

Neural Correlates of Primate Social Behavior

Michael J. Raleigh

During the past decade, there has been an increasing interest in the neurological foundations of primate social behavior. These recent studies have extended the more traditional investigations which focused on the relationships between ablations, stimulations, recording electrical activities and drug administrations, and the cognitive performances of single caged animals. Such investigations have demonstrated that a wide variety of brain structures are involved in the mediation of socially important behaviors such as grooming, huddling, aggression, playing, sexual behavior, utilization of space and access to limited resources (Brody and Rosvold 1952; Butter and Snyder 1972; Ervin 1975; Raleigh and Steklis 1975; Frazen and Myers 1973a, 1973b; Kling 1972a, 1972b; Kling, Lancaster and Benitone 1970; Kling and Mass 1974; Kling and Steklis 1977; Mass and Kling 1975; Mirsky 1960; Myers 1972; Myers, Swett, and Miller 1973; Snyder 1970a, 1970b; Steklis, Kling and Ervin, 1977; Warren, 1972). Recently, however, it has been suggested that the temporal pole, amygdala and orbital frontal cortex (Kling and Steklis, 1977) are three structures most intimately associated with the integration of nonhuman primate social behavior. These structures are either part of or closely connected with the limbic system, which integrates and mediates the expression of emotions in animals and humans (MacLean 1970; Mark and Ervin 1970). Unfortunately, little is known about the relationship between stimulation of or recording from these structures and alterations in social behavior: nearly all the data are derived from lesion studies. As a consequence, this discussion will focus on the lesion data in exploring three issues. First an attempt will be made to underscore the interplay between the social environment (free ranging, semi-natural enclosures and laboratory cages), the animal's prior social history (its age, sex and position in the social group) and the postoperative alterations in social behavior. The effect of a brain lesion on aggression, grooming, playing, huddling, sexual behavior and other social activities is not a unitary phenomenon: Rather the behavioral consequences of a lesion vary with the social setting and with the animal's preoperative social history. Subsequently, the postoperative alterations in the social behavior of the unlesioned animals will be discussed. Living in social groups, nonhuman primates establish long term stable social relations (Dolhinow 1972). Postoperatively the existing relationships between the normal and

lesioned animals are shattered and the resulting changes in the normal animals may provide useful cues about the nature of the behavioral deficits exhibited by the operates (Ervin, Raleigh and Steklis 1975). Finally, the contributions that these types of studies make to understanding human neuropsychiatric disorders will be discussed. While findings from nonhuman primates cannot be extrapolated directly to the human situation, this experimental approach does suggest a strategy for evaluating human neurobehavioral dysfunction.

Environment, Social History and Brain Damage

As has been pointed out (Kling 1972a 1972b; Mass and Kling 1974; Myers 1972; Frazen and Myers 1973a, 1973b; Steklis, Kling and Ervin 1977) two important conclusions emerge from studies of the social behavioral consequences of brain lesions. These are namely, 1) the effects of an intervention on an animal's affiliative and aggressive behaviors vary with the environment in which the animal is tested and, 2) an animal's social history (age, sex and position in the social network) is a useful predictor of its postoperative alterations in social behavior. The importance of the immediate social environment has been underscored by Kling, Lancaster, and Benitone's (1970) demonstration that following amygdectomy free-ranging vervets failed to rejoin their social group. In contrast, in caged situations amygdectomized monkeys exhibit striking tendencies to engage in unusual sexual behavior and increased oral exploration of their environment (Kling, 1972b). The effects of amygdectomy on free-ranging animals could not have been predicted on the basis of what was known about the alterations in caged animals (and vice-versa). Similarly the importance of the immediate social environment was shown to be a key variable in assessing the effects of orbital frontal lesions. For example, when housed in small laboratory cages, vervets with orbital frontal lesions manifested an increase in aggressive behavior and won a greater percentage of fights than they had prior to surgery. However, upon return to their social group, the operates exhibited decreases in aggression and won few, if any fights. As Kling and his colleagues have repeatedly demonstrated (Kling and Mass 1974), the effects of a lesion are contingent upon the environment in which the animal is tested.

Recent investigations have also underscored the importance of the operates' social history in determining

the effects of brain damage on social behavior. It has been suggested that the most vulnerable social behaviors are those which characterize animals of a particular age, sex and social position. For instance, following orbital frontal lesions, juvenile vervets living in a quarter-acre enclosure, manifested dramatic deficits in the form and frequency of play although aggression, grooming and access to desired foods and shelter was not altered. Furthermore, in female juveniles "play-mothering," which consists of carrying, restraining, holding and retrieving the infants of adult females is a prominent social activity (Lancaster 1971; Struhsaker 1967, Gartlan 1969; McGuire 1974). Postoperatively juvenile females with this lesion no longer exhibited this behavior. Among adult female operates grooming and participating in aggressive coalitions, two of their most characteristic social behaviors (Lancaster 1975) were severely disrupted. In contrast, dyadic aggression, access to limited foods and shelter and other aspects of their social behavior were not strikingly altered. Among adult males, sexual behavior, success in dyadic aggression and access to limited resources were severely reduced postoperatively although grooming, playing and other social activities remained unaltered (Ervin, Raleigh, and Steklis 1975). In sum, although orbital frontal damage did not alter locomotion, perception and feeding, the behaviors critical for animals maintaining their position in the social group were those most strikingly altered. Similar observations have been reported in studies of the effects of amygdectomy (Kling 1972a), dorsolateral frontal lesions (Mass and Kling 1975) and temporal pole damage (Myers 1972).

In brief, recent studies emphasize the environmental liability of the consequences of the brain lesions. It is difficult to connect, for example, the observation that following frontal lobotomy free-ranging rhesus monkeys fail to rejoin their social group, to their deficits in cognitive tests (Kling and Mass 1974). These studies have also suggested that the postoperative alterations are contingent upon the animals preoperative age, sex and position in the social system. While, as has long been recognized (Sherrington 1906), it is likely that the variety of social behavioral deficits can be related to disturbances in some underlying process(es), without an appreciation of the complexity of the social behavioral alterations, it is premature to form conclusions regarding the nature of these processes. As Warren (1972:582) has stated, "only by studying many species in a variety of situations can we hope to differentiate specific and general lesion effects and to establish unequivocal similarities across species."

Response of Normal Animals

In a social group, the behavior of operated and unlesioned animals is intimately related: both sets of animals are members of a complex social network and the responses of the unoperated animals to the

lesioned subjects greatly influences the operates' expressions of their social deficits. Unfortunately few previous studies have commented upon the undamaged animals' treatment of the operates. Kling, Lancaster, and Benitone (1970) did note that the unlesioned members of the free-ranging vervet troop did approach and investigate the amygdectomized animals. Myers, Swett and Miller (1973) reported that following frontal lobotomy rhesus monkeys appeared to have been forced out of their troop by other members. In both studies, control animals rapidly reintegrated into their groups. At this time, however, it is unclear whether the operates' failure to rejoin their social group is primarily due to their loss of social skills or the unlesioned animals' aggressive responses to them, or both. In captivity only one study has emphasized the importance of the response of the unaltered individuals to the experimentals (Ervin, Raleigh, and Steklis 1975). These data suggest that the response of the normal animals is contingent upon the preoperative relationships between operates and unlesioned animals. When the preoperative relationship is primarily antagonistic, the normal animals' behavior exacerbates the operates' deficits. In contrast, when the preoperative interactions are primarily affiliative (involving much play, grooming and huddling), the normal animals will ignore but not aggress against the operates. In these situations, their behavior does little to exacerbate or alleviate the operates' deficits. Finally, it is only rarely that normal animals behave in a fashion that alleviates the operates' alterations. These three types of interrelationships — competitive, indifferent and mitigating — between lesioned and unoperated animals are discussed below.

Aggression between operates and unlesioned animals magnifies the operates' social deficits, particularly when agonism was instrumental in maintaining their preoperative relationship. For example, Mass and Kling (1975) found that dorsolateral frontal lesions resulted in the loss of rank among a colony of stumptailed monkeys and that this decrement was proportional to the operates' previous rank. The higher the animals' preoperative rank, the more severely it was aggressed against and the further its fall in the dominance hierarchy. A similar finding was reported in vervets which sustained orbital frontal lesions (Ervin, Raleigh, and Steklis 1975). In that study, the highest ranking male (as determined by percentage of aggressive episodes won) was lesioned. Postoperatively, this animal, OM1 underwent a dramatic reversal of his relationship with the second and third ranking animals NM1 and NM2. Preoperatively OM1 defeated NM1 and NM2 in aggressive encounters, limited their access to limited foods, prevented them from engaging in sexual behavior with receptive females and occasionally broke up the grooming bouts in which they were involved. During this time, NM1 and NM2 would respond to his threats submissively,

frequently avoiding him and watch him while they were attempting to initiate sexual behavior. Preoperatively the other group members were less obviously effected by OM1 but were still clearly responsive to his presence. In the postoperative phases, NM1's and NM2's relationships with OM1 were dramatically reversed. The change in their relationship was apparent immediately upon OM1's return to the enclosure, at which time they threatened and challenged him. By the end of four days, it was obvious that NM1 and NM2 had become dominant to OM1. They won dyadic aggressive encounters with him, prevented him from engaging in sexual behavior and limited his access to desired foods. After a month, the rate at which NM1 and NM2 aggressed against OM1 declined. At that time, however, other normal animals began to aggress against and displace OM1. By the end of seven weeks, OM1 had become a sort of a "scapegoat" with displaced aggression often being directed towards him. A typical instance occurred when NM1 displaced NM2 from the feeding bin. NM2 then threatened a juvenile normal animal which in turn threatened and chased OM1.

Throughout the preoperative period there was considerable tension between OM1 and NM1 and NM2, and OM1's rapid drop in status may be related to the amount and intensity of the threats and challenges he received from these two animals. Apparently, operated animals deal with challenges to their social position less effectively and the amount of threats directed towards an operate appears to be a crucial variable in determining how rapidly he loses status. If NM1 and NM2 had not repeatedly challenged OM1, it is likely that he might retain his high status.

In contrast to such dramatic reversals of an antagonistic relationship, when the preoperative relationship was mainly positive involving frequent play and grooming, the normals generally ignored the operates and did little to effect the operates' deficits. For instance, after members of an enclosed vervet group were subjected to orbital frontal damage, the operates no longer engaged in the types and amounts of play which characterize young vervets. However, the unlesioned animals did not respond aggressively towards young animals that were not fulfilling their preoperative social role. Rather, during the first two weeks after surgery, the undamaged animals would attempt to engage the operates in play groups. The invitations to engage in play were typically of the same form as those exhibited preoperatively. They included tail pulling, exaggerated bouncing and the like. Although the operates did not respond to the normal animals, the unlesioned animals did not direct any more aggression towards them than in the preoperative period. Unable to play with the operates, beginning about the fourth week, the normal animals began to play exclusively with each other. The primary alteration in the normals was in the choice of their play partners: on the whole

they ignored the operates and by the end of five weeks the frequency of their play had returned to preoperative levels.

The third type of interactions between operates and normals was that which tended to reduce the operates' social deficits. Because operates tend to withdraw from the group, there are few field observations relating to this issue. However, on the basis of a captive study, Kling (1972b) suggests that neonatally amygdectomized macaques are able to survive primarily because their mothers continue to care for them. Among adult animals even fewer reliable observations are available. However, observations of Ervin et al. (1975) suggest that certain activities of the normal animals can alleviate the operates' deficits. In the orbital lesion study previously discussed, after four months, NM1 and NM2 were removed from the group and the behavior of OM1 was monitored. While NM1 and NM2 were absent, OM1 regained his access to limited foods and shelter, was approached by receptive females and engaged in sexual behavior. OM1's increased sexual behavior and improved success in aggressive encounters appeared to be triggered by changes in the remaining normals towards him. His return to preoperative levels was preceded by the increased approaching of receptive females and by other animals being submissive to him. In short, when treated as if he was a high ranking animal, OM1 began to behave like one.

In summary, the deficits of lesioned animals are expressed in a social context. Their postoperative behavioral profiles are clearly affected by the behavior of the unlesioned animals. When these normal animals challenge and aggress against the operates, their deficits become more pronounced. When normal animals ignore the operates, the lesioned animals' deficits are limited to those inherent in themselves: they are not exacerbated by this type of treatment. Finally when the normals initiate affiliative activities such as grooming, playing and sexual behavior, the operates' deficits are diminished.

Relationship to Human Psychopathology

In comparing brain dysfunction in humans and animals, it is important to stress that the animal work suggests a strategy, a way of approaching problems. For at least four reasons, specific animal findings do not translate directly to the human situation. First, even in animals there is considerable species and environmentally determined variability in the manifestations of brain dysfunction. For instance, data (Ervin, Raleigh, and Steklis 1975; Snyder 1970a, 1970b) suggest that the alterations which follow orbital frontal lesions vary depending on the paradigm in which the animals are tested. It is very difficult to generalize from one paradigm to another even when the same animals are used in both tests. For instance, when caged individually, operates engaged in hyperactive

spacing, yet in the social group there was no evidence of such behavior. In a similar fashion, the operates exhibited an increase in aggression directed toward humans; however, this alteration did not parallel the changes manifested in a social setting. In that setting, the orbital-frontally lesioned animals were less aggressive and more submissive.

Second, much of human behavior is mediated by language. The more that human affiliative and aggressive behaviors depend on language, the less likely it is that there will be nonhuman analogs to them. Primate communication is very different from human language and this contrast underlies many of the differences between human and animal social behavior (Lancaster 1975; Washburn and McCown 1972).

A third factor is that in humans it is frequently impossible to specify either the location of the lesion or the social context in which the behavioral changes are expressed. Tumors and gunshot wounds rarely result in precisely delimited lesions. In addition it is often difficult to systematically observe the patients' behavior. Often alterations in a patient's behavior are reconstructed from interviews.

Fourth, those patients who do receive precise lesions are being treated for dysfunctions of the brain. Neurological interventions, including leukotomies, lobotomies and stereotaxic lesions are not performed on people with intact brains. All of Mark and Ervin's (1970) patients, for instance, exhibited evidence of previous neural damage. Postsurgical changes in such patients are unlikely to be comparable to the social behavioral changes manifested by animals which had no evidence of prior neural damage. Thus while the contrast between human and animal data is striking, it is not surprising. In brief, it is impossible to extrapolate specific animal findings to the human situation.

Nonetheless, the animal data do suggest a strategy for assessing the effects of brain dysfunction in humans. It was noted that the relationship between changes in social behavior following frontal lobe damage and deficits in standard cognitive tests has yet to be fully specified (Kling and Mass 1974). Similarly variability between the postoperative alterations in social behavior and formal learning settings has been documented for other structures. For example, Kling and Mass (1974:377) suggest that in amygdalotomized animals "increasing social environmental complexity tends to result in increased social fear, withdrawal from social interactions and social isolation in free-ranging settings." On the other hand, the behavioral deficits are not always more striking in the social setting. For instance, Steklis, Kling and Ervin (1977) found that infero-temporal lesions did not have major consequences on social behavior, although they profoundly affect the animals' performance on formal discrimination tests (Gross 1973). Such variability appears to suggest that it is judicious to assess the behavioral consequences of brain damage in a variety

of circumstances. A single standardized test is unlikely to reveal the extent of the behavioral alterations. A particularly vivid instance of this phenomenon was the use of intelligence tests to determine the effects of frontal lobotomies. As pointed out by Greenblatt and Solomon (1953) and by Blumer and Benson (1975) such lesions tend to result in prominent alterations in personality, ability to plan for the future and a host of other deficits although IQ scores are left intact. Such major deficits in human social behavior can be readily detected by observing humans in social settings: it seems highly inappropriate to rely exclusively on formal tests to ascertain the nature of the alterations in behavior.

The relationships between individual brain dysfunction, environmental factors, species typical social behavior, the structure of the social group and alterations in behavior are exceedingly complex. In humans, it is very unlikely that such a complicated interactive system can be fully specified. However, in monkeys, it is possible to create discrete lesions and to control the social and environmental settings in which the operate is tested. In such situations, combining naturalistic observations and formal testing pre-and postoperatively might facilitate the teasing apart of these variables. Such experimental manipulations might clarify the interaction between the social and biological correlates of behavior. Social behavior is the product of functioning brains and in order to understand the factors that influence its expression not only the environmental causes but also the neural circuits that mediate it should be examined. This point of view was expressed in Washburn's (1973:182) statement that a major contribution of primatology is its "repudiation of the 'black box' philosophy and an insistence that the study of behavior must include an effort to understand internal mechanisms."

Acknowledgement

The cooperation and encouragement of the government and people of St. Kitts-Nevis-Anguilla is gratefully acknowledged. Much of the research reported was made possible by a pre-doctoral traineeship grant GMS-1224. The support, guidance and advice of the Behavioral Science Foundation is acknowledged.

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