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Effects of social manipulations and environmental enrichment on behavior and cell-mediated immune responses in rhesus macaques

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Abstract

This paper reviews a series of studies that have examined the effects of manipulations to the social and the inanimate environments on the behavior and cell-mediated immune responses of rhesus macaques of various ages living in different settings. In general, enrichment of the inanimate environment with toys, structures, foraging devices, and/or videotapes increased the amount of species-typical behavior expressed by the monkeys, but did not affect their immune responses. Housing monkeys socially, on the other hand, not only resulted in increased time spent in species-typical activities, but also resulted in (1) decreases in time spent in abnormal behavior and (2) changes in a number of immune parameters. Additionally, attempts to directly influence the affiliative interactions of socially housed adult rhesus have resulted in systematic changes in affiliative behavior, although anticipated accompanying systematic alterations to cell-mediated immune responses have yet to be realized. The data suggest that aspects of the physical and social environments influence behavioral and immunological parameters in captive macaques in the absence of other experimental manipulations. As such, these influences need to be appropriately managed and/or controlled in order to minimize potential confounds in experimental designs. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

It is clear that aspects of the inanimate environment and the social environment influence the behavior and immune responses of laboratory animals (Bohus and Koolhaas, 1991; Novak and Suomi, 1991; Segal, 1989). In fact, this entire special issue is devoted to analyses of the effects of the environment on pharmacology, biochemistry, and behavior in select species of laboratory animals. The goal of the present paper is to review some of the data that we have collected, which focus on assessing the behavioral and immunological effects of systematic manipulations to the inanimate and social environments of captive rhesus monkeys (*Macaca mulatta*). Rhesus monkeys are both an extremely social species and an exceptionally important species for many biomedical investigations, particularly AIDS-related investigations (Capitanio et al., 1998; Sastry et al., in press). While groundbreaking immunodeficiency virus and vaccine work is currently being done using the rhesus monkey model (Joag et al., 1998), it is our contention that certain uncontrolled aspects of the captive laboratory environment are not being accounted for. We feel that some of these uncontrolled aspects could be controlled and/or accounted for, thereby permitting the data collected to more directly address experimental hypotheses. The expense of establishing such control might be high, but it is our opinion that the payback in enhanced research quality is worth the additional cost.

The need for the provision of a variety of environmental enhancements for nonhuman primates maintained in laboratory settings has been recognized by many (Segal, 1989) and has been empirically investigated by several research groups, including our own (i.e., Line and Morgan, 1991; Parks and Novak, 1993; Schapiro and Bloomsmith, 1995). Virtually all nonhuman primates currently maintained in laboratories benefit from some form of environmental enrichment program. These programs range in complexity from the provision of simple toys, perches, and/or feeding devices to complex plans involving rotations and combinations of multiple sensory, occupational, physical, and foraging enhancements.

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Many of these enrichment programs also include options for social enrichment (Crockett et al., 1994, 1997; Eaton et al., 1994; Reinhardt, 1989), in addition to those more traditional enhancements to the inanimate environment just mentioned. Extremely creative solutions to the dilemma of single housing vs. social housing have been devised (full contact/part time: Capitanio et al., 1998; partial contact/full time: Crockett et al., 1997; Coelho et al., 1991). Most cage manufacturers now produce caging systems that include a variety of techniques (grooming bars, Crockett et al., 1997; mesh panels, playrooms, etc.) for providing partial or full contact between neighbors. Such systems allow for the control over critical experimental variables typical of the single cage situation, while simultaneously providing opportunities for social contact. Many groups suggest social housing for nonhuman primate subjects when experimental protocols permit it (Novak and Suomi, 1991; Reinhardt et al., 1995), and some have even provided experimental data to suggest that pair housing is beneficial to the monkeys (Eaton et al., 1994; Schapiro et al., 2000). However, if social housing is judged to make it impossible to achieve the goals of an experimental protocol, then the benefits to the monkeys may not always supply sufficient justification for pair or other forms of social housing.

We will now present behavioral and immunological data that we have collected in a number of studies over the last decade. Our goal has always been to improve the behavioral management of captive primates by *empirically* analyzing the effects of experimental manipulations of the inanimate and social environments. Manipulations that were effective/beneficial have been incorporated into our standard operating procedures and those found ineffective were not introduced. By utilizing behavioral management strategies that have been shown to improve the care and well being of our subjects, we feel we are enhancing the quality of the data and research using the rhesus macaque model.

2. Method

2.1. Animals and housing

This is essentially a review article, so the methods utilized in the various studies will be presented in only their most general form. Precise details concerning specific studies and results can be found in the original publications cited. All of the studies to be presented were conducted as part of the specific pathogen-free (SPF) derivation program at The University of Texas M. D. Anderson Cancer Center (Buchl et al., 1997; Schapiro et al., 1994) and were devised by M. Bloomsmith and M. Keeling. Most of the data collection procedures and analyses were performed by the author in collaboration with M. Bloomsmith.

Our goals from the inception of this program were to assess the effects of both the inanimate and the social environments on the behavior and stress responses of rhesus monkeys that were participating in an NIH-funded program to establish a breeding colony of rhesus monkeys free of several designated pathogens (*Cercopithecine herpsesvirus 1*, Simian Immunodeficiency Virus, Simian Retrovirus, and Simian T-Cell Lymphotrophic Virus). Our strategy involved a period of social restriction, a notoriously stressful environmental manipulation for rhesus macaques (Harlow and Harlow, 1962), but one that seemed necessary in order to achieve our SPF goals (Buchl et al., 1997; Schapiro et al., 1994). Our program evolved from one in which we were simply assessing the effects of environmental manipulations on behavior into one in which we prospectively altered aspects of both the inanimate and the social environments to more definitively characterize relationships between the environment, and behavior and immunology (Schapiro and Bloomsmith, 1995; Schapiro et al., 1998, 2000).

In general, our housing strategy consisted of a period of socialization, followed by a period of social restriction that was then followed by progressively more complex social opportunities (Buchl et al., 1997; Schapiro et al., 1994). Young rhesus monkeys spent their first year of life in unimale–multifemale breeding groups with their parents and half-siblings. At 1 year of age, subjects were removed from their natal group and singly caged until they were 2 years of age. From 2 to 3 years of age, subjects were housed in pairs, and from the age of 3 years, subjects were housed in social groups for the rest of their time in the colony. All females lived in unimale–multifemale breeding groups from 3 years onward (Schapiro et al., 1995a). Most males also lived in breeding groups, but excess males spent 1–3 years in all-male groups as required (Schapiro et al., 1995b). All subjects were studied for a minimum of 4 years [from ages 1 (late infant) to 5 (subadult)], and many were studied for several years in adulthood as well.

In general, when studying the effects of environmental enrichment, we maintained experimental groups of 16 subjects that received the various enhancements and control groups ($n = 16$) of monkeys of similar age and experience who did not receive the target enhancements (Schapiro and Bloomsmith, 1994, 1995). By using this between-subjects technique, we were able to isolate the effects of environmental enrichment. Each subject was observed for between one and three 15-min focal animal samples per week during each year in each housing condition (Schapiro et al., 1996a).

Rhesus monkeys give birth seasonally (Lindburg, 1987) and most of the early data were collected from up to five different birth cohorts (those infants born during the birth seasons of 1988–1992 and observed between 1989 and 1997). The first four cohorts participated in the housing scheme mentioned above. Later cohorts were simply group-housed in mixed-sex peer groups (Schapiro et al., 1996b) from the time they were removed from their natal groups (1 year of age) until the time they were put into breeding or all-male groups (3 years of age). These later cohorts were never singly housed nor pair-housed and serve as age-matched control groups for assessing the effects of single (and pair) housing (Schapiro et al., 1996b).

2.2. Data analysis

In general, behavioral and immunological data were analyzed using analysis of variance (ANOVA) and/or multivariate analysis of variance (MANOVA) techniques (Schapiro and Bloomsmith, 1995; Schapiro et al., 2000). The primary independent variables in the analyses were aspects of the inanimate environment (e.g., enriched vs. control subjects; Schapiro and Bloomsmith, 1995), aspects of the social environment (e.g., single vs. pair vs. group housing; Schapiro et al., 1996a), and aspects of prospective manipulations (e.g., trained vs. untrained subjects; Schapiro et al., 2001). While a variety of behavioral measures served as dependent variables, most of the results discussed will focus on changes in species-typical behaviors (e.g., play and social grooming; Schapiro et al., 1996a) and abnormal activities (e.g., self-directed aggression and repetitive locomotion; Schapiro and Bloomsmith, 1995). A variety of cell-mediated immune responses were also analyzed, including proliferation responses to mitogens, cytokine production, natural killer cell activity, and lymphocyte subset distributions (Schapiro et al., 1998, 2000). In one study (Schapiro et al., 1993), we examined plasma cortisol as a measure of stress, but we opted not to continue this line of investigation for reasons that will become clearer below.

3. Results

Since we will be reviewing a large number of studies, only the most relevant findings will be discussed, and specific significant behavioral effects will be presented primarily in the accompanying tables.

The first result of interest (see Table 1) is that inanimate environmental enrichment increased the amount of time that singly housed yearling rhesus macaques spent in positive species-typical behaviors (i.e., playing) compared to control subjects that received no enrichment (Schapiro and Bloomsmith, 1995). Oddly enough, a fairly intense environmental enrichment program that included various combinations of physical, foraging, and sensory enhancements had no effect on the amount of time that subjects spent engaged in abnormal activities.

A comparison of conditions external to the single cage (Schapiro et al., 1995c) revealed that the behavior of yearlings that lived in indoor rooms (sensory contact only with other singly caged monkeys) differed significantly in a number of ways from yearlings that lived in single cages in outdoor buildings (sensory contact with other singly caged monkeys and with social groups). Specifically, indoor housing resulted in increased time spent inactive and playing, but decreased time spent feeding (see Table 2). Additionally, singly caged yearlings housed indoors displayed significantly more self-aggression, but significantly less pacing, than did singly caged yearlings housed outdoors. These differences in abnormal activities are discussed in more detail in the original paper (Schapiro et al., 1995c), but it is interesting to note that the pacing that was common in monkeys outdoors usually occurred in response to “capture” procedures taking place somewhere in the outdoor colony. Pacing in response to a perceived capture threat is a more effective coping strategy and less abnormal response than is self-directed aggression by monkeys singly caged indoors.

While some aspects of the external environment seemed to affect behavior, light levels did not. Light levels experienced by individual monkeys varied considerably, depending on the position of their cage within the room. Although some maintain that monkeys housed in cages on the darker, bottom row of two-tiered racks differ behaviorally from monkeys housed in cages on the lighter, top row in certain situations (specifically in the presence of fear-inducing human personnel: Reinhardt and Reinhardt, 2000), our data do not support this interpretation (Schapiro and Bloomsmith, 2001).

Table 1
Selected behaviors that differed significantly in mean percent of observation time across conditions (control vs. enriched)

Housing condition behavior	Control subjects[a]	Enriched subjects
Single cage[b]		
Self-grooming	11.5	9.1
Playing	0.6	1.5
Pair housing[c]		
Inactivity	4.5	7.1
Playing	4.4	5.7
Group housing[d]		
Social grooming	12.6	12.3
Playing	2.2	1.5
Abnormal behavior	0.9	1.3

[a] Control subjects in the group housing condition received a “light” enrichment program.

[b] Complete data set contained in Schapiro et al. (1995c).

[c] Complete data set contained in Schapiro and Bloomsmith (1994).

[d] Complete data set contained in Schapiro et al. (1997).

Table 2
Selected behaviors that differed significantly in mean percent of observation time for singly caged yearlings across external environments (indoors vs. outdoors)[a]

	Indoors		Outdoors	
	Control	Enriched	Control	Enriched
Inactivity	6.4	5.5	2.9	4.3
Feeding	24.9	25.7	27.0	26.4
Playing	0.8	2.2	0.4	0.4
Pacing	5.6	4.9	9.1	9.6
Self-aggression	0.5	0.5	0.2	0.1

[a] Complete data set contained in Schapiro et al. (1995c).

During pair housing, juvenile monkeys (between 2 and 3 years of age and who again received a combination of physical, foraging, and sensory enhancements) engaged in significantly more play than did control juveniles (see Schapiro and Bloomsmith, 1994 and Table 1). Enriched subjects also spent more time inactive than did control subjects, but there were no significant differences in abnormal activities. Neither species-typical nor abnormal patterns of behavior (see Table 1) were influenced in a study of group-housed subadult monkeys where the comparison of interest was between an intensive enrichment program and a “light” enrichment program (Schapiro et al., 1997). In general, the behavior patterns of socially housed monkeys were more representative of the patterns seen in more naturalistic settings than were the behavior patterns of singly caged monkeys. Additionally, the beneficial effects of inanimate enrichment were diminished when monkeys were housed socially, suggesting that social enrichment was more valuable than inanimate enrichment.

We used several techniques to assess the effects of the social environment on behavior. In one study (Schapiro et al., 1996b), we compared the behavior of four cohorts of singly caged yearlings to a cohort of yearlings that had spent the period from 1 to 2 years of age in mixed-sex groups of similarly aged monkeys. In this comparison, not only did the socially housed monkeys display higher levels of species-typical activity (feeding and playing), but they also displayed greater than a 10-fold decrease in levels of abnormal behavior (see Table 3). These data suggest that manipulations to the social environment of young rhesus monkeys have greater impact on their behavior than do manipulations to aspects of the inanimate environment. This study is of particular relevance since the sample size was quite large, the study spanned a long period, and the subjects in the two conditions were matched for age.

We also compared the behavior of subjects across their three consecutive years of single, pair, and group housing (Schapiro et al., 1996a). As one might expect, subjects differed in the amount of time they spent engaged in both species-typical (inactivity, self-grooming, playing) and abnormal activities as a function of housing condition (and/or age), with socially housed subjects displaying patterns that were more representative of the behavioral repertoires of wild conspecifics (see Table 4).

Table 3
Selected behaviors that differed significantly in mean percent of observation time for yearlings across social environments (singly caged vs. group housed)[a]

	Singly caged		Group housed	
	Control	Enriched	Control	Enriched
Sexual behavior	0.6	0.5	0.1	0.1
Feeding	27.9	28.4	33.8	34.5
Playing	0.5	1.3	3.6	3.2
Abnormal behavior	9.0	8.0	0.6	0.1
Self-grooming	11.5	9.4	4.9	5.1

[a] Complete data set contained in Schapiro et al. (1996b).

Table 4
Selected behaviors that differed significantly in mean percent of observation time across housing conditions (single vs. pair vs. group housing)[a]

	Single		Pair		Group	
	Control	Enriched	Control	Enriched	Control	Enriched
Inactivity	4.5	4.5	4.7	6.3	5.7	7.0
Playing	0.6	1.6	4.5	5.1	2.4	1.5
Abnormal behavior	8.5	8.4	3.2	3.3	0.9	1.0
Self-grooming	11.4	9.0	6.3	4.6	7.2	7.4

[a] Complete data set contained in Schapiro et al. (1996a).

Since the primary purpose of our program was to establish a breeding colony of SPF monkeys, we were concerned with whether the housing strategy that we were utilizing to minimize infection with the target pathogens was adversely affecting the breeding and parenting abilities of the monkeys in the program. Comparisons of both breeding males (Schapiro et al., 1995b) and females (Schapiro et al., 1995a) that had gone through the SPF housing paradigm of the initial four cohorts, with breeders who had been socially housed their entire lives, revealed no significant differences in reproductive output. This finding applies both to short-term (Schapiro et al., 1995a, 1995b) and long-term (Bernacky and Schapiro, unpublished data) measures of reproductive output. While we occasionally like to think that some active component of the enrichment or resocialization strategies that we designed “caused” the SPF animals to be acceptable breeders and parents, it seems more probable that the initial decision to allow youngsters to remain in their family groups until 1 year of age was responsible. One year of age is a fairly late weaning timepoint in most captive production colonies and increases the likelihood that an infant would become infected with one of the target pathogens (Lerche et al., 1994; Ward and Hilliard, 1994). However, the increased behavioral experience gained during this time appears to have been worth the investment and risk (Schapiro et al., 1994). Virtually none of the young animals that met our SPF criteria at 6 and 9 months of age failed to meet these same criteria at 12 months of age (Buchl et al., 1997).

While behavioral measures can certainly provide valuable data concerning the effects that environmental manipulations can have on captive primates, it is often additionally illuminating to have more physiologically based data to confirm the behavioral findings. Our first foray into physiologically based data sets was an examination of body weights in a subset of our singly caged monkeys (Schapiro and Kessel, 1993). In one cohort, enriched and control monkeys did not differ in weight prior to enrichment (age 12 months). However, beginning at age 16 months (4 months into the enrichment program) and continuing until at least 40 months of age, enriched subjects weighed

Table 5
Mean body weights (kg) that differed significantly at selected time points across conditions (control vs. enriched)[a]

	Control subjects	Enriched subjects
12 months[b]	2.02	2.11
16 months	2.30	2.55
24 months	2.90	3.24
36 months	4.14	4.63
40 months	4.90	5.33

[a] Complete data set contained in Schapiro and Kessel (1993).

[b] No significant difference in weight at 12 months prior to enrichment.

significantly more than controls at virtually all timepoints (see Table 5).

We also examined plasma cortisol as a measure of stress in singly and pair-housed monkeys (Schapiro et al., 1993). Using a dexamethasone suppression–ACTH activation technique (Kaplan et al., 1986) to combat some of the problems inherent in plasma cortisol sampling in captive monkeys, we found no differences in cortisol levels as a function of either inanimate enrichment or social housing condition (Schapiro et al., 1993). We did, however, find a difference in cortisol levels as a function of the environment outside of the cage (see Table 6).

Although we were able to sample cortisol values, we were not confident in our ability to use and interpret cortisol levels as a measure of the effects of environmental manipulations. We felt that since our monkeys were likely to participate in investigations in which cell-mediated immune responses would be evaluated (Sarkar et al., 1999; Sastry et al., 2001), we should obtain information about environmental effects on these types of responses (lymphocyte subset distributions, proliferation responses to mitogens, cytokine production, and natural killer cell activity). In this way, we could address the most relevant effects of potentially "stressful" manipulations—effects on cell-mediated immunity—without becoming embroiled in the problems surrounding the sampling, measurement, and interpretation of cortisol data in nonhuman primates.

We have examined cell-mediated immunological effects of our inanimate environmental enrichment strategies (Schapiro et al., 1998) and have found no statistically significant effects on our battery of cell-mediated assays (see Table 7). It is important to note, however, that these data, unlike all of the behavioral data, were collected after enrichment, rather than concurrent with it. Social housing condition, on the other hand, significantly affected a number of the immunological parameters we measured, including CD4$^+$/CD8$^+$, proliferation responses to *Shigella flexneri* and *Campylobacter jejuni*, natural killer cell activity, and production of IFN-γ (Schapiro et al., 2000; see Table 8). Most of our findings demonstrate significant differences between singly and socially housed subjects, and many, but not all, of our findings suggest that single caging has negative immunological consequences. The fact that housing condition alone can influence subjects' cell-mediated immune responses has important implications for biomedical research, presenting a major potential confound for studies of infection, disease progression, therapeutic interventions and/or vaccination protocols that use singly caged subjects.

Table 6
Mean activation scores[a] for plasma cortisol that differed significantly across external environment (indoors vs. outdoors)[b]

	Indoors		Outdoors	
	Control	Enriched	Control	Enriched
Activation score	14.7	15.2	10.8	12.0

[a] Activation score obtained by subtracting the raw baseline score from the raw score at $t=15$ min post-ACTH infusion.

[b] Complete data set contained in Schapiro et al. (1993).

Table 7
Mean values for selected cell-mediated immune responses for group housed subadults that did NOT differ across conditions (control vs. enriched)[a]

	Control subjects	Enriched subjects
CD4$^+$/CD8$^+$	1.04	1.20
Con A (1:100)[b]	5.8	5.8
PWM (1:50)[b]	32.4	32.7
Natural killer activity (100:1)[c]	22.4	15.4

[a] Complete data set contained in Schapiro et al. (1998).

[b] Stimulation index.

[c] Percent lysis.

One of our more interesting sets of immunological data is one that shows that pair-housed monkeys had significantly higher proliferation responses to *S. flexneri* and *C. jejuni* ($P<.08$), two common diarrhea-inducing pathogens in primate colonies, when compared to single- and group-housed subjects (Schapiro et al., 2000). Interestingly, an earlier study by our group (Schapiro and Bushong, 1994) showed that pair-housed monkeys required the fewest veterinary interventions and days of treatment for diarrhea when compared to both single- and group-housed monkeys. Whereas most proliferation assays are performed on mitogens that stimulate immune responses, but do not necessarily have much relevance to the actual health of the animals, our data were collected using pathogens that were typical and problematic for the species. In this case, the cell-

Table 8
Mean values for selected cell-mediated immune responses that differed significantly across housing conditions (single vs. pair vs. group)[a]

	Single	Pair	Group
CD4$^+$/CD8$^+$	0.68	0.83	1.15
Con A (1:100)[b]	5.07	4.68	2.59
PWM (1:50)[b]	6.79	1.46	1.41
Natural killer activity (100:1)[c]	15.3	17.2	13.3
S. flexneri[b]	4.54	7.11	1.83
C. jejuni[b]	3.02	3.72	2.89
Salmonella typhimurium[b]	3.24	4.26	2.05
IFN-γ production[d]	28.2	32.5	75.3

[a] Complete data set contained in Schapiro et al. (2000).

[b] Stimulation index.

[c] Percent lysis.

[d] At micrograms per deciliter.

Table 9
Mean percent of observation time spent affiliating with adults across study phases (baseline vs. training), experimental conditions (trained vs. untrained), and observation times (during training vs. outside of training)[a]

	Baseline phase	Training phase	
		During training	Outside training
Trained low affiliators	6.7	4.5	12.5
Untrained low affiliators	8.2	–	11.2
Trained high affiliators	17.9	2.9	14.3
Untrained high affiliators	15.1	–	13.7

[a] Complete data set contained in Schapiro et al. (2001).

mediated findings were fairly well corroborated by the actual health data.

With all these data in hand, it became apparent to us that the best technique for definitively analyzing the effects of the social environment on behavior and immune responses was to try to prospectively manipulate behavior. To this end, we attempted to alter the affiliative patterns of our subjects using positive reinforcement training techniques, since a number of retrospective studies had demonstrated that levels of affiliative activity were correlated with certain immunological responses (Capitanio et al., 1998; Line et al., 1996). We started by training monkeys that affiliated infrequently to affiliate more frequently (Schapiro et al., 2001). We had several control conditions in this study including groups of (a) low affiliators that were not trained, (b) high affiliators that were trained to affiliate less frequently, and (c) high affiliators that were not trained. We were hoping that by training low affiliators to affiliate more, we would enhance the cell-mediated immune responses of these animals. While our training techniques successfully affected affiliative interactions (Schapiro et al., 2001; see Table 9), the immunological data are not all in agreement with the hypothesis. Low affiliators significantly increased their affiliative interactions as a function of training (specifically outside of training sessions; Schapiro et al., 2001), but there were no significant correlations between affiliative behavior and responses on the battery of cell-mediated immunity assays.

4. Discussion

Clearly a review of this type, focusing on the work from only one laboratory, presents a fairly biased picture of the area of discussion. However, our data are, for the most part, in agreement with the other data available addressing the effects of the inanimate and the social environment on laboratory primates (Capitanio et al., 1998; Eaton et al., 1994; Segal, 1989). An advantage of presenting a review of a number of studies from a single laboratory is that similar methods and philosophies are involved in the development, implementation, and analysis of all of the studies discussed.

The data we have presented seem to address many of the key aspects for which this special issue was designed. We have empirically examined the effects of a number of different components of the inanimate and social environments on behavior and selected immunological responses. We have examined these effects on male and female rhesus macaques ranging in age from late infancy to adulthood. Overall, the results suggest that the environment influences behavior and immune responses in relatively young macaques, not an unexpected finding, but one that is rarely applied to the design, implementation, and analysis of biomedical/physiological research using nonhuman primate models. We consider this potentially problematic, particularly for studies that use singly housed rhesus macaques and measure immune responses (many AIDS-related and infectious disease studies). Given the immunological effects of single caging alone (Schapiro et al., 2000), it seems likely that single caging effects may be a potential confound in many such studies. While it may not be necessary to ensure that all potential environmentally related influences are identified and controlled, it may be appropriate to account for and manage environmental influences that have been shown to influence behavior and/or immune responses. Specifically, given some of the data obtained for pair-housed animals in our studies (Schapiro and Bushong, 1994; Schapiro et al., 2000), pair housing may present a particularly viable housing option for macaque subjects maintained for a variety of, but not all, research purposes.

To summarize the data in a reasonably concise fashion, it seems that enhancements to the inanimate environment, such as climbing structures, toys, foraging opportunities, and videotapes, positively impact young monkeys. This beneficial effect is typically evidenced by increased amounts of time spent in species-typical behaviors, such as playing, compared to control monkeys that received no environmental enhancements. These same enhancements seem to have no significant effect on the amount of time that monkeys spend engaged in abnormal activities or on their immune responses. Providing full contact social opportunities to the monkeys, on the other hand, not only increases time spent in species-typical activities, but also decreases time spent behaving abnormally and seems to enhance certain cell-mediated immune responses. Additionally, a housing strategy that involves considerable social experience followed by social restriction and then gradual resocialization appears to have few adverse consequences on later reproductive output. The general conclusion would be that enhancing the social environment by providing a partner or partners is a more effective enrichment technique than is providing inanimate enhancements. There are even some data which indicate that specifically manipulating aspects of the social environment using positive reinforcement training techniques for group-housed animals can be applied to alter monkeys' patterns of affiliative interactions. Therefore, the interpretation that enhancement of the inanimate environment is of greater importance to singly caged monkeys than it is to pair- or group-housed ones seems reasonable. While we are not advocating denial of inanimate enhancements to socially housed monkeys, the data suggest a hierarchy of needs, in which if a monkey's social requirements are met, it may be somewhat less critical to provide elaborate enhancements to the inanimate environment.

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