Environmental Enrichment for Nonhuman Primates: Theory and Application

Corrine K. Lutz and Melinda A. Novak

Abstract

Investigators have an obligation to promote the psychological well-being of nonhuman primates used in research. Considerable emphasis has been placed on providing nonhuman primates with enriched environments as a means to achieve this objective. A framework is provided that consists of a set of hypotheses about well-being, and the extent to which exposure to various enrichment devices and procedures actually promotes well-being is evaluated. Two hypotheses are concerned with fostering species-typical behavior: use (versus nonuse) of the enrichment, and whether use of enrichment helps normalize other aspects of the behavioral repertoire. Two additional hypotheses are concerned with abnormal behavior: whether currently existing enrichment lowers levels of abnormal behavior, and whether it prevents the behavior. This framework is applied to various enrichment strategies ranging from toys and foraging devices to social interaction. Most devices are used by nonhuman primates and thus constitute an important way to enrich the captive environment. However, enrichment devices vary as to their effectiveness in normalizing the behavioral repertoire and eliminating abnormal behavior. Only social contact satisfies the goal of promoting a wide variety of species-typical activities while at the same time reducing or preventing the development of abnormal behavior.

Key Words: auditory stimulation; enrichment; foraging devices; mirrors; primate; social contact; toys; videotapes

Introduction

Investigators who use animals in biomedical and behavioral research have an obligation not only to conduct high-quality research but also to promote the health and well-being of their animal subjects to the greatest extent possible given the research objectives. Although these obligations may at times appear to conflict, it is essential to maintain this dual focus. Data are only as meaningful as the health of the subjects and the conditions under which they are studied. Thus, such an emphasis is borne not only out of personal concern for the psychological well-being of the organism but also for the empirical well-being of the underlying science.

Although major strides were made in biomedical research during the past few decades, efforts to promote the well-being of laboratory animals, particularly nonhuman primates, largely lagged behind. This situation changed in 1991, when federal legislation required researchers to "provide a physical environment adequate to promote the psychological well-being of primates." The revision of the Animal Welfare Act was associated with increased attention to animal well-being. Since the early 1990s, there have been substantial efforts to improve the housing conditions of laboratory primates. Terms such as "psychological well-being" and "environmental enrichment" now appear in the scientific literature. However, as is the case with a fledgling research enterprise driven by legislation, there are both methodological and theoretical obstacles to overcome. One significant methodological issue is determining the optimal length of assessment. Because environmental manipulations are likely to yield different short- and long-term effects, judgments about the effectiveness of enrichment can be compromised by an inadequate exposure period. Although methodological issues are important, the objective of this article is to provide a theoretical framework for enrichment research. The theoretical obstacles include the difficulty of defining terms such as psychological well-being and environmental enrichment, and the failure to study enrichment using hypothesis testing.

A significant challenge of work in this area is to understand the relationship between psychological well-being and environmental enrichment and be able to define adequately what is meant by these constructs. The most simple way to view the relationship between psychological well-being and environmental enrichment is to consider them as dependent and independent variables, respectively. Thus, psychological well-being is what you measure after you have manipulated the environment through some kind of enrichment. These terms are not interchangeable but instead, are separate components of hypothesis-driven experiments. An operational definition of environmental enrichment is simply any change to the cage environment that would appear to be positive from our human perspective (e.g., an increase in cage size). Assessments of individual animals are then used to determine whether the change is indeed beneficial for them. Here beneficial is legislatively defined as "promoting

Corrine K. Lutz, Ph.D., is a Postdoctoral Research Fellow in the Division of Behavioral Biology, New England Primate Research Center, Harvard Medical School, Southborough, Massachusetts. Melinda A. Novak, Ph.D., is the Chair of the Psychology Department, University of Massachusetts, Amherst.

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psychological well-being." Despite the difficulty in defining this term, an operational definition as noted by Novak and Suomi (1988) includes assessments of behavior (both positive and negative), stress, and the ability to adapt to changing conditions.

Perhaps the greatest challenge is the development of a rational hypothesis-driven approach to the study of promoting psychological well-being. Much too often the approach has been to try whatever is available at the time and record what happens. However, with this approach, virtually any modification of the captive environment will be associated with some changes in behavior. Thus, a framework in which to understand and evaluate the changes is required. Below, we provide a tentative framework, first in the form of a prescription of connecting enrichment strategies to species based on their natural history, and second with respect to providing a set of testable hypotheses. We then assess the literature on environmental enrichment to determine how these hypotheses generally fare.

Establishing a Framework for Environmental Enrichment Research

Primate species are extraordinarily variable, particularly with respect to morphology, habitat, diet, and social organization, and would therefore be expected to vary in their response to environmental change. An enrichment strategy that is optimal for one species might not be as beneficial for another. Thus, the starting point should be adequate knowledge of the species' natural history. For example, some species are primarily arboreal whereas others are primarily terrestrial. Some species have thumbs that permit fine motor manipulations whereas others do not. Species-typical information can then be used to select enrichment strategies that are morphologically feasible and behaviorally relevant for the animal under consideration.

The second step is to assess the effectiveness of environmental enrichment. Because most changes to the environment elicit some behavioral response, it is important to test specific hypotheses about behavioral change. Here we derive hypotheses from the two explicit goals of environmental enrichment. These goals, as described in the Animal Welfare Act of 1991, are to promote species-typical behavior and eliminate abnormal behavior.

Hypotheses Related to Species-typical Behavior

For fostering species-typical behavior, we articulate two hypotheses—one quite specific and the other more general—that can be and have been used to test the effectiveness of various enrichment strategies. The first hypothesis is the "usage" hypothesis, which is based on the premise that using an enrichment device requires species-typical behavior. Specific predictions can be made for different kinds of enrichment. Thus, when monkeys are given toys, manipulation should increase. When monkeys are provided with foraging devices, foraging should increase. These examples are obvious, and the usage hypothesis is typically tested in enrichment research.

A second hypothesis, the "normalized repertoire" hypothesis, has broader significance and predicts that the addition of enrichment will alter or promote other kinds of species-typical behavior in addition to those associated directly with usage of the devices. For example, the addition of a foraging device is predicted to alter time budgets and activity levels such that laboratory animals look more like their free-ranging counterparts in relevant and desirable behaviors. The value of testing the normalized repertoire hypothesis is that it assesses the overall impact of enrichment on the animal. Therefore, decisions about keeping or modifying an enrichment strategy can be based both on usage and on whether it promotes a desirable behavioral repertoire in the animal (e.g., increases in positive behavior along with either no change or a reduction in aggressive behavior).

Hypotheses Related to Abnormal Behavior

A second goal of environmental enrichment is to reduce the occurrence of abnormal behavior. The two hypotheses that can be derived from this objective differ in their presumptive effect on abnormal behavior. The first hypothesis, termed "therapeutic intervention," is based on a pre-existing condition of abnormal behavior. This hypothesis specifically predicts that enrichment strategies should reduce the levels of abnormal behavior. Most studies of environmental enrichment test this hypothesis.

The second hypothesis, concerned with "prevention," applies to situations in which the level of abnormal behavior is extremely low or not yet present (e.g., in very young animals or in animals imported from free-ranging populations). As the name implies, this hypothesis predicts that enrichment should prevent the development of abnormal behavior. Testing this hypothesis requires creating groups of animals that initially do not show abnormal behavior, instituting an enriched environment in one group but not the other, and then comparing the two groups at a later point in time with respect to abnormal behavior. This hypothesis has been tested infrequently.

Types of Enrichment

Enrichment strategies can be divided into two general categories: providing the animals with inanimate forms of enrichment, and providing the animals with social contact. Inanimate enrichment can be further divided into those that require some physical activity on the part of the animal (active enrichment) and those that provide only passive kinds of stimulation. Active forms of enrichment include, but are not limited to, toys, foraging devices, swings, and

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grooming boards. Passive forms of enrichment include exposure to pictures, slides, videotapes, and sounds. This distinction is somewhat arbitrary inasmuch as passive forms of enrichment can be converted to active forms of enrichment if the animal can control the onset or offset of exposure. Furthermore, active forms of enrichment may provide only passive stimulation if the animal does not use them.

Evaluation of Inanimate "Active" Enrichment

Toys and Manipulanda

Primates in the wild are naturally curious animals; they explore and manipulate various kinds of objects they encounter in the natural environment. Much of this exploration and manipulation occurs in the context of searching for food, and includes activities such as cracking open nuts (Anderson 1990; Hannah and McGrew 1987; Ottoni and Mannu 2001) or gouging holes in tree trunks for exudates (Lacher et al. 1981). However, not all manipulation is associated with feeding. Japanese macaques innovated a form of stone handling that included behaviors such as gathering, rolling in hands, rubbing, and carrying the stones (Huffman and Quiatt 1986). Wild capuchin monkeys have been observed to use leaves as cups to retrieve water (Phillips 1998), and one capuchin used a branch as a cane while standing up on his hind legs (Urbani 1999). In the laboratory, opportunities for exploration and manipulation can be severely limited. To help compensate for the comparatively sparse environment, various toys and portable objects can be provided to captive primates to give them opportunities for manipulation and exploration.

Types

A wide variety of manipulable objects are available as enrichment devices for laboratory primates. Many of these items are relatively durable and include rubber dog toys, polyvinyl chloride pipes, nylabones, and boomer balls (Figure 1). Less durable items include wrapping paper and telephone books. Children's toys and "activity boxes" can be used for smaller monkeys such as marmosets and tamarins (Renner et al. 2000) and for infant monkeys (Champoux et al. 1990). Children's toys are generally not suitable for larger adult monkeys or chimpanzees because of the risks created by broken pieces. However, even exposure to suitable toys can lead to health risks. Microbial growth can persist on toys even after sanitation (Bayne et al. 1993), and parts or fibers from enrichment devices may be ingested, leading to potentially severe intestinal ulcerations or perforations (Etheridge and O'Malley 1996; Hahn et al. 2000).

Usage

In general, many primates explore and manipulate objects. However, an animal's age, sex, and housing condition can influence how much it interacts with inanimate toys. For example, Kong® toy usage by chimpanzees was negatively correlated with age (Bloomsmith et al. 1990a; Brent et al. 1989a), and in rhesus monkeys, only 64% of adults compared with 94% of adolescents manipulated wood branches (Reinhardt 1990). Toy use may also vary in part as a function of sex. Female rhesus monkeys have been observed to manipulate and handle objects more than males (Novak et al. 1993; Parks and Novak 1993), whereas the reverse was true for longtailed macaques (Turner and Grantham 2002). This sex difference in toy manipulation may be due in part to sex differences in toy preference. For example, male vervet monkeys appeared to prefer more "masculine" toys (e.g., trucks), and females preferred more "feminine" toys (e.g., dolls) (Alexander and Hines 2002). However, no sex difference has been identified in toy ball manipulation by chimpanzees (Bloomsmith et al. 1990a). Social facilitation may play an additional role in toy manipulation. Although the level of toy manipulation was low in adult singly housed rhesus monkeys (Line et al. 1991), toy use was considerably higher in adult, socially housed rhesus monkeys (Novak et al. 1993) and baboons (Brent and Belik 1997).

Although most captive primates respond to toys, interest in individual toys tends to wane as a function of exposure. Manipulation of toys is usually greatest on the first day, and significantly declines in response on subsequent days (Bloomsmith et al. 1990a; Brent et al. 1989a; Crockett et al. 1989; Pruetz and Bloomsmith 1992), or even within the first hour of exposure (Pruetz and Bloomsmith 1992). When objects provided to chimpanzees were rotated in the afternoon, object usage was greater than when the objects remained the same throughout the day (Sanz et al. 1999). Toy usage was also shown to increase when a larger variety of toys was provided (Schapiro and Bloomsmith 1995). For example, when several toys were provided to individually housed adult pigtailed macaques, they were used for 27% of the 30-min observation periods compared with 16% of the time when only two toys were available. However, response to the multiple toys also declined over the 5-wk test period (Kessel and Brent 1998). Adding novel objects to those already present in the cage increased manipulation by chimpanzees from 8% of the time (0 novel objects) to 54% of the time (10 novel objects). In addition, the number of days to decline to a level of 15% took longer for 10 novel objects (7 days) than it did for a single novel object (3 days) (Paquette and Prescott 1988). These results suggest that a number of toys should be provided initially and rotated on a regular basis to maintain interest.

In general, the more destructible the object is, the more it is manipulated. For example, captive chimpanzees manipulated sheets of paper 27% of the available time compared with less destructible toys (10% of the time). Furthermore, although paper-directed behavior tended to decrease during the first hour of exposure, the overall rates did not decline during the 13 days of exposure (Pruetz and Bloomsmith 1992). Durable objects yielded lower manipu-

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Figure 1 Novel toys promote manipulation, but interest wanes with time.

lation scores. For example, only 10% of 34 animals in a room manipulated a nylon ball during a half-hour observation period (Bayne 1989). Similarly, the use level of sticks was low—approximately 4.8% of the observation time (Reinhardt 1990)—and decreased sharply by the second day of exposure (Line et al. 1991).

Normalized Repertoire

Although usage rates can be somewhat low, even simple, inanimate objects can have an impact on an animal's subsequent behavior. This impact can start at an early age. For example, play behavior increased when yearling rhesus monkeys were provided with various toys and manipulable objects (Schapiro and Bloomsmith 1995).

Abnormal Behavior

Conflicting evidence exists regarding the efficacy of toys in reducing abnormal behavior in laboratory primates. When simple toys and sticks were provided to adult rhesus monkeys, only one of six types of abnormal behaviors decreased during toy exposure. Furthermore, there was no relationship between toy use and stereotypic behavior (Line et al. 1991). Similarly, there was no difference in abnormal behavior displayed by adult macaque monkeys during a control condition (no toy present) and a toy condition (Crockett et al. 1989). Some animals even incorporated the enrichment toy (e.g., nylon ball) in their stereotypic pacing or self-abusive biting patterns (Bayne 1989). However, the provision of toys yielded significant decreases in abnormal behavior in individually housed chimpanzees and pigtailed macaques (Brent et al. 1989a; Kessel and Brent 1998) and in group-housed baboons (Brent and Belik 1997). One unexpected benefit of toy use was observed in a laboratory baboon with a pre-existing history of self-injurious behavior (SIB[1]). Toys were incorporated into biting rituals such that the animal bit the toy rather than itself (Crockett and Gough 2002). Unfortunately, this pattern emerges only rarely in monkeys with SIB.

Very few studies currently address whether the provision of toys can prevent the development of abnormal behavior. In one study, infant rhesus macaques raised in an enriched setting with an activity board, a swing, and hanging chains showed more self-mouthing but less self-clasping and less stereotypy than controls without the enrichment (Champoux et al. 1990). However, rearing monkeys alone in sensory-enriched environments (with toys, manipulanda, and video) or alone in sensory-poor environments yielded no differences in behavior (Sackett et al. 1982). In both cases, the monkeys exhibited profoundly abnormal behavior.

Foraging Devices

Free-ranging nonhuman primates spend a considerable amount of time searching and foraging for food. The percentage of total waking time spent foraging depends in large part on the quality of the environment. In rhesus monkeys, for example, food seeking can range from approximately 16% in urban areas to nearly 50% in rural areas (Goldstein and Richard 1989; Seth and Seth 1986; Teas et al. 1980). When humans provided food for the monkeys, this percentage decreased further to between 7 and 8% (Malik 1986). A similar pattern has emerged for free-ranging baboons. Baboons provisioned via a garbage dump spent approximately 20% of their time foraging, whereas more rural baboons spent closer to 60% of their time foraging for food (Altmann and Muruthi 1988). In contrast, captive primates are fed balanced diets placed in a readily accessible food dispenser once or twice a day. This procedure essentially eliminates foraging behavior, a major source of activity for free-ranging primates. Given the substantial discrepancy in time budgets between free-ranging and captive primates, providing foraging opportunities may substantially promote species-typical behavior and improve the well-being of captive primates.

Types

Many devices and methods have been developed to achieve the goal of extending feeding time and complexity for cap-

[1]Abbreviation used in this article: SIB, self-injurious behavior.

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tive primates. Although these methods do not necessarily replicate foraging in the wild, they do simulate the process of working for food. Foraging devices can vary in complexity. Some devices require simple extraction of small pieces of food from a surface. Artificial turf boards (Bayne et al. 1992a) contain crumbled pieces of food that are sprinkled onto a horizontal piece of Astroturf, whereas artificial fleece boards (Bayne et al. 1991; Lam et al. 1991) are arrayed vertically and have bits of food pressed into the fleece (Figure 2). Other foraging devices require extraction of food from a container. A simple device is the puzzle foraging ball, a hollow ball containing holes through which monkeys can extricate food (Crockett et al. 2001). Food puzzles, which are much more complicated devices, have been used successfully with chimpanzees (Bloomstrand et al. 1986) and macaque monkeys (Bloom and Cook 1989; Heath et al. 1992; Murchison 1991). The food puzzle typically has three to four levels and can be filled with food treats such as peanuts. The subject moves the food from the upper to the lower levels by inserting a finger into small holes in the front of the feeder. The food can then be retrieved from the bottom level via a large hole.

More specialized devices include artificial gum feeders (McGrew et al. 1986; Roberts et al. 1999) and mealworm feeders (Vignes et al. 2001; Voelkl et al. 2001) for marmosets, and devices that simulate termite fishing for chimpanzees (Maki et al. 1989). In situations where an apparatus is not available, foraging time can be increased by spreading food items through woodchips or straw on the floor of the pens or cages (Baker 1997; Byrne and Suomi 1991; Chamove et al. 1982; Lutz and Novak 1995). Due in part to increased processing time, simply feeding captive primates whole (vs. chopped) fruit and vegetables can increase time spent feeding (Smith et al. 1989).

Figure 2 A fleece board allows for foraging activities.

Usage

When attached to the cage for 6 mo, both turf and fleece boards were shown to increase foraging time effectively. During 30-min observation periods totaling 80 hr, rhesus monkeys foraged from these apparatuses for an average of 40% (fleece board) to 52.2% (turf board) of the session. In addition, the time spent foraging actually increased across the 6 mo when the boards were in place (Bayne et al. 1991, 1992a).

Food puzzles require more skill. Although both monkeys and chimpanzees were able to solve food puzzles and extract food (Bloomstrand et al. 1986; Heath et al. 1992; Murchison 1991), individual differences in aptitude were observed. Of nine macaque monkeys exposed to puzzle feeders, only three were able to retrieve all of the peanuts during the 30-min observation period (Heath et al. 1992). Marmosets were not able to solve the puzzle, but they still extracted food from the puzzle feeder by pulling food from the finger holes and not from the bottom opening as designed (de Rosa et al. 2003). Thus, choice of enrichment device should depend in part on the skill level of the individual or species being enriched. Nevertheless, even in a species that can solve the puzzle, not all animals have equal access to enrichment devices. For example, in group-housed chimpanzees, access to the puzzle-feeder varied as a function of rank. During a 2-hr session, those rated as high-ranking spent an average of 20 min with the puzzle-feeder, whereas low-ranking animals spent approximately 10 to 11 min with the puzzle-feeder (Bloomstrand et al. 1986). Therefore, it may be necessary to provide a number of devices to group-housed animals so that more animals have access.

Sophisticated devices were not necessary to increase foraging time when animals were housed on shavings. When woodchips and either grain or mealworms were added to the bare floor for both Old World and New World species, time spent on the ground increased. For example, the time spent on the ground increased from 0 to 11% for marmosets, and from 9 to 87% for lemurs (Chamove et al. 1982). Combinations of foraging activities appeared to be particularly successful in increasing foraging time. When turf boards, food puzzles, frozen juice, and produce were rotated throughout the day, singly housed rhesus monkeys spent approximately one third of the observation period eating and foraging (Schapiro and Bloomsmith 1995). Similarly, when chimpanzees were presented with foods requiring processing time, food puzzles, items dispersed for foraging, and a filled monkey biscuit dispenser, mean feeding durations ranged from 6 to 10.9 min

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within the 30 min after presentation (Bloomsmith et al. 1988).

Normalized Repertoire

The use of foraging devices appears to alter other kinds of species-typical behavior. Squirrel monkeys given access to turf boards showed an increase in locomotion and a reduction in inactivity (Fekete et al. 2000). In some rhesus monkeys, exposure to a foraging/grooming board elicited grooming behavior and solicitation postures directed toward the fleece—actions associated with grooming other animals (Bayne et al. 1991). Exposure to foraging devices has also been associated with a decrease in aggressive behavior in many primate species housed in social groups (Chamove et al. 1982). Both aggressive behavior and grooming behavior decreased in chimpanzees when they were exposed to a combination of foraging methods (Bloomsmith et al. 1988). Simply adding sunflower seeds and other forage material to a wood chip substrate increased feeding and exploration and decreased passivity and social interaction in rhesus monkeys (Byrne and Suomi 1991; Novak et al. 1995).

Abnormal Behavior

It is unclear whether the use of foraging devices is effective in reducing abnormal behavior. Outcomes appear to vary as a function of species and individual characteristics. For example, turf boards did not alter stereotypic behavior in squirrel monkeys or female longtailed macaques (Fekete et al. 2000; Lutz and Farrow 1996), whereas exposure to turf boards and fleece boards was associated with a decrease in stereotypic behavior and pacing in rhesus monkeys (Bayne et al. 1991, 1992a). Although the addition of food items to a shavings substrate reduced the frequency of abnormal behavior in chimpanzees (Baker 1997), it did not reduce abnormal behavior in rhesus macaques (Byrne and Suomi 1991). In another study of eight different species, the addition of shavings decreased abnormal behavior in seven of the species tested (Chamove et al. 1982). When a number of foraging devices (foods requiring processing time, food puzzles, items dispersed for foraging, and a filled biscuit dispenser) were utilized and rotated for chimpanzees, abnormal behavior (coprophagy, feces spreading, and hair pulling) was reduced (Bloomsmith et al. 1988). However, a different outcome was reported for squirrel monkeys. Abnormal behavior was not reduced when singly housed or group-housed squirrel monkeys were exposed to a rotation of various foraging devices (Spring et al. 1997).

Individual differences in response to novelty have been well documented in macaques (Suomi 2000), thus one would expect to see individual variation in response to foraging devices. Such variability has been noted in similarly ranked chimpanzees exposed to a puzzle feeder containing peanuts. In this study, one male ceased to display abnormal behavior (e.g., coprophagy, regurgitation, excessive grooming, fecal smearing, and the consumption of wood), one female showed an increase in abnormal behavior, but two others showed no change (Bloomstrand et al. 1986).

The picture is further complicated by the fact that some forms of abnormal behavior may decrease following exposure to enrichment devices whereas others may be unaffected. One would predict that foraging devices should have the greatest impact on abnormal behavior that was incompatible with foraging (e.g., pacing and back-flipping) and have less of an effect on other kinds of abnormal behavior (e.g., self-biting). This prediction was confirmed for individually housed rhesus monkeys exposed to a food puzzle feeder (Novak et al. 1998). During the first hour of exposure to a puzzle feeder, there was a substantial decrease in pacing although self-biting behavior was unaffected. In fact, in two of the animals, the presence of a puzzle feeder precipitated an increase in self-biting behavior.

At the present time, the use of foraging devices appears to have a somewhat unpredictable effect on pre-existing abnormal behavior. Effectiveness varies as a function of species, type of device or method, and individual. No study to date has assessed the effectiveness of foraging devices in preventing the development of abnormal behavior.

Evaluation of Inanimate "Passive" Enrichment

Visual Enrichment

Under free-ranging conditions, monkeys are continuously exposed to complex and shifting visual scenes. Therefore, it is reasonable to assume that visual stimulation might be an important form of enrichment for captive primates. Early experimental research supports this assumption and has shown that monkeys will actually work for the opportunity to view various scenes, either live or on television. When five adult rhesus monkeys were allowed to control what they viewed using a lever, the monkeys pressed the lever more frequently to see another monkey than to see an empty room (Butler 1958). Similar results were obtained when rhesus monkeys had access to viewing a monkey, a toy train moving on a track, and an empty cage. Monkeys pressed the panel to view the train and monkey more than the empty cage (Butler 1954). When pushing a lever to view videotapes or slides, rhesus monkeys preferred watching videos over slides, and in-focus over out-of-focus videotapes (Butler 1961). Similarly, young bonnet macaques maintained consistently high levels of lever pressing to obtain visual access to a color videotape of an adult female conspecific (Swartz and Rosenblum 1980).

Types

The type of visual enrichment can vary from simple changes, such as pictures mounted on the walls, to more

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complex changes. Examples of these changes include the presentation of slides (Haude and Detwiler 1976) and videotapes (Figure 3; Platt and Novak 1997).

Usage

Usage is more difficult to assess when the enrichment is primarily visual. Two basic approaches have been adopted to deal with this problem. In the first approach, monkeys are provided with some visual stimulus, and looking behavior is measured. In the second approach, monkeys must work (e.g., press a lever) for a visual stimulus, and lever pressing rates are measured.

When looking behavior is used as a measure of interest, studies show that some primates appear to gaze at slides and videotapes. At issue is the time spent watching. Animals housed in individual cages tended to watch more than animals housed in social groups. Individually housed chimpanzees viewed videotapes an average of 74% of the time compared with 20% for the socially housed chimpanzees (Bloomsmith et al. 1990b). Socially housed rhesus monkeys, like chimpanzees, watched videotapes on average 25% of the time when the tapes were available (Platt and Novak 1997).

The amount of exposure is also important inasmuch as primates habituate to tapes that operate either repeatedly or continuously in long time blocks. The mean percentage of time socially housed chimpanzees watched a videotape was approximately 40% lower for the fourth viewing than it was for the first presentation (Bloomsmith et al. 1990b). When singly housed chimpanzees were presented with a single television programmed to a local channel for 6 hr daily, television viewing was highest on the first day (52% of scans) but averaged 20% of scans on subsequent days (Brent et al. 1989a). Similarly, when videotapes were presented to individually housed yearling rhesus monkeys for approximately 7.5 hr per day over a 3-mo period, the level of watching was low and averaged only 3.2% of the time (Schapiro and Bloomsmith 1995). Viewing time was higher overall (25-42%) when videotapes were presented for a shorter period of time (20-60 min per day) to group- and singly housed rhesus macaques and chimpanzees (Bloomsmith et al. 1990b; Platt and Novak 1997).

Figure 3 Animals housed in single cages tend to watch more television than those housed in social groups.

Viewing time appears to be partly related to content. When slides were used, monkeys preferred unfamiliar scenes to familiar ones (Haude and Detwiler 1976). Furthermore, looking time was positively correlated with the frequency of slide presentation (Haude and Ray 1967). A similar pattern has emerged with videotapes. Rhesus monkeys preferred tapes of unfamiliar animals and people and were most attracted to tapes with frequent scene changes (Platt and Novak 1997). However, this preference for unfamiliar animals was not observed in chimpanzees (Bloomsmith et al. 1990b).

The second approach to evaluating the effectiveness of visual stimulation requires monkeys to work for access to videotapes. Numerous studies have shown that monkeys not only press a lever to watch videotapes of other monkeys, but also show sophisticated comprehension of the actions on the tapes (i.e., they can discern social relationships; Bovet and Washburn 2003). However, the strength of the preference for visual stimulation may vary as a function of the testing situation. When five adult male bonnet macaques used a joystick to receive food rewards or to view videotapes of a social group of conspecifics, there was no overall preference for video reward. Two subjects showed a preference for videotapes whereas the remaining subjects preferred pellets (Andrews and Rosenblum 1993). In a later study (Washburn et al. 1997), food reinforcement was held constant while visual stimulation was varied. Rhesus monkeys used a joystick to select either a blank screen or videotape of a monkey, and both choices yielded a food pellet. Under these conditions, monkeys preferred the blank screen compared with the videotape. Brannon and colleagues (2004) also noted a preference for food reinforcement over video reinforcement. However, when monkeys received only videotape reinforcement, they clearly preferred to watch a videotape of a novel social group compared with a familiar group (Brannon et al. 2004).

Other studies suggest that videotape exposure is weakly reinforcing. Even after 75 wk of continuous access to joystick-controlled videotapes of conspecifics, three bonnet macaques continued to respond at modest levels to the tapes (Andrews and Rosenblum 2002). However, monkeys were less likely to watch videotapes as the "price" of viewing increased (as measured by number of lever presses) (Harris et al. 1999). Complicating the picture is the finding that the lever or joystick itself may elicit interest (Kiyama et al. 2003), thereby providing inflated estimates of videotape usage.

Normalized Repertoire

As with any form of enrichment, the effects of television viewing on other kinds of behavior vary by sex, age, and

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species. Brief daily exposure to videotapes was associated with increased activity and decreased social behavior in adult rhesus monkeys (Platt and Novak 1997). In contrast, when a television was presented to individually housed yearling rhesus monkeys for approximately 7.5 hr per day, levels of self-grooming and exploration were higher and playing was lower compared with toys and feeding enrichment combined (Schapiro and Bloomsmith 1995). However, in chimpanzees presented with a television showing a local television channel for 6 hr per day, no significant behavioral changes were observed (Brent et al. 1989a).

Abnormal Behavior

At present, only a few studies have examined the relationship between videotape exposure and abnormal behavior. In yearling rhesus monkeys, the presence of a television did not appear to influence the display of abnormal behavior (Schapiro and Bloomsmith 1995).

Mirror Enrichment

Mirrors are suggested as a possible form of primate enrichment in the Animal Welfare Act (1991). Although mirrors can be considered a form of visual stimulation, we include a separate section for this form of enrichment because of the unique properties of mirrors. Unlike chimpanzees (Gallup 1970), monkeys typically have not been reported to recognize themselves in mirrors (Anderson 1983). However, mirrors can be used in at least two additional ways: angled to see normally out-of-sight areas of a colony room, and directly to see a strange monkey (i.e., one's own image). There are relatively few parallels to mirror enrichment in nature. It is possible that monkeys might briefly view their image at a water hole, but the water would have to be both clear and undisturbed.

Types

Mirrors vary only with respect to size and location. They range from large wall-mounted units to small round discs attached directly to the animal's cage.

Usage

There is no question that monkeys use mirrors to locate objects, to see areas of a colony room that they normally cannot see, and to view the "stranger" in the mirror. Capuchin monkeys manipulated and transported small portable mirrors significantly more than similar-sized nonreflective objects (Marchal and Anderson 1993). When chimpanzees were given access to mirrors, they used the mirror during 30% of the scans during 12-min observation periods (Lambeth and Bloomsmith 1992). Mirrors have also been used by both chimpanzees and monkeys to locate a target or food treats that were out of direct line of sight (Anderson 1986; Itakura 1987; Menzel et al. 1985). More treats were obtained when the mirror was present than when the mirror was absent (Marchal and Anderson 1993).

However, as with many enrichment devices, monkeys can become habituated to mirrors. When a mirror was attached to the cages of individually housed longtailed and lion-tailed macaques, response levels to the mirror were highest on day 1 of a 2-wk exposure period (Clarke et al. 1995). However, it has been reported that interest can be restored simply by moving the mirror to a new location (Suarez and Gallup 1986) or by removing it for a period of time and then reinstating it (Gallup and Suarez 1991).

Mirror viewing time also varies both by age and by sex. In chimpanzees and capuchin monkeys, adult males used the mirror the least, subadult males used the mirror the most, and females demonstrated an intermediate level of use (Collinge 1989; Lambeth and Bloomsmith 1992). Mirror usage may also vary as a function of age; however, there is no clear pattern. In one study, immature chimpanzees showed an increase in mirror use over time, whereas adults showed a decrease in mirror usage over the same period (Lambeth and Bloomsmith 1992). In contrast, viewing by adult capuchin monkeys increased across a 5-wk study, whereas subadult viewing decreased (Collinge 1989).

Normalized Repertoire

The general effect of mirror stimulation is to increase both affiliative and agonistic communicative patterns of behavior. This increase in behavior can be substantial. When a mirror was removed from the cage of two adult rhesus monkeys and then replaced 5 days later, social behavior increased 28 fold (Gallup and Suarez 1991).

Captive primates often view their mirror reflection as a conspecific, and they behave accordingly. For example, the duration and frequency of social responses exhibited by stumptailed macaques (e.g., threats, grimaces, lipsmacking, and teeth chattering) were higher when the mirror was present compared with when it was covered (Straumann and Anderson 1991). Similarly, capuchin monkeys directed threats toward their mirror images, and the number of threats were greatest toward the largest mirror (Marchal and Anderson 1993). The responses directed toward a mirror were more frequent when the mirror was attached to the cage mesh than when it was placed 1 m from the cage (Anderson and Roeder 1989).

Mirrors can also be used to view other animals in the room. When chimpanzees were able to utilize a mirror to view neighboring conspecifics, sexual behavior, agonism, and facial expressions increased whereas play behavior declined (Lambeth and Bloomsmith 1992). When a mirror was attached to the cages of both longtailed and lion-tailed macaques, they displayed both submissive and aggressive responses to the mirror. However, responses differed by species. The longtailed macaques showed more submissive behavior whereas lion-tailed macaques showed more ag-

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gressive behavior in response to the mirror (Clarke et al. 1995).

Abnormal Behavior

Although little research has been conducted to demonstrate the effect of mirrors on abnormal behavior, mirror exposure did not significantly reduce the display of abnormal behavior in one study (Lambeth and Bloomsmith 1992). In addition, mirrors do not appear to be a useful means of preventing abnormal behavior. When infant stumptailed macaques were reared with a mirror between the ages of 2 and 7 mo, they exhibited less social exploration and less social play with the mirror than paired infants exhibited with one another. Furthermore, mirror exposure did not protect the infants from developing the isolation syndrome. Infants raised with mirrors showed autoeroticism, self-clasping, stereotypy, and bizarre posturing, patterns similar to those exhibited by infants reared in total isolation (Anderson and Chamove 1986).

Auditory Enrichment

In nature, primates are exposed to a variety of sounds they do not normally encounter in a laboratory environment. These natural sounds include auditory signals produced by other species (e.g., insects, birds, and mammals) and weather-related noises (wind, thunder, rain). At the present time, little is known about the effects of natural sounds on the behavior of laboratory primates. Instead, auditory enrichment of the captive primate environment is achieved primarily through the presentation of music.

The selection of music as a form of enrichment is based in part on the benefits of music for humans. The strongest case for this benefit comes from clinical studies. For example, in human patients, music heard prior to clinical procedures was associated with significantly lower anxiety scores (Hayes et al. 2003; Wang et al. 2002) and lower heart rates (Augustin and Hains 1996). The question of whether nonhuman primates can also derive similar benefits from music is unresolved to date. The finding of decreased heart rate in four baboons exposed to music (Brent and Weaver 1996) provides some support for this idea.

Types

Auditory enrichment presented to animals typically involves some form of music. Because little research has been conducted to determine the music preferences of laboratory primates, the choice of music is typically based on the preference of the caregiver or technician. Although the animals may not have control over music type, some apparatuses allow them to have control over turning the music on or off (Line et al. 1990; Novak and Drewson 1989).

Usage

Determining the "usage" of auditory stimulation can be quite complicated. Unlike visual stimulation, exposure to sounds cannot be avoided or ignored easily although animals can become habituated to some sounds over time. Thus, usage is typically assessed in an operant paradigm where the presentation of music is controlled by the actions of the monkeys. Most studies show that when given the opportunity, captive primates will press a lever for musical sounds. In one study, rhesus monkeys were presented with a radio they could operate. Although their usage varied from week to week, the monkeys continued to turn the radio on and off through the 20th wk of the study. In addition, the amount of time the radio played each day was as high in the 20th wk as it was in the 1st wk of the project (Markowitz and Line 1989). In another study, socially housed monkeys provided with access to a music box played the music for 45 to 60 min of the 2-hr exposure period (Novak and Drewson 1989). This pattern prevailed even with a longer exposure period. Rhesus monkeys given 24-hr access to a radio played the radio more than 12 hr per day (Line et al. 1990).

Normalized Repertoire

Music presented to captive primates appears to have an influence on behavior; however, the influence can vary. When group-housed chimpanzees were exposed to music, both agitated/aggressive and solitary active/explore behaviors decreased, and these changes persisted even when the music was removed (Howell et al. 2003). In group-housed rhesus monkeys, the levels of affiliative behavior increased with music exposure, but there was no change in other species-typical patterns of behavior (Novak and Drewson 1989). In contrast, music did not have any obvious effect on the behavior of four singly housed baboons (Brent and Weaver 1996).

The type of music may also play a role. Rhesus monkeys were more affiliative and less active when exposed to slow jazz compared with dixieland. Furthermore, when given the opportunity, monkeys chose to play slow jazz more than Dixieland (Drewsen 1990). A similar pattern between activity and beat was noted for chimpanzees. Activity increased when "fast-beat" music was played compared with "slow-beat" music (Harvey et al. 2000). It should be noted that different forms of music usually vary along a number of dimensions, not only beat. At present, there is very little information on how specific features of music (e.g., loudness, rhythm, pitch, range) influence nonhuman primate behavior.

Abnormal Behavior

It is unclear whether exposure to music reduces abnormal behavior. In some of the studies described above, abnormal behavior was either not affected (Brent and Weaver 1996) or not analyzed (Howell et al. 2003). However, in two

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studies, abnormal behavior appeared to decrease in the presence of sound. A decrease in stereotypic behavior was noted when rhesus monkeys were exposed both to different kinds of music and to animal sounds (Drewsen 1990). Furthermore, self-injurious behavior was inversely related to use of the radio apparatus (Line et al. 1990). At present, there is little information on whether music can prevent the development of abnormal behavior.

Evaluation of Social Contact

Primates are social species that exist in a variety of different social structures in the wild. Group size varies from monogamous pairs (e.g., gibbons) and family units (e.g., marmosets) to large multimale troops consisting of more than 100 individuals (e.g., baboons; DeVore and Hall 1965). Primates spend most of their time throughout the day and night interacting and communicating with other members of their social group (Lindburg 1971; Teas et al. 1980). These interactions range from brief communicative interchanges at a distance (e.g., location calls) to prolonged patterns involving extensive physical contact (e.g., grooming bouts and consort pairings). Interactions include affiliative as well as aggressive responses, although the most severe forms of aggression are generally reserved for strangers.

Because sociality is a key feature of most primate species, social stimulation in the form of social housing is considered by many to be the single most effective form of enrichment for captive primates. Social stimulation has unique and dynamic properties; it is seldom constant or completely predictable. It stimulates all of the basic sensory systems and is less likely to produce habituation than all other forms of environmental enrichment (Novak and Suomi 1991). Furthermore, social housing provides the greatest opportunity for the expression of species-typical behavior because many forms of social interaction are possible (Schapiro et al. 1996; Spring et al. 1997). These interactions include passive body contact, play behavior, grooming, copulatory behavior, and parental behavior.

Types

A number of options are available for housing primates together in laboratory settings. These options are necessarily constrained both by species differences in social behavior and by space. For example, it is easier to provide caging and space for small primates living in small groups (e.g., family groups of marmosets) than to provide caging and space for large social groups of large primates (e.g., troops of rhesus monkeys or baboons). Thus, social organization will be better approximated for some species than for others in the laboratory environment. At the most basic level, options include pair housing, small group housing (3-20), and large group housing (>20). Large group housing usually requires a set of large indoor rooms or an outdoor enclosure. Within each of these options, housing arrangements can also vary as a function of sex (same vs. mixed sex) and age (peers vs. mixed ages). In the text below, discussion focuses primarily on pair or small group housing in contrast to individual housing.

Usage (Success Rates)

Unlike other forms of enrichment, social interaction is dynamic, thus making it difficult both theoretically and methodologically to test the "usage" hypothesis. For the purposes of this discussion, the focus is on the success of pairing monkeys (primarily macaques) that were previously housed alone in individual cages. Success is based on compatibility. Incompatible pairs are those that fight, show high levels of aggression, and/or high levels of competition in which one monkey prevents the other monkey from gaining access to food or water. Current research suggests that pairing can be quite successful as long as behavioral assessments are used to determine the likelihood of compatibility prior to pairing (Reinhardt et al. 1988).

The most common way to assess compatibility is to examine the responses of potential pairs to one another through a Plexiglas barrier or a grated partition (Eaton et al. 1994; Reinhardt et al. 1988). In the largest study of the effectiveness of pair housing, pairing unrelated adult monkeys at the Wisconsin National Primate Center was successful in 92% of the cases (671 of 726 pairs) (Reinhardt 2002). Similar success was achieved by pairing adult female rhesus macaques, with only three of 21 pairs requiring separation due to fighting (Eaton et al. 1994). However, success rates can vary as a function of species and sex. In adult longtailed macaques, all 15 female/female pairs were compatible, but only eight of the 15 male/male pairs were still together after 2 wk (Crockett et al. 1994).

Pairing alone would not be considered beneficial unless the partners interacted in a positive manner. For example, in one study (Eaton et al. 1994), paired rhesus females preferred to spend time in close proximity to one another not only during the day, but also at night, where they spent an average of 80% of the time together. Pair-housed juvenile rhesus monkeys also were observed to spend approximately one half of their time in socially directed or socially located behavior (Schapiro and Bloomsmith 1994). After more than 1 yr housed together, paired rhesus monkeys spent significantly more time interacting with their companion (23.5% of time) than with an inanimate branch segment (4.8% of the time) (Reinhardt 1990).

One unique alternative to pair housing is the use of widely spaced bars between the cages of compatible pairs (Crockett et al. 1997). The benefits of this housing arrangement relate to the allowance of limited physical contact without the risk of food competition or severe aggression. Nine male/female pairs tested in this situation spent an average of 12% of their time grooming each other, and pairs spent more than 15% of the time either within an arm's length or in physical contact with their partner (Crockett et al. 1997).

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Normalized Repertoire

There is no question that social housing promotes species-typical behavior. When monkeys were paired, they sat in close proximity to each other, and groomed and played with each other (Schapiro and Bloomsmith 1994), activities that could not be expressed by individually housed monkeys. Exposure to a partner was also associated with increased activity levels (Eaton et al. 1994). Species-typical sex differences were also observed. As with wild monkeys, female pairs spent more time grooming each other than did male pairs (Crockett et al. 1994). Group housing yielded similar benefits. Compared with individual housing, socially housed squirrel monkeys (*Saimiri sciureus*) exhibited higher levels of grooming (Spring et al. 1997). Socially housed yearling rhesus monkeys spent more time feeding and exploring and less time grooming themselves and vocalizing than their individually housed counterparts (Schapiro et al. 1996).

Despite the enormous benefits gained from housing primates socially, there are also risks, the most significant of which is incompatibility leading to severe aggression and wounding. Compatibility is not a static state; outbreaks of severe aggression can occur seemingly without much warning (Samuels and Henrickson 1983). However, these risks are not unique to the captive environment. Free-ranging monkeys also experience aggression and may be wounded in altercations with others (Lindburg 1971). From a cost:benefit perspective, the primary benefits of social housing—an increased species-typical behavioral repertoire along with a reduced incidence of abnormal behavior—are thought by many to outweigh the increased risk of aggression.

Abnormal Behavior

Converging lines of evidence suggest that social housing reduces the incidence of abnormal behavior. In one approach, direct comparisons were made between individually and socially housed monkeys. Paired or group-housed adult rhesus monkeys were less likely to engage in abnormal behavior than monkeys housed in individual cages (Bayne et al. 1992b). Similarly, squirrel monkeys housed in social groups exhibited lower levels of stereotypic behavior than monkeys housed alone (Spring et al. 1997). Group-housed yearling rhesus monkeys also exhibited less abnormal behavior than individually housed yearlings (Schapiro et al. 1996).

Other approaches have examined the effects of changing the housing situation—either moving socially housed animals into individual cages or moving individually housed animals into social groups. Abnormal behavior was predicted to increase in response to individual cage housing, and this prediction was confirmed for chimpanzees. Relocation of chimpanzees to individual cage housing was associated with a marked increase in stereotypic behavior (e.g., rocking, pacing, spinning), but not in self-directed behaviors such as self-orality and eye saluting (Brent et al. 1989b). Social housing was predicted to ameliorate abnormal behavior, and this prediction was also generally confirmed. Introduction of a compatible partner was associated with significant decreases in hair pulling and overall abnormal behavior in adult female rhesus monkeys (Eaton et al. 1994). Group housing of individually housed baboons also resulted in a marked reduction in abnormal behavior (Kessel and Brent 2001). Recent reports indicate that social housing may reduce more serious forms of abnormal behavior such as self-injury (Reinhardt 1999; Weed et al. 2003); however, social housing does not eliminate self-injurious behavior in all animals (Crockett and Gough 2002).

Social housing is also known to be a powerful deterrent to the development of abnormal behavior. Extensive research on isolation rearing in rhesus monkeys has shown that adverse rearing conditions (namely, rearing infants in isolation without any exposure to conspecifics) can have devastating effects on behavior (Harlow and Harlow 1962a,b). Monkeys reared in this manner developed behavioral characteristics that came to be known as the "isolation syndrome" (Mason 1968). Compared with control animals, isolates showed highly abnormal behavior such as rocking, crouching, and clutching themselves. They also showed heightened fear responses, inadequate motor coordination, and deficits in social interaction. These patterns persisted as the isolates grew older (Mitchell 1968; Sackett 1967).

Although isolation rearing is not currently practiced as a general rule, individual housing as adults with visual access to conspecifics is a common occurrence in the laboratory. Possible benefits associated with this type of housing may include easy access to the animal, reduction in disease transmission, and elimination of wounding from fights. However, there is also a cost associated with this practice. A recent survey of individually housed rhesus monkeys at the New England Primate Research Center revealed the following two important risk factors for self-injurious behavior: increased time spent individually housed, and placement into individual housing at an early age (Lutz et al. 2003). Similarly, in pigtailed macaques, abnormal behavior was positively associated with the proportion of the first 48 mo singly housed (Bellanca and Crockett 2002). These findings support the view that social housing is a very effective form of enrichment for captive primates. In the case of macaques, social housing serves to normalize the behavioral repertoire and is extremely effective both in reducing abnormal behavior and in preventing its occurrence.

Conclusions

Primates housed in a laboratory can be subject to environments that are impoverished compared with the natural environment. These conditions may include restrictions in movement, sensory stimulation, social interaction, and/or

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cognitive challenges. This case applies particularly to animals housed individually in small cages.

As demonstrated by many laboratory studies, enrichment helps to increase the complexity of the environment. Ideally, inanimate forms of enrichment should promote usage, facilitate a more normal behavioral repertoire, and reduce or prevent the development of abnormal behavior. Most devices, whether they are toys, foraging units, videotapes, or mirrors, are used by nonhuman primates and thus constitute an important way to enrich the captive environment. However, devices vary as to their effectiveness in normalizing the behavioral repertoire and eliminating abnormal behavior. Some increases in species-typical behavior may be observed, but the effects on abnormal behavior are inconsistent. This inconsistency may be due in part to the fact that reaction to enrichment devices can vary both between and within species as a function of sex, age, and individual preferences.

At present, the most effective form of enrichment for captive primates is social housing. Extensive research shows that many animals can be paired successfully, even as adults. Social housing has been shown to normalize the repertoire and reduce the levels of pre-existing abnormal behavior. Furthermore, it is the single most effective way to prevent the development of abnormal behavior in young animals.

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