

yield photosynthates with an isotope composition of -27 per mil. In this case, the composition of the total photosynthetic products would be the resultant of the combination of the fraction at -11 to -31 per mil and the fraction at -27 per mil. The isotope composition of the total extract would be the combination of the compositions of the total photosynthate and the accumulated malic acid (-11 per mil). When the number of short days increases, the composition of the insoluble fraction will be progressively modified by the contribution of the newly formed carbon chains.

It has been reported (23) that environmental changes could shift the isotope composition of a CAM plant from values typical of a C_4 plant to values typical of a C_3 plant. Our results establish that such a shift can be obtained by photoperiodic control. However, we emphasize the importance of measuring different fractions instead of total leaf tissue for evaluating the metabolic pathways in a CAM plant. Analyses of extracts provide information about the relative contribution of each of the carboxylating enzymes to the primary CO_2 fixation, while the difference between the δ values of the insoluble fractions and extracts gives information concerning the size of the malate pool. Analyses of total tissue might produce, for example, values intermediate between those typical of plants of the C_3 and C_4 type (for example, -14 to -22 per mil), suggesting large contribution of both enzymes, while in reality such leaves fix all CO_2 via PEPC [see Table 1 and (20)].

Thus, a biophysical method facilitates the understanding of biochemical data in the study of metabolic responses. Environmental parameters such as temperature (24) and thermoperiod (21) produce similar biochemical changes, and will also leave a characteristic δ imprint in CAM plants (8, 25). This suggests that the isotope method might be applied in ecological studies of recent and fossil CAM plants, in particular, to reconstruct the past climate by isotope analyses of fossil remains of CAM plants (25, 26).

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Redirection of Filial Attachments in Rhesus Monkeys: Dogs as Mother Surrogates

Abstract. *Rhesus infants raised from birth with their mothers, age-mates, or cloth surrogates for periods varying from 1 to 10 months were separated from these objects and placed with dogs. Contrary to previous suggestions that were consistent with the notions of a critical period for attachment formation and irreversibility of filial bonds, the monkeys formed strong and specific attachments to their canine surrogates.*

The newborn of many species of birds and mammals form an attachment to a parent or appropriate substitute. The strength of attachment is usually inferred from behaviors that maintain proximity to the parent figure and from reactions to separation. Such bonds are often described as though they were once-in-a-lifetime events—restricted to a narrow period early in life, specific

to a particular object, exclusive, and enduring (1). Actually, these aspects of attachment behavior have been systematically examined mainly in birds but almost never in mammals, including the nonhuman primates.

We investigated the specificity, exclusiveness, and reversibility of filial bonds in an initial experiment with eight immature laboratory-born rhesus

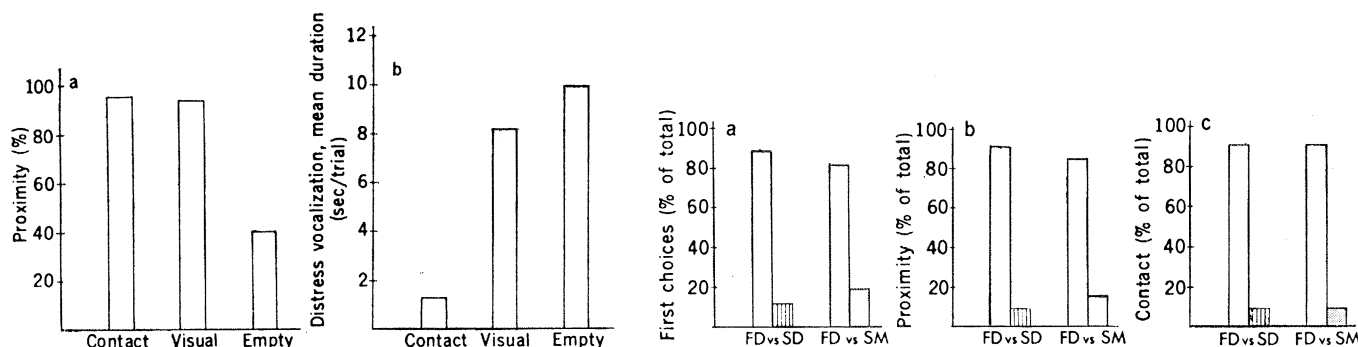


Fig. 1 (left). Proximity (a) and distress vocalizations (b) in a novel environment. Proximity was measured with reference to a restraining cage that contained the familiar dog, either available for physical contact (*Contact*) or for visual contact (*Visual*), or was empty (*Empty*). Each monkey received a total of nine 30-second trials per condition, presented in balanced order. Fig. 2 (right). Percentage of total choices (a), total time in proximity (b), and total time in contact (c) for familiar dog (*FD*), stranger dog (*SD*), and a young stranger monkey (*SM*). Each condition (*FD* versus *SD*, *FD* versus *SM*) was presented on twenty 30-second trials, with the position of the incentives balanced across trials. Tests with the familiar versus unfamiliar dog were completed first, and the second condition was presented approximately 4 days later.

monkeys. All animals had formed attachments to cloth surrogates or monkeys and were separated from these figures and individually exposed to dogs as potential substitutes. In every case a new attachment was formed.

We selected subjects that differed broadly in age and rearing history. Four monkeys were raised from birth in enclosed isolation cages with cloth surrogates, two for less than 1 month and two until 10 months of age. Four monkeys had prolonged contact with other monkeys; two were raised by their natural mothers until approximately 3 months of age, and two were raised in an enclosed cage with a single peer monkey until age 7 months. All subjects, after separation from the original attachment figures, underwent a series of graduated exposures to spayed adult female mongrel dogs, culminating in continuous cohabitation in outdoor kennels (1.2 by 3.2 by 1.8 m). During the exposure and cohabitation periods, narrative data were collected. Systematic tests of the specificity and exclusiveness of the monkeys' attachment behavior started after they had lived with the dogs for 6 to 8 weeks.

Initially, most monkeys reacted to the dogs with fear, expressed in grimaces, distress vocalizations, crouching, and withdrawal. These behaviors usually disappeared quickly, however. All but one of the eight subjects approached the dog within 2 hours (five within 30 minutes), and all approached within 7 hours. Clinging to the dog occurred within the first 4 hours of exposure in seven monkeys; one monkey did not cling until after about 13 hours of exposure.

During the continuous cohabitation phase of the experiment, the monkeys

and dogs were in frequent contact. They rested together, played together, and groomed each other—the monkeys, with their hands; the dogs, by licking the monkeys' fur and anogenital area. The monkeys presented to the dogs for grooming and exhibited social facilitation of feeding, drinking, and investigatory behaviors initiated by the dogs. They often accompanied the dogs when they were taken from the kennels for an exercise period. Most monkeys would cling to the dog, although some of the older ones walked or ran with it, usually keeping within a few feet. If they were prevented from going along, they characteristically vocalized, paced, attempted to escape from the cage, and showed other signs of agitation. Thus, the monkeys displayed the basic features of attachment behavior described by Bowlby (2), Cairns (3), and others. These observations were confirmed and extended by formal tests.

In the first test, the monkeys were observed in a novel room (3.7 by 2.4 by 2.4 m) containing a box (61 by 122 by 85 cm) with walls and ceiling of clear plastic. They were tested under three conditions: (i) The box was empty ("empty"); (ii) it contained the familiar dog but could not be entered ("visual"); or (iii) it contained the familiar dog, which could be reached through passages at the front and ends of the box ("contact"). A record was obtained of the amount of time in, on, or within 61 cm of the box ("proximity") and of the duration of distress vocalizations (such as coo or scream). The effectiveness of the familiar dog in eliciting approach and reducing distress vocalizations were unequivocal (Fig. 1) ($P < .01$ for both measures, Friedman test).

To test the specificity of attachment, the monkeys were given a choice between the familiar dog and a stranger—either another mongrel dog or a rhesus monkey of similar age. The far end of the novel room was partitioned into two presentation areas (each 1.2 by 0.9 m) in which the animals used as social incentives were restrained by short leashes attached to the rear wall. The presentation areas first entered and the amount of time in each area and in contact with the incentives were recorded. The familiar dog was clearly preferred to either stranger. A presentation area was entered on 89 percent of the trials (combined conditions), and on 85 percent of these, the area containing the familiar dog was entered first (Fig. 2a) ($P < .01$, t -test for correlated measures). Comparable results were obtained for measures of proximity and contact (Fig. 2, b and c); 88 percent of total time in proximity and 91 percent of total time in contact were with the familiar dog ($P < .05$). Scores for the unfamiliar dog and the unfamiliar monkey were similar and did not differ significantly for any of these measures. The four monkeys having extensive early exposure to monkey companions resembled the other subjects in all important respects; they selected the familiar dog over the monkey stranger (94 percent of choices) and spent more time in proximity to it (88 percent).

Finally, to determine whether the attachment to the familiar dog was also exclusive, the monkeys were given a choice between an unfamiliar dog and an unfamiliar inanimate surrogate (cloth-covered plastic horse). This test was completed in the period between the first and second series of preference

tests, and identical procedures were followed. The data suggest a tendency toward exclusiveness. A presentation area was entered on less than 50 percent of the trials compared to 89 percent for trials with the familiar dog ($P < .01$, combined preference tests). The dog stranger was contacted on only 25 percent of the trials in this test compared to 72 percent for the familiar dog ($P < .02$, combined tests). Even though the stranger was much less effective than the familiar dog, it received substantially more approaches and contacts than did the inanimate surrogate. On 84 percent of the trials in which a presentation area was entered, the dog stranger was chosen first, and it received 88 percent of total time in proximity and 95 percent of total time in contact.

These results bear directly on several important issues related to early social attachments. First, they emphasize the fundamental importance of distinguishing between the attributes of strength, specificity, exclusiveness, and permanence (that is, irreversibility) in discussions of attachment behavior. Conceivably, these attributes can vary independently. We have found that an existing attachment may be strong, specific, and exclusive, and yet can be redirected to an object that is physically quite different from the original attachment figure. Eventually, the new attachment also becomes strong, specific, and exclusive. In addition to the evidence presented, we separated five of the monkeys from their original dogs and housed them with new canine companions. In every case the new dog became an effective parent substitute. Clearly, a prior bond does not preclude the formation of a strong new attachment by young rhesus monkeys.

Second, conclusions that the original attachment abides indefinitely in rhesus monkeys and shows little or no reduction in strength (4) must be reexamined in the light of the evidence presented here. The four monkeys in this experiment that were raised with conspecifics consistently preferred the familiar dog over an unfamiliar young monkey. Furthermore, subsequent tests indicated that the two peer-raised monkeys preferred the dog over the original cage mate.

Third, the suggestion that the capacity to form new filial attachments diminishes sharply during the first 2 months of life and all but disappears by 250 days of age is clearly at variance with our results (5). All of our subjects, including two that were raised

individually in enclosed isolation cages until 10 months of age, showed unequivocal evidence of infantile attachment to the dog—including approach, following, a sharp increase in vocalization upon separation, and active clinging to the dog in situations eliciting fear or distress.

Finally, our data suggest that the ease with which new attachments will be formed depends upon properties of the social substitute which are yet to be fully determined. Although a large measure of stimulus equivalence may be expected in the earliest stages of ontogeny, it seems unlikely that all claspable objects will support the development of strong filial attachments in older infant monkeys. In another experiment in which rhesus monkeys were given cloth surrogates at 10 months, no evidence of attachment formation was obtained (5), whereas our monkeys of a comparable age showed strong attachment to their canine companions. A dog obviously provides more varied stimulation and

subtle feedback during the affiliation process than an inert cloth surrogate. This probably accounts for the discrepant results. In any event, a gentle, accepting dog can be a highly effective mother substitute for young rhesus monkeys, even for those that have had experience with the real mother.

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Site of Neural Attenuation of Responses to Self-Vocalized Sounds in Echolocating Bats

Abstract. *Bats of the genus Myotis emit intense orientation sounds for echolocation. If such sounds directly stimulated their ears, the detection of echoes from short distances would be impaired. In addition to the muscular mechanism in the middle ear, the bat has a neural mechanism in the brain for attenuation of responses to self-vocalized orientation and nonorientation sounds. This neural attenuating mechanism operates in the nucleus of the lateral lemniscus, reducing its activity by about 15 decibels, and it is synchronized with vocalization.*

Sensory systems often receive stimulation produced by the animal's own activities. For instance, the retina is stimulated by movement of images introduced by eye and head movements, and the lateral-line system of fish is activated by water displacement caused by body movement. Such self-stimulation may not be absolutely necessary for monitoring the movements of the eye or body, and it may even disturb the perception of external sensory stimuli. Apparently, the visual and lateral-line systems have mechanisms for attenuating such self-stimulation. Visual perception in humans is suppressed before and during eye movements (1). A comparable phenomenon has also been observed in arthropods (2). When fish and aquatic frogs move, the activity of sensory cells in the lateral line organ is suppressed by efferent fibers before and during body movements (3).

The auditory system is stimulated by the animal's self-vocalized sound. This self-stimulation is important in controlling vocalization, as evidenced by the abnormal variability in intensity of speech sounds from deaf persons (4) and by the interference with normal development of songs in birds that are deafened (5). Acoustic self-stimulation, however, would be unnecessarily intense for simple monitoring of vocalization, if the auditory system were not equipped with mechanisms for attenuating its sensitivity. Attenuation of self-stimulation appears essential to hearing; such attenuation occurs both at the receptors and in the brain. In humans, cats, and bats, the muscles of the middle ear have been shown to contract synchronously with vocalization to attenuate self-stimulation (6, 7). In addition to this muscular attenuation, neural attenuation by the olivo-