies involving isolated infants in the 1950s and 60s.[16] Since then, there have been studies with mobile compared with stationary surrogates,[25] inanimate compared with living heterospecific surrogates,[26] and behavior in response to separation from a surrogate,[27] as examples. The goal of our current study was to add to this plethora of knowledge by investigating whether we could create less fearful and clingy infant monkeys that were more calm and exploratory by introducing a surrogate for each macaque that provided nestling contact, nutrition, kinesthetic movement, vocal and tactile stimulation, and response contingent learning opportunities in combination with continuous peer pairing.

Our findings confirmed our hypothesis and revealed that a complex surrogate with features that emulate a natural mother can influence various developmental behaviors, especially exploration of the environment, foraging, partner affiliation and clinging behavior. The feedback contingencies (heartbeat and sound) of the RS did not appear to promote improved behavioral development over NRS infants. However, mechanical problems such as disconnected wires and battery failure causing the heartbeat and sound to perform inconsistently may have contributed to the lack of differences. In addition, the response feedback may have needed to be stronger and more obvious to the infant.

However we noted significant differences between the CS and NS treatment groups, indicating that other design features of the surrogate affected the infants' behavior. Both surrogates (RS and NRS) had 2 textures of fur, movable arms, a nursing bottle on top, a pacifier, side handles, and in the large surrogate, 3D movement and a resting base. These features gave the infant an object to cling to, sleep on, nurse from, explore, play with, and run to for comfort when startled or distressed. The last behavior, although not recorded as a behavior on our ethogram, was reported by nursery staff anecdotally. Additional research is warranted to investigate this behavior.

Compared with stationary surrogates, simple mobile surrogates can increase comfort level[10,11] but may not increase environmental exploration of infants.[25] In addition to mobility, we added other features as previously described and which did increase exploratory behaviors. Results of the current study show that CS infants had higher rates of species-typical behaviors of tactile–oral exploration and foraging, providing evidence that, when paired with a peer-mate, infants with a surrogate that emulates some features of a natural mother are more confident and less fearful.

Also indicated in the results are important differences in partner clinging between CS and NS treatment groups. CS infants had a lower rate of overall clinging frequency than did NS infants. Considering how detrimental obsessive clinging can be to nursery-reared infants' social development and overall well-being, including decreased exploratory behavior, less reciprocal social behavior, and delay in development, this result is very promising. Other studies have shown that continuously paired infants with no surrogates do indeed have very high clinging behavior, and that one way to decrease this clinginess is to pair infants intermittently, for 8 h daily.[34] However infants in these rearing conditions may display increased levels of abnormal behaviors, such as floating limb and self-biting.[34] We noted no abnormal behaviors in either the surrogate or control infants. Because of anecdotal reports by nursery staff indicating that CS infants continued to cling less overall when moved to outdoor group-housed cages and seemed to display more appropriate

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social behavior, follow-up longitudinal research would be interesting to investigate whether the surrogate–peer rearing condition did indeed have long-term effects.

In addition, CS infants showed less affiliative behavior toward their partners than did NS infants. More research is necessary to determine whether there is actually less affiliative behavior overall or whether the affiliative behaviors are instead directed toward the surrogate, other macaques within visual sightlines, or nursery staff. Such refocusing of affiliative behavior could perhaps indicate a higher comfort level with directing positive behaviors toward more than one social partner.

Furthermore, we investigated the change in behavior rates over time, and results indicated differences between treatment groups in the expression of behaviors as a function of age for partner affiliation, partner contact, and self-sucking. In partner affiliation, there was a near-significant interaction, with CS infants displaying increased affiliation after period 4 and into period 5, when the surrogates were being removed. In a previous study, self-sucking behavior was shown to be equivalent in subjects with a moving compared with a stationary surrogate.[25] In the current study, self-sucking, although not significantly different between the 2 treatment groups overall, was significantly higher in NS infants during periods 1 and 2, after which it was statistically the same in both treatment groups, showing a slow and steady decline. Self-sucking is a very common behavior seen in nursery-reared infants, likely as a replacement for a mother's nipple, so it is reasonable to expect that in the initial months after birth, self-sucking would be higher in NS infants compared with CS infants, which have a surrogate to cling to and nurse from.

The development of abnormal behaviors such as motor stereotypies and self-biting in nursery infants is well documented. Although these behaviors may start exhibiting themselves as early as the first month,[4,25,34] they typically do not appear at a high and consistent frequency until after infancy and into the juvenile and adult years. We saw no evidence of abnormal behaviors, other than self-sucking, through age 5 mo. Longitudinal data could be collected in follow-up studies of infants to see whether CS infants develop less abnormal behavior than do NS infants if these behaviors begin to emerge at a greater frequency.

Although our study did not reveal a statistically significant effect from the mechanically responsive features of the surrogate (heartbeat and sound), additional research using a larger sample size and an improved mechanical surrogate is warranted. Nevertheless, the remaining nonmechanical features (including movement, tactile stimulation from various textures, a place to rest, and the ability to nestle and grasp while nursing) could still provide a complex surrogate. It is encouraging that when used in conjunction with continuous peer pairing and with a surrogate for each monkey in the pair, this complex surrogate had a positive effect on specific aspects of a nursery-reared infant's wellbeing. Although mother rearing is optimal for the behavioral wellbeing of infants and cannot be replaced by even the most complex surrogate design, we recommend that facilities with nurseries work toward implementing surrogate rearing with moderating features that help to fulfill some of the needs that normally would be met by the presence of a mother. Biomechanically responsive surrogates may be difficult for some facilities to implement due to the sheer number of infants and costs associated with design, construction, and maintenance, but facilities with smaller populations may be amenable to adopting this technology. The determination of features discovered from surrogate studies to improve infant development might be introduced in less complex ways with larger populations of nursery-reared infants.

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