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# SOCIAL AND EMOTIONAL BEHAVIOR IN MONKEYS FOLLOWING ORBITAL FRONTAL ABLATIONS

by

Daniel Raphael Snyder

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in
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Doctoral Committee:

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ABSTRACT

SOCIAL AND EMOTIONAL BEHAVIOR IN MONKEYS
FOLLOWING ORBITAL FRONTAL ABLATIONS

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Male rhesus monkeys were tested for alterations in social and emotional behavior before and after bilateral orbital frontal (OF) ablation. Each monkey's behavior was compared to his own preoperative reactions in the same situations and to the reactions of sham operated control monkeys.

When preoperatively introduced into a monkey colony, all the Ss assumed the most dominant position in the social hierarchy. Postoperatively, three of the monkeys fell to the bottom of the hierarchy with a latency of 11 days to 6 months. After OF ablation, aggression directed toward humans was abolished and there was a correspondence between the onset of stereotyped locomotion in both home cage and social colony and the loss of aggression. In three Ss, OF ablation disrupted a conditioned avoidance response but produced strong resistance to extinction of the same response. Compared to the sham operated monkeys, the OF Ss were more likely to accept and ingest new or typically rejected food as well as nonfood items. They also performed an instrumental response for a longer period of time in

order to obtain a nonfood item, showed heightened orality, and had increased resistance to instrumental extinction.

The fourth OF monkey maintained his dominance in the social colony for over 8 months through continued aggression, regained his aggression toward humans, and showed no postoperative decline in conditioned response frequency. Histological analysis revealed that this monkeys' lesion selectively spared the medial portion of posteromedial OF cortex, although he sustained the greatest overall OF lesion. This suggests that the critical focus of the cortical mechanism controlling aggressive behavior may be some region within posteromedial OF cortex.

Various interpretations of the results of these experiments are discussed. Neither the hypothesis that OF ablation results in a loss of inhibitory control over hypothalamic drive centers nor the hypothesis that OF ablation produces a failure to suppress previously dominant responses and a reversion to these responses can account for all of these results. We suggest that there is a negative relationship between level of environmental threat and the duration of the latent period before the deficit in aggression appears and that OF ablation produces an inability to react appropriately to threat or stress. A mechanism is suggested in which OF ablation removes the suppressive influence of OF cortex over the amygdala which, in turn, regulates the sensitivity of autonomic centers in the hypothalamus to external stimulation. Thus, in the presence of external threat, autonomic excitation is discharged into the cortico-limbic system and blocks the neural integration of agonistic behavior. This stress hypothesis postulates that (in OF Ss) the greater the degree of external threat or stress, the greater the uninhibited internal arousal, and the greater the disruption in socioemotional behavior.

In memory of my father,

Arthur M. Snyder, M.D.

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A doctoral dissertation represents the culmination of a graduate education and is the direct product of the training and personal contact the candidate receives from his teachers, research advisors, and colleagues. It is my hope that these chapters convey to the reader the excellence of the professors and students in the Departments of Anatomy, Physiology, and Psychology at The University of Michigan with whom I was privileged to associate.

I am particularly indebted to those who contributed to the design and execution of this research and this manuscript. It is with gratitude that I acknowledge my obligation...

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Chapter I

# INTRODUCTION

> ... "the frontal cortex [may be] a functional unit, although the definition of that function must be left to the future"....
>
> von Bonin and Bailey (1947)

This dissertation presents a series of experiments on the effects of damage to orbital frontal cortex on the emotional and social behavior of primates. These studies were aimed at furthering our understanding of forebrain control of emotion.

## Alterations in Activity and Affective Behavior

Many investigators have reported the following sequelae of orbital frontal (OF) damage in monkeys. Immediately following OF ablation and for up to three weeks thereafter, monkeys have been variously described as confused, passive, apathetic, lethargic, hypokinetic, hypoactive, drowsy, depressed, stuporous, or somnolent (Brutkowski, 1965; Butter, Snyder, & McDonald, 1970; Kennard, Spencer, & Fountain, 1941). They may show anorexia to varying degrees ranging from finickiness in food selection to complete rejection of all foods.

During this initial phase following surgery, one may observe that OF monkeys spend an inordinate amount of time sitting in sleep posture (balling) and even lying on the cage floor. When approached

slowly (and not stared at directly) they frequently maintain their relaxed posture and fail to react, unlike the normal monkey. They can, however, be aroused, but less readily than normally. While the OF monkeys seem drowsy, they do not appear to spend more day time sleeping during this immediately postoperative hypoactive phase than do normal monkeys. In addition, there is evidence (Livingston, Fulton, Delgado, Sachs, Brendler, & Davis, 1948) that OF damage produces permanent activity changes in daytime but not at night, when, like normal monkeys, they are less active than during the day. Thus, OF monkeys, like unoperated monkeys, show a diurnal activity pattern.

OF monkeys are extremely hyporesponsive to strong, even noxious, external stimulation during this period of behavioral depression. Startle responses to loud noise and light flashes are abolished as is resistance to direct handling and manipulation of limbs and head by humans. Objects (e.g., capture net and handler's gloves) introduced directly into the cage, the mere sight of which elicit violent aversive and escape behavior preoperatively, evoke but the mildest head and eye aversion and oral exploration.

Absence of affective expression also characterizes the initial phase after OF ablation. The OF subjects' facies are devoid of expression and they neither transmit nor react to the quick, subtle facial and body gestures which are so much a part of primate social communication (e.g., Altmann, 1962, 1968). The implications of this for the loss of social dominance will be discussed in Chapter III. During this stuporous period, OF monkeys are loathe to move about the cage, but when they do, they make slow, deliberate movements in a

quadrupedal, flat-footed gait. None of the spontaneous, jerky, darting head and body movement so characteristic of the rhesus monkey is present.

The duration of the hypoactive period shows considerable variability and indeed sometimes may not occur at all. However, its severity does not appear to be related to any specific locus on the dorsolateral or OF surfaces. Hypoactive states have been reported to result from large prefrontal lesions involving areas 6, 7, and 8 (Kennard, Spencer, & Fountain, 1941), prefrontal lobotomy (Wade, 1952), restricted bilateral area 9 lesions (Richter & Hines, 1938), lesions of the anterior portion of the cingulate gyrus (Bianchi, 1895), and orbital lesions (Butter, Snyder, & McDonald, 1970).

Many of the affective changes seen following OF ablation in monkeys also occur following prefrontal lobotomy and lobectomy in nonhuman primates (Brutkowski, 1964, 1965; Jacobsen, 1935; Kennard, 1956; Pribram, Ahumada, Hartog, & Roos, 1964; Warden, Barrera, & Galt, 1942) as well as in man (Fulton, 1951). Additionally, tumors of the orbital surface (Hecaen, 1964) and orbital cortex undercutting in man (Levinson & Meyer, 1965) are said to typically produce a hypokinetic syndrome involving loss of initiative, disinterest in the environment and abnormal fatigability. Such behavior presents a striking parallel to the lack of emotional expression, increased tameness, and initial depression following amygdalectomy in monkeys (Klüver & Bucy, 1937, 1938, 1939; Pribram & Bagshaw, 1953; Weiskrantz, 1956) and in man (Terzian & Ore, 1955).

A more commonly reported consequence of OF as well as dorsolateral frontal cortex ablation is hyperactivity (French, 1959a, 1959b; French

& Harlow, 1955; Gross, 1963; Isaac & De Vito, 1958; Kennard et al., 1938, 1941; Richter & Hines, 1938; Ruch & Shenkin, 1943; Symmes, 1963) which follows hypoactivity, if the latter occurs. Most often hyperactivity takes the form of incessant locomotor pacing. With unilateral damage, it is expressed as "forced circling" or rotary locomotion toward the side of the lesion (Kennard & Ectors, 1938). Differential increases in gross locomotor activity may be partially due to individual differences between animals, degree of familiarity with the environmental situation (French, 1959a, 1959b) and degree and kind of environmental stimulation (Gross, 1963; Isaac & De Vito, 1958). Hyperactivity is reported following bilateral ablation of prefrontal cortex anterior to the arch of the arcuate sulcus, including cortex buried in sulcus principalis (Jacobsen, 1936; Symmes, 1963; French, 1959a), following selective ablation within sulcus principalis only (Gross & Weiskrantz, 1964), but not following selective ablation of area 6, excluding sulcus principalis (French, 1959a), area 8 or areas 10, 11, and 12 (Richter & Hines, 1938).

There is also evidence that the hyperactivity produced by OF lesions may have a focus in posteromedial orbital cortex. Ruch and Shenkin (1943) found that bilateral ablation of ventral posteromedial orbital cortex (area 13) produced marked hyperactivity of rapid onset (no depressed period) while selective ablation of other portions of the orbital surface (areas 10, 11, and 14) had no effect on hyperactivity.

French (1959a) reports that while monkeys with dorsolateral frontal ablation (area 9) showed rapid increases in motility, they also showed progressive decrements in rate of locomotion within

sessions. This is not typical of the results of radical frontal lobectomies and ablations (e.g., French & Harlow, 1955), nor of either radical or restricted OF damage involving area 13 (Ruch & Shenkin, 1943). Furthermore, because of the rapid onset of the activity changes and the delayed-response deficit following prefrontal lesions (Orbach, 1956), French eliminates the possibility that retrograde degeneration in structures removed from the lesion site are responsible for these two symptoms of prefrontal damage.

What role, then, do structures surrounding and related to area 13 play in the control of activity? In both baboon (Mettler, 1945) and monkey (Richter & Hines, 1938), the addition of either anterior basal ganglia or caudate damage to frontal cortical lesions produced a further heightening of hyperactivity. Furthermore, rostral striatal ablation by itself produces hyperactivity (Glees, Cole, Whitty, & Cairns, 1950). Electrical stimulation and electrocoagulation (Delgado & Rosvold, 1953a) of area 13 produced excessive hyperactivity, similar to that reported for isolated damage to area 9 and 13, which was not found after selective extirpation of the bordering areas. Thus, the anatomical evidence supports the notion of separate dorsolateral and ventral cortical foci concerned with locomotor activity while the surrounding cortex (at least on the orbital surface) does not appear to contribute to hyperactivity. Moreover, the basal ganglia to which OF cortex projects (Johnson, Rosvold, & Mishkin, 1968) are apparently part of the same system for controlling activity.

Another problem is the determination of the nature and neurological basis for the other affective products of frontal damage. Ruch and Shenkin (1943) were the first to consider this issue. They

stated that beginning several weeks after selective area 13 ablation ..."the animals became more reactive, perhaps over-reactive to the observer but excitement still produces an abnormal response, which is to accelerate the rate of running. This seems to take the place of the usual fear or aggressive responses." Butter, Snyder, and McDonald (1970) have made similar observations. However, Butter et al. (1970) also reported that in the presence of highly threatening stimuli, OF monkeys may interrupt their locomotor pacing and display intense aversion. It is to be concluded, therefore, that OF monkeys do act emotionally and that this behavior is somehow related to the degree of threat in the situation. This, in turn, suggests that their thresholds to threat were lowered.

Does the hyperactivity of the OF monkey represent a rise in its baseline of spontaneous locomotor output, or is it an abnormal response to environmental stimulation (i.e., hyperreactivity)? Isaac and De Vito (1958) reported that monkeys with dorsolateral lesions do not show hyperactivity in the presence of low-level stimulation (i.e., darkness, quiet), that they show a disproportionate increase in response to increments in the absolute level of stimulation, and that stimulation across sensory modalities summates to further increase activity. However, familiarity is also an important determining factor: Gross (1963) indicated that in both light and darkness the activity of monkeys with dorsolateral lesions is enhanced in the presence of a familiar acoustic stimulus and depressed to novel acoustic or tactile stimuli. French (1959a) and French and Harlow (1955) reported that locomotion decreased to almost normal levels when frontal monkeys were exposed to long-term stimulation in a

familiar environment. When placed in unfamiliar surroundings, however, high rates of activity persisted for several months. As previously mentioned, Butter, Snyder, & McDonald (1970) have suggested that the degree of environmental threat might represent an alternative dimension to stimulus intensity and familiarity which would incorporate the complementary findings described above. It remains to be determined in which manner familiarity and mode interact to influence the activity of OF monkeys.

## Research Plan

These experiments were intended to study the role of orbital frontal cortex in the control of social and emotional behavior. The aim is to describe the alterations in social and emotional behavior produced by ablation of OF cortex and to specify the nature of the impairments underlying these effects.

Many of the alterations in emotionality and activity produced by OF lesions have long been recognized as being expressed in perseverated feeding and movement (Bianchi, 1895). Thus, hyperactivity has been regarded by many as perseverations of normal exploratory tendencies. The concept of abnormal perseverations of ongoing activity has also been successfully applied to learning impairments in monkeys with frontal lobe lesions (Battig, Rosvold, & Mishkin, 1960, 1962; Brush, Mishkin, & Rosvold, 1961; Butter, Mishkin, & Rosvold, 1963; Mishkin, 1964). Moreover, monkeys with OF lesions show more severe perseverative impairments than monkeys with dorsolateral lesions (Mishkin, 1964).

One explanation of the emotional changes seen in monkeys with OF damage is that, as in the learning situations, the monkey reverts

to earlier, formerly dominant responses which then tend to perseverate. Our research plan, then, was partially designed to provide various tests of the reversion hypothesis as applied to social and emotional behavior. An earlier application of the reversion hypothesis to emotional behavior directed toward humans (Butter, Mishkin, & Mirsky, 1968) established the response pattern for only a short time prior to surgery instead of from the time of introduction into the laboratory. In the present experiment (Table 1, experiment 1; Chapter IV), the monkeys' emotional reactions toward human observers were recorded at regular intervals from arrival in the laboratory to surgery and for several months thereafter. Thus, we were able to record as closely as possible the initial responses to humans so that any reversions to emotional responses initially observed in the laboratory occurring after OF damage could be adequately observed.

A reversion to formerly dominant responses also implies a loss or reduction of recently acquired behaviors. This aspect was tested in a conditioned aversion situation using a classically conditioned posture (CR) and emotional reactions to inescapable shock (Table 1, experiment 6; Chapter V) as well as in the responses to human Os (Chapter IV).

Most primate emotional behavior occurs in a social context. Furthermore, OF cortex is anatomically and physiologically related to the anterior limbic system in which lesions are known to cause emotional disruption and changes in social behavior. Therefore, the effects of OF cortex damage on emotional and social behavior (specifically, the dominance hierarchy) were recorded in a stable, conspecific colony (Table 1, experiment 7; Chapter III).

Another product of anterior limbic (amygdaloid) damage is an increase in oral exploratory and consummatory behaviors together with an apparent decrease in the ability to discriminate the appropriateness of stimuli toward which to direct these behaviors. In view of these changes, the OF monkeys were postoperatively tested in two feeding situations in which altered orality and food preferences would be indicated and in one instrumental situation in which perseveration of an appetitive response for a nonfood object would be indicated (Table 1, experiment 8; Chapter VI).

In a sense, however, all of the experiments listed in Table 1 (except experiment 8) are potential tests of the reversion hypothesis in that the frequency of initially dominant behaviors in novel situations could change over repeated sessions in which identical measures were taken before and after surgery with each S as his own control. In summary, our effort was to determine more clearly the nature of the orbital frontal contribution to the control of socioemotional behavior and the influence that changing situational demands have on a primate's emotional repertoire before and after OF removal. A wide range of behavioral reactions were recorded before and after OF or sham surgery in a variety of novel, stressful, threatening, or fearful situations. Table 1 provides the order in which these tests were run and a brief, identifying phrase for each. The following chapters present the results and conclusions to be drawn from experiments 1 (human observer "stare" testing), 6 (conditioned aversion), 7 (social dominance testing with conspecifics), and 8 (orality and preference behavior).

Footnotes for Table 1

[a] Continued throughout the entire testing period from the day of arrival from the supplier to the week before the Ss were sacrificed (about 17 months).

[b] Manufacturer's trade name for this doll-like plastic figure.

[c] Thanks are due to Miss Heide Rosvold for providing a more respectable designation.

[d] Social behavior testing was the final preoperative test and the first postoperative test. Otherwise, the experimental order was kept intact.

[e] Done postoperatively only, after the conclusion of the preoperative test schedule.

Table 1

Experimental Situations and Order of Testing Before and After Orbital Frontal or Sham Surgery

| Experimental Order | Behavioral Reactions Recorded Toward | Animal Observed In | Name Given to Test |
|---|---|---|---|
| 1[a] | Human observers | Home cage in colony | Stare Test |
| 2 | Nonthreatening, plastic crib toys | Observation cage in isolation | Exploration/ Curiosity |
| 3 | Threatening, inanimate objects | Observation cage in isolation | DamnThing[b]; Michigan Troll[c] |
| 4 | Localizable, auditory threat | Observation cage in isolation | Lion Roar |
| 5 | Naturalistic, predator film | Observation cage in isolation | Predator Film |
| 6 | Inescapable pain (electric shock) | Gridded shock cage | Conditioned Aversion or Aggression |
| 7[d] | Conspecifics | Group cage in colony | Social Colony; Dominance Testing |
| 8[e] | Food and nonfood objects | Wisconsin General Test Apparatus; home cage in colony | Orality Testing; Food Preferences |

Footnotes on facing page.

## Chapter II

## SURGICAL PROCEDURE, GROSS BEHAVIORAL ALTERATIONS, AND HISTOLOGICAL ANALYSES

### Subjects

The Ss were eight feral, male rhesus monkeys (Macaca mulatta), ranging in weight from 4.4 to 5.6 kg. at the initiation of this series of experiments. Ss were housed in individual cages throughout pre- and postoperative testing except for the periods during which they were with the social colony before and after surgery (Chapter III). Throughout the course of testing the Ss were maintained at full diet of 45 cal/kg/day (Purina Monkey Chow) supplemented occasionally with fruit and vegetable. Only for the final food preference tests (Chapter VI) was their ration restricted to approximately 30 cal/kg/day.

### Surgery

Surgery was performed within one week following the preoperative test series (10-13 months after arrival). Ss were divided into two groups of four animals each on the basis of a qualitative rank-ordering of their level of aggression in tests 1, 3, and 4 (see Table 1): an orbital frontal (OF) and a sham group (S).

The animals were given an IM tranquilizing dose (2.0 mg/kg) of Sernylan (Parke-Davis and Co.) followed by slow IV administration of sodium pentobarbital until the cutaneous pain reflexes were abolished.

One-stage bilateral operations were performed under aseptic conditions. Following incision and retraction of the scalp, fascia, and temporal muscles, craniotomies were performed in the frontal bone. The dura was then incised and reflected forward and back through the opening and the orbital surface was visualized by retracting the frontal lobes. The orbital cortex was ablated under visual control by subpial aspiration with a narrow gauge suction pipette. Hemostasis was achieved by packing with saline-soaked pledgets, gelfoam, and the judicious use of electrocautery. The intent was to remove all cortex on the orbital surface including the banks and depths of the orbital and fronto-orbital sulci. The wounds were thoroughly irrigated with saline to check for any residual bleeding or seepage before the dura, muscle, and scalp were closed in separate anatomical layers with silk sutures. Before the final, continuous skin suture was begun, the incision was sprayed with a mixture of hydrocortisone and tetracycline (Terra-Cortril Spray courtesy of Pfizer Laboratories) followed by Terramycin Powder (Pfizer) after the incision was sealed. All Ss were also given 500,000 units of Bicillin IM after surgery as prophylaxis. The four sham operated monkeys received exactly the same procedure as the OFs except that no cortical tissue was removed.

Postoperative Care

Beginning the first day after surgery, all Ss were routinely given a selection of fruit and monkey chow mixed with condensed milk, water, Karo syrup and multiple vitamins (0.3 cc. Zymadrops) three times during the day plus additional appetite incentives such

as raisins or peanuts as required. None of the animals required force-feeding.

Gross Behavioral Changes

As mentioned previously, the postoperative depressive phase is reported to last up to three weeks. During this period of apathetic lethargy, the affected OF Ss showed a lack of orienting or startle responses to external stimulation, anorexia, a lack of locomotor activity, and a total lack of aggression. In the present study, three of the OF animals (Jim, Walt, and Ben) showed progressive abatement of apathy and hypoactivity by the eighth day after surgery. The fourth OF monkey (Willie) showed only a mild hypokinesis for less than 24 hours and no anorexia.

By the thirteenth postoperative day, all of the OF animals had clearly entered the hyperreactive phase. The three monkeys who had displayed some anorexia eagerly accepted any mouth-sized object which was either immediately ingested or stored, sometimes for hours, in their cheek pouches. Two of these OF monkeys displayed occasional copraphagia, the third showed only intermittent and brief ingestion of feces.

For several months, events such as other monkeys barking and shaking their cages or humans entering the colony area induced stereotyped, quadrupedal pacing in the OF monkeys. When approached directly (more intensely stimulated) their pacing increased. Our observations, like those reported previously, suggest that the OF monkey's forced pacing is a form of hyperreactivity to certain aspects of the environment such as degree of threat. They had the blank facies described

previously but two OF Ss (Walt and Ben) did show fleeting grimaces as they were pacing in response to human stare. The OF monkeys did, however, occasionally engage in overtly aggressive exchanges with neighboring animals. During these bouts of agonistic barking, cage shaking, and aggressive gestures, the OF animals appeared just as aggressive as non-OF monkeys. Furthermore, when placed in a social colony (Chapter III) the OF animal is at least initially capable of maintaining a dominant position through direct aggression. When engaged in conspecific aggression, however, the approach of a human (Chapters III and IV) usually intimidates the OF monkey who withdraws immediately and, typically, begins to pace despite the other animal's continued threats. This immediate withdrawal from humans is not usually observed in normal or sham operated monkeys.

Neither hyperphagia, hyperactivity, hyperreactivity, nor any qualitative alterations in emotional responsivity were observed in the sham operated monkeys.

## Histological Analyses

At the conclusion of the postoperative test series the OF animals were anesthetized with Sernylan (2.0 mg/kg IM) and Nembutal (IV to effect), and intracardially perfused with 0.9% saline followed by 10% formalin solution. The brains were removed immediately after perfusion and prepared for celloidin embedding. Coronal sections 40μ thick were cut through the frontal lobes and thalamus, and every tenth section was stained with thionine and mounted.

Results

Figure 1 contains reconstructions of the rostral halves of the four lesioned brains along with representative tracings through the lesioned areas and through thalamic areas of retrograde degeneration. Examination of Figure 1 reveals that each of the four animals sustained extensive OF damage. The anterior part of OF cortex, especially the medial portion, was partially spared in Jim, Walt, and Ben; the posterolateral portion of OF cortex was more severely lesioned in Jim than in Willie while Walt and Ben showed intermediate damage. The posteromedial portion was partially spared in all Ss; Walt showed the most while Ben showed the least damage to this region.

In order to evaluate the degree of damage to three different portions of OF cortex, the percentage of surface area ($mm^2$) within the lesion boundaries as projected onto the ventral surface reconstructions was computed. The orbital surface was divided into four quadrants (Figure 1), with the posterior limit arbitrarily set 480$\mu$ behind the most anterior section, a point near the caudal limit of OF cortex. A line was drawn crosswise at this point on the reconstruction. The division between the anterior and posterior quadrants was set halfway between the posterior limit and the frontal poles. The final division between the medial and lateral portions was set by a line in the A-P plane which bisected the posterior boundary. Because of the lateral curvature of the brain, the anterolateral quadrants were much smaller in total area than any of the other three quadrants. Consequently, the anterolateral portion was combined with the anteromedial to form a single anterior portion.

Fig. 1 Lateral and ventral reconstructions of orbital frontal (OF) lesions and cross-sections through lesions and through thalamus showing regions of retrograde degeneration. On ventral views, solid regions indicate damage in depths of temporal lobe and dashed lines indicate quadrants for estimating lesion area described in text.

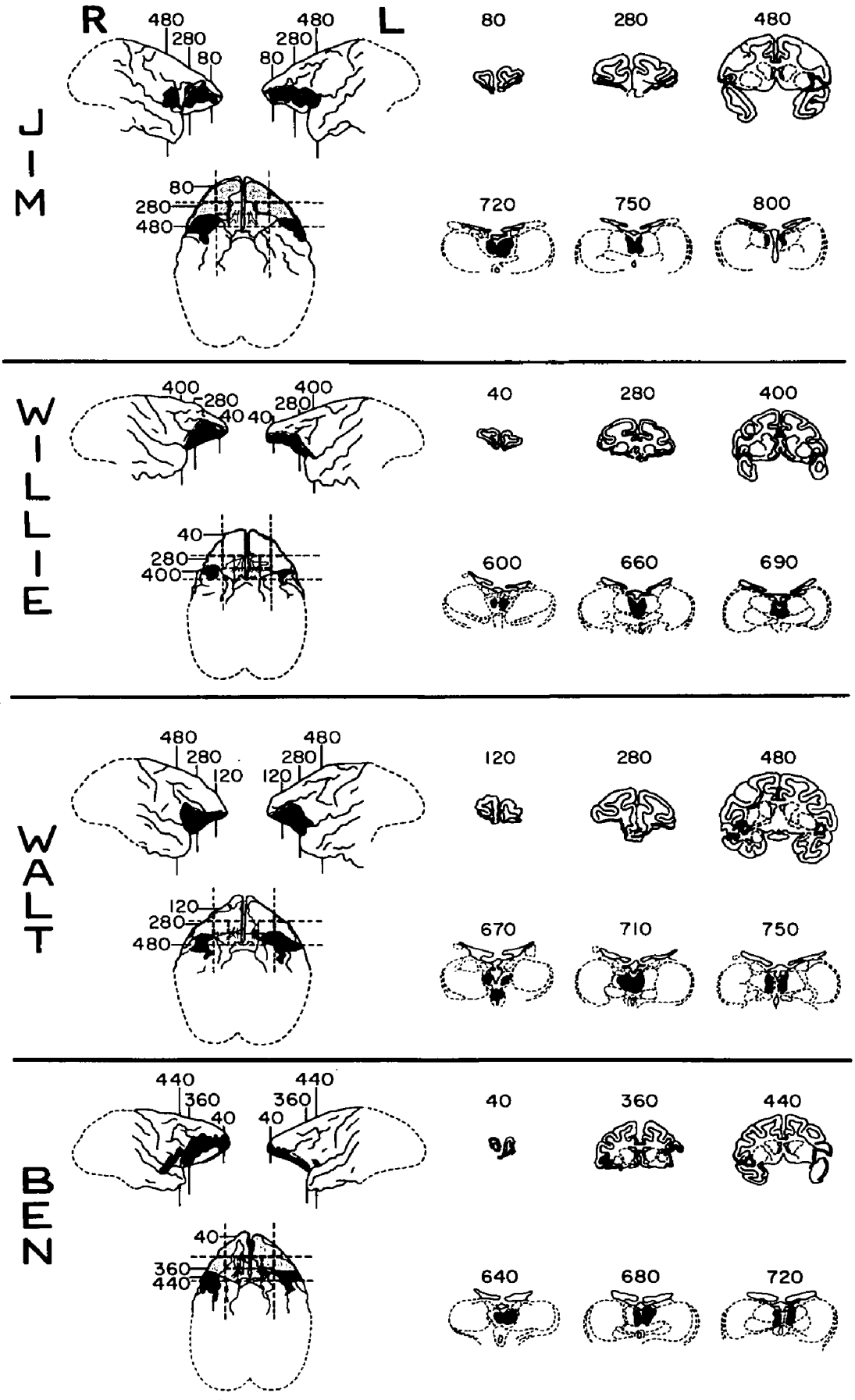

R
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690
WALT
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280
120
120
280
480
670
710
750
BEN
440
360
40
440
360
40
40
360
440
640
680
720

Table 2 is a summary of the lesion extent in each of the three areas and of total OF damage combined to provide bilateral estimations for each S and the rank orders from greatest (1) to least (4) damage.

Table 2

Percentage Estimates and Rank Order of Bilateral Damage to OF Cortex Surface

| S | Total % OF Damage | Anterior % | Rank | Posterolateral % | Rank | Posteromedial % | Rank |
|---|---|---|---|---|---|---|---|
| Jim | 73 | 81 | 2 | 88 | 1 | 42 | 2 |
| Willie | 70 | 95 | 1 | 69 | 3 | 35 | 3 |
| Walt | 70 | 70 | 4 | 80 | 2 | 61 | 1 |
| Ben | 63 | 76 | 3 | 80 | 2 | 32 | 4 |

It is apparent both from Figure 1 and Table 2 that the four ablations were quite uniform in the total amount of tissue destroyed if not in the configuration of the lesions. Similar uniformity is apparent in the retrograde degeneration in the thalamus.

Degenerative changes and gliosis were noted in the following midline nuclei of the anterior thalamus: n. centralis medialis, n. paracentralis, and n. reuniens, as well as n. parafasicularis of the intralaminar group. The heaviest degeneration, however, was found in pars medialis of n. medialis dorsalis which has repeatedly been shown to be the primary diencephalic projection area for orbital frontal cortex (Johnson, Rosvold, & Mishkin, 1968; Mettler, 1947;

von Bonin & Green, 1949). Table 3 provides the total bilateral area of retrograde degeneration ($mm^2$) from tracings of the three representative dorsomedial nucleus sections given in Figure 1. There was no correspondence between the thalamic degeneration pattern and damage to structures other than OF cortex.

Table 3

Areal Estimates of Retrograde Degeneration in the Dorsomedial Nucleus Sections Given in Figure 1

| S | Degenerated Area ($mm^2$) | Rank |
|---|---|---|
| Jim | 545 | 2 |
| Willie | 444 | 4 |
| Walt | 629 | 1 |
| Ben | 531 | 3 |

Other, non-OF structures were for the most part spared during the surgical ablation. Only the anterior claustrum received moderate to severe damage in all Ss. Other areas such as anterior caudate, putamen and amygdala were untouched or very slightly involved. Table 4 summarizes the estimated damage to eight structures adjacent to orbital cortex on the left and right sides separately.

## Discussion

Results presented in forthcoming chapters indicated that Jim was, in some situations, much less affected or not at all in comparison with the other three OF monkeys. Earlier evidence (Butter,

Table 4

Estimates of Subcortical Damage[a] in OF Monkeys

| S | Anterior caudate | | Anterior putamen | | N. accumbens | | Anterior claustrum | | Olfactory tubercle | | Amygdala | | Temporal polar cortex | | Substantia innominata | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L | R | L | R | L | R | L | R | L | R | L | R | L | R | L | R |
| Jim | N | Sl | N | Sl | N | N | M | Se | N | N | N | N | Sl | Sl | N | N |
| Willie | N | N | Sl | Sl | N | N | Se | M | Sl | N | N | N | Sl | N | N | N |
| Walt | Sl | N | M | N | Sl | N | Se | Se | Sl | Sl | N | N | Sl | Sl | Sl | Sl |
| Ben | N | N | N | N | N | N | M | Se | N | N | N | N | Sl | N | N | N |

[a]
N = Normal
Sl = Slight Damage
M = Moderate Damage
Se = Severe Damage

Snyder, & McDonald, 1970) suggested that such behavioral savings might result from a sparing of the posteromedial portion of OF cortex. However, Table 2 indicates that far from having an incomplete lesion, Jim had more extensive overall damage than any other lesioned monkey and, specifically within the posteromedial portion, more damage than two other OF Ss. In view of this contradictory result, a more detailed analysis was required to determine if these findings and those of our earlier experiments could be reconciled.

Based on the ventral surface reconstructions (Figure 1), the posteromedial quadrant of OF cortex (as defined prior to Table 2) was further subdivided into four unequal rectangles such that the posteromedial subdivision of the posteromedial quadrant now completely included the olfactory tubercle. The area of bilateral damage to each of these four subdivisions of the posteromedial quadrant of OF cortex is presented in Table 5.

Table 5

Percentage Estimates and Rank Order of

Bilateral Damage to the Posteromedial OF Cortex

| S | Anterolateral % | Rank | Anteromedial % | Rank | Posterolateral % | Rank | Olfactory Tubercle % | Rank |
|---|---|---|---|---|---|---|---|---|
| Jim | 95 | 2 | 8 | 4 | 26 | 2 | 0 | 3 |
| Willie | 78 | 3 | 36 | 2 | 12 | 3 | 2 | 2 |
| Walt | 100 | 1 | 64 | 1 | 43 | 1 | 6 | 1 |
| Ben | 67 | 4 | 31 | 3 | 12 | 3 | 0 | 3 |

As mentioned previously, all Ss showed little or no bilateral damage to the olfactory tubercle. Only Jim, however, was spared damage to the anteromedial subdivision, just rostral to the olfactory tubercle. No similar differences were seen in the two lateral subdivisions. Our suggestion, therefore, is that the behavioral differences described by Butter et al. (1970) and in the upcoming chapters may be the result of differential destruction to the area of posteromedial OF cortex immediately anterior to the olfactory tubercle and very near the midline. It is, perhaps, fortuitous that Jim sustained the greatest overall lesion for his "atypical" behavior compared to the other three OF monkeys cannot be explained simply on completeness of the ablation.

## Chapter III

## CONSPECIFIC SOCIAL DOMINANCE

Primate social behavior and ecology have been subjected to scientific scrutiny since the pioneering contributions of Dr. C. Ray Carpenter over three decades ago. Judging from the flood of field studies appearing over the past fifteen years or so, the importance of acquiring information about naturally occuring, species-specific behavior patterns to the theoretical anthropologist, social, physiological and comparative psychologist, zoologist, and the behaviorally-oriented clinical psychologist and psychiatrist can hardly be overemphasized: In 1962, DeVore and Lee reported that 48 major primate field studies were underway or recently completed which involved workers from each of the above academic disciplines.

The Old World monkeys (Cercopithecidae), particularly the rhesus monkey (Macaca mulatta), have been the most intensively studied of all primate species (including Hominidae) largely because there exists a relative wealth of background information, because there are good observational opportunities in several locations, and because of their intensely social nature, they are, in terms of data collection, rewarding to study (Altmann, 1967).

Of all the behaviors that occur between and among males and females of all ages in a free-ranging social group, the preponderance of attention has been directed at the analysis of dominance hierarchies. Many of these papers have attempted to categorize the species-specific agonistic repertoire into meaningful, cause-and-effect

sequences, to provide some knowledge of the effects on social behavior of changing ecological conditions (such as population density, altered food supply, or predation), or to explore some of the seasonal changes in social interactions which accompany mating, birth, and maternal care (e.g., Altmann, 1962, 1968a; Carpenter, 1942a, 1942b; Chance, 1956; Hinde & Rowell, 1962; Kaufmann, 1967; Koford, 1963, 1965; Marsden, 1968b; Sade, 1967; Southwick, 1962; Vandenbergh, 1968; Vessey, 1968).

Once a foothold was gained on the "vocabulary" of the rhesus' agonistic language, it became possible to manipulate controlled aspects of the social environment to yield ever finer analyses of discrete behavior mechanisms. Many of the fundamental social and biological phenomena such as home range utilization and changes in rank associated with maturation, breeding, and spacing (e.g., Kaufmann, 1967) or intergroup relations (Marsden, 1968a; Southwick, 1962; Vandenbergh, 1968; Vessey, 1968) are still best studied in very large outdoor enclosures or in the field. It has become exceedingly profitable, however, to bring small groups of macaques into the laboratory where rigorous environmental controls and observational methods can be utilized. Under controlled conditions, the order and stability of the dominance hierarchy has been determined by a variety of measurement techniques which include: primacy in food getting as measured in a competitive feeding situation (Brody & Rosvold, 1952; Miller & Murphy, 1956; Mirsky, 1955, 1960; Mirsky et al., 1957; Rosvold et al., 1954; Varley & Symmes, 1966), restriction of feeding areas (Bernstein & Sharpe, 1966), competitive drinking (Boelkins, 1967), competitive avoidance (Hamilton, 1960), cooperative avoidance

(Miller, Caul, & Mirsky, 1967), relative fighting ability (Brody & Rosvold, 1952; Delgado, 1966, 1967a, 1967b; Mirsky, 1955, 1960; Mirsky et al., 1957; Rosvold et al., 1954; Varley & Symmes, 1966), cooperative aggression (Maslow, 1936, Masserman, Wechkin, & Woolf, 1968; Varley & Symmes, 1966; Zola, 1968), grooming pattern (Varley & Symmes, 1966), conditioned fear (Murphy & Miller, 1956), conditioned avoidance responses (Buddington, King, & Roberts, 1967), group competitive stiuations involving both positive and negative reinforcement (Hamilton, 1960; Plotnik, 1968a) manipulatory incentives (Schusterman, 1964), social restriction (Mason, 1960, 1963), and living space restriction (Southwick, 1967). These procedures are neither equally valid nor reliable in isolating the dominance hierarchy nor are they equally potent in eliciting generalized aggression. When replications of the same test yield different hierarchical orders it may be argued that it is the hierarchy itself that is flexible; that the alpha male changes rank within a series of tests (e.g., Boelkins, 1967). The mass of field-work evidence cited above unanimously disagrees with this, however, and indicates that over any given short period (of, say, about one month) the social hierarchy is rigidly stable and that the rank orders of all animals in the male and female central and peripheral hierarchies are easily identifiable, <u>especially</u> the identity of the alpha male. If, in fact, the alpha male is challenged and loses status it usually takes at least one month for the fall to become evident in all social interactions and for his new (lower) position to cease being ambiguous (Kaufmann, 1967). Of course, it is still possible that the pressures of captivity so disrupt social behavior that the

dominance hierarchy is rendered ineffectual and in a permanent state of flux. However, the fact that most social behaviors in captivity are indistinguishable from those observed in the wild (e.g., grooming, hetero and homosexuality, play, maternal care) renders that interpretation untenable.

Many of the competition situations used so often in the past, particularly eating and drinking, produce very unreliable results if the social hierarchy is assumed to coincide perfectly with either the feeding or drinking order or with the actual number of pellets or volume of fluid consumed. (The more important studies which have utilized these procedures are listed above.) There are several reasons why the alpha male may not choose to assert his dominance in a competitive feeding situation thereby giving "misleading" information about the rank ordering of the group: because of recent successes in obtaining more than his share of food or fruit, the alpha male might be more satiated than his subordinates and, therefore, relatively reluctant to work for more; the palatability of various incentives may vary on a daily basis and, unless regularly deprived, monkeys, especially dominant monkeys, may temporarily refuse previously highly preferred foods; during a competitive feeding test the alpha male might be otherwise occupied with leader-type chores such as protecting a female in estrus with whom he is in consort, breaking up fights between subordinates, or threatening other monkeys and/or intruders in the laboratory. All of the results from experiments in which the E directly approached the colony to distribute hand-held or hand-delivered food claiming that acceptance of food followed hierarchical lines should be used with caution (Brody &

Rosvold, 1952; Mirsky, 1955, 1960; Mirsky et al., 1957; Rosvold et al., 1954). Firstly, it is to be expected that each of the subordinates would have (repeatedly) come forward long before the alpha monkey (and possibly one or two other high ranking males) ceased threatening the human, and secondly, even the order in which the subordinates came forward is very likely meaningless since the relationship between aversion to humans and conspecific social rank is uncertain, although Rosvold et al. (1954) reported a negative relationship between aggressive dominance behavior in a colony and aggressiveness in the home cage toward humans. It is probably safe to assume that one or more of the above conditions is always in effect markedly reducing the predictive power of feeding competition tests of social dominance. (This is not to say that these previous experiments are not valid. While the feeding competition portions are open to scrutiny, the aggressive-submissive interactions, which were recorded in each of these studies, can certainly be assumed to have followed the linear dominance hierarchy and provided an accurate rank order indentity for each S. Misconceptions arise when feeding or some other selective social behavior is used alone as an indicator of rank.) Unfortunately, similar criticisms of some of the other methods could also be made but since they have been used so rarely they will not be reviewed here.

Let us turn, instead, to a combination of observational techniques that have yielded valid, reproducible results. The compilation of well verified, extensive inventories of the rhesus repertoire of agonistic behaviors has already been documented (e.g., Altmann, 1962; Sade, 1967). All that remained was to find a situation which could

be repeated as often as necessary and was always sure to provoke intense socioemotional behaviors—whatever form they may take.

Occasionally, a feral group of rhesus monkeys becomes too large for the home range and it divides into two or more subgroups which expand into new territories or merge with adjoining, smaller groups (Carpenter, 1942a). More often, isolated animals leave one group to join another, sometimes after having been driven from their natal groups (Southwick, 1962). Bernstein and Mason (1963) artificially created a rhesus monkey group in toto using animals that had not previously been housed together. They reported frequent and unidirectional aggressive interactions which implied immediate recognition of each animal's social rank by all members of the group.

In a situation in which the same measure is to be repeated (for example, before and after surgery) it is easier to control and more economical to introduce a single monkey at a time into an existing social group whose hierarchy is known instead of forming new groups of unknown stability. The social reactions of stabilized groups during the integration of individual conspecifics has been observed in chimpanzees (Wilson & Wilson, 1968), baboons (Hall, 1964), squirrel monkeys (Rosenblum, Levy, & Kaufman, 1968), Japanese monkeys, Macaca fuscata, (Kawai, 1960), as well as adult, adolescent, and juvenile male and female rhesus monkeys, Macaca mulatta, (Bernstein, 1964; Bernstein & Draper, 1964; Hansen, Harlow, & Dodsworth, 1966; Southwick, 1967). From these studies it is clear that more intense, lengthy, and widespread aggression occurs during the integration of a new animal into the group than occurs when either many animals feed in a small area or when total living space is seriously compromised—

the other two situations that are known to regularly induce high levels of aggression (Jay, 1965; Southwick, 1967). During the integration process, Bernstein (1964) reported that all types of social interactions were highest upon release and decreased slowly over the following two days. Immediately upon introduction all the group members spent much less time in close spatial proximity (probably because of the heightened intragroup aggression) and only gradually returned to their preintroduction levels; and the same pattern applies to time spent in body contact and social grooming. As for the direct effects on aggression, Bernstein (1964) states, "Agonistic and sexual behaviors show a pronounced increase on the release of new animals with the severest forms of agonistic behavior (fighting, screaming, and crouching) showing the most rapid declines. In each case where severe fighting took place upon the introduction of a newcomer, the newcomer submitted to additional punishment without resistance after an initial period of reciprocal fighting." There is a short period, then, when aggression directed at the newcomer may result in reciprocal fighting which is not seen together with a lowered overall level of aggression when the whole group undergoes simultaneous introduction (Bernstein & Mason, 1963; Kawai, 1960). These reports from captive colonies plus parallel observations of rhesus hostility towards nongroup members in the field (Carpenter, 1942a; Southwick, 1962) indicate that a strange monkey is, at first, an intruder and may be threatened or simultaneously attacked by many of the troop members. That this does not occur in the simultaneous introduction procedure where the recognition of status is immediate and the aggression unidirectional suggests that ultimate status of

the intruder has little to do with the initial attempts to protect the integrity of the group.

Once the intruder submitted and resistance ceased, Bernstein (1964) noted that the alpha and other high ranking males began to threaten and attack those subordinates who persisted in attacking the intruder. It is as if the dominant seniors were protecting the "sanctity" of the dominance hierarchy; that the meaning of properly signalled submission, albeit from a stranger, should not be violated.

Paranthetically, there is an interesting, somewhat analogous situation which often occurred during a stressful test of emotional behavior (Butter, Snyder, & McDonald, 1970). Monkeys were threatened by a doll-like figure which was intermittently thrust at them within an observation cage which allowed the Ss to retreat only one or two feet from the doll when it "attacked." After many presentations, when repeated threats and attacks had no influence on the doll's aggressive behavior, many of the normal monkeys began to submit (head and eye aversion, cower, body turn, and perineally present) to it. Occasionally, the animals happened to be in a submit posture near the doll when it moved forward and struck them. The first few times this happened the Ss exhibited a violent mixture of intense fear and overt aggression: the animals flinched, crashed against the cage, wheeled, and attacked the doll—sometimes leaping on it to bite the head and arms. Again, it was as if the doll broke a social taboo by continuing aggression in the face of submission; the behavioral base of the dominance hierarchy had been challenged. The parallel between the "inappropriate behavior" of the threatening inanimate object and the violation of properly given submission

signals by the subdominant aggressors toward the lone intruder is obvious.

It seems that once the integration-learning process is complete and an animal's status is secure, the agonistic relations in both directions are not subject to rapid forgetting even in the absence of continual reinforcement. Bernstein (1964) noted that the re-introduction of a low ranking female after a 60 day absence produced little aggression, especially when compared with her first confrontation with the group. Almost immediately after reintroduction, she was groomed by several group members, she approached the alpha male and was mounted by him and by a juvenile male. In fact the only threats of any substance came from monkeys subordinate to the female before her absence and who appeared to be "taking advantage" of a temporary social instability to direct some aggression at a higher ranking S who, it follows, they must have immediately recognized. Additional evidence is provided by Carpenter (1942a) who observed the free-ranging behavior of a rhesus group whose alpha male was returned after a three week absence. He reported apparent immediate recognition of and submission to the dominant male by all the group members and also by some members of nearby groups. The evidence indicates, then, that the social dominance hierarchy is based upon firmly established behavior patterns, that it is remarkably stable over a period of weeks, and that any changes in rank tend to occur slowly over several months with the rare exception of a leader losing a challenge and suffering abrupt expulsion from the group. Because of the high frequency of unambiguous social interactions and the rigidity of the dominance hierarchy in Macaca mulatta as compared with many other

primates, investigators have made this behaviorally prolific species the primary subject in which to study the neural mechanisms of social and emotional behavior. Prefrontal lobotomy (Brody & Rosvold, 1952) was reported to have had a variable and unclear effect characterized as a reduction in the "rigidity and stability of the social structure" because the lobotomized low status monkeys ceased submitting to and avoiding more dominant animals and began aggressing upwardly. In reply, the dominant animals provided "violent retaliatory attacks, the ultimate effect of which was to increase the intensity of downward aggressive action throughout the social structure, and to decrease the animals' postlobotomy tendency to upward mobility in the hierarchy. The lobotomized animals soon abandoned direct attacks on upper-status monkeys, although they continued to enter situations such as food snatching which invited attack upon them." The postlobotomy Ss showed a permanent loss of the submission and avoidance behaviors appropriate to their social rank and, thereby, destroyed the social stability of the group. It is worth repeating, however, that prior to the strong retaliations by the upper status animals, operated low status animals exhibited "an increase in upwardly directed aggression, and a tendency to upward mobility in the hierarchy."

Lesions of the amygdala (Mirsky, 1960; Rosvold, Mirsky, & Pribram, 1954) appear to have effects on social behavior opposite those suggested by prefrontal lobotomy: a sharp decline in the operated S's aggressiveness and dominance behavior, and a fall in hierarchical rank. Confirmation of these results has been provided by Plotnik (1968) in the squirrel monkey. Mirsky suggested that amygdaloid injury caused a loss or weakening of "previously learned

connections between complex social stimuli and socioemotional responses." Upon return to the colony after surgery, the operated animal is assumed to have "forgotten" how to express his dominance. According to this interpretation, the subordinate Ss took advantage of the operated animals uncertainty to "get in a few licks" while the danger of retribution was relatively slight. However, it is not surprising that the subordinate's frequency of agonistic interactions should increase following a sudden loss of rank-reinforcing aggression from a formerly dominant peer. In other words, Mirsky suggested that while the amygdala lesion caused an "impairment or forgetting" of social behavior it did not block the ability to relearn so that the postoperative animals learned submission and suffered a corresponding fall in the dominance hierarchy. Mirsky (1960) tested this interpretation by placing preoperatively low ranking amygdalectomized Ss with a group of easily dominated juveniles immediately following surgery. If all the social experiences soon after surgery were supportive of dominance behavior, he suggested, the operated animals might relearn to be even more socially dominant than they were preoperatively and this might carry over to their behavior in their former peer group. Some support for this is suggested by the fact that out of three animals involved in this procedure the first rose one rank in the peer group hierarchy and remained there, the second rose temporarily, the third showed a transient increase in the frequency of downward directed aggression, and none subsequently fell. (The implications of these results vis-a-vis the orbitofrontal effects will be discussed later in this chapter.)

The role of the cingulate gyrus (Mirsky, Rosvold, & Pribram, 1957; Ward, 1948) in emotional behavior is not as obvious as that of other limbic structures and OF cortex. Following cingulectomy there is a suggestion of a temporary rise in aggression toward humans (see Chapter IV) but there is no effect on conspecific social behavior.

In addition to the psychosurgical procedures, electrical stimulation of the brain (ESB) has been used to explore the role of discrete neural structures in modifying or controlling socioemotional behavior in the monkey. ESB in many cortical sites (excluding temporal lobe-amygdaloid structures) is reported to have evoked a variety of motor and autonomic responses, but did not modify the social relations of monkeys in a colony (Delgado, 1966). There was one earlier experiment, though, in which Delgado and Rosvold (1953a, 1953b) reported that ESB of the ventromedial frontal lobes inhibited aggression while food intake was disrupted by stimulating more superior points of the frontal lobe. In contrast, stimulation of many diencephalic and midbrain structures including Forel's field, fimbria of the fornix, central gray, nucleus ventralis posterior lateralis, and midline thalamus induced highly reliable changes in aggressive and escape behavior (Delgado, 1966, 1967a, 1967b; Plotnik & Delgado, 1968). The elicited behaviors, however, were not rigidly stereotyped motor acts independent of environmental pressures. Rather, the responses were considerably modified when the S was stimulated in a restrained chair, alone in a cage, or in his social colony. The aggression elicited by ESB in the colony was indistinguishable from naturally occurring agonistic interactions: it was directed against individual colony members, always downward in the hierarchy, and often bypassing

preferred grooming or sexual partners. Furthermore, the frequency and intensity of agonistic behavior which could be elicited from the same neural site in the same animal depended on his social rank and was altered accordingly when the social structure of the group was changed (Delgado, 1967a; Plotnik & Delgado, 1968).

From other laboratories (Perachio & Murray, 1969; Robinson, Alexander, & Bowne, 1969) there is recent evidence which questions the one-way control that prior social experiences and the powerful dominance hierarchy seem to exert over the expression of agonistic behavior. These experimenters have evoked directed attack and sexual behavior using radio-controlled ESB to sites in hypothalamus, brain stem, and extrapyramidal structures in rhesus monkeys within a social colony. Their results indicate that attacks elicited from a subordinate animal may be directed upward toward a more dominant animal (although not necessarily the alpha male). Furthermore, after a series of submissive-to-dominant attacks, the dominance structure undergoes a permanent reversal and once this has occurred no further stimulations (elicited attacks) are required to maintain the new hierarchical order.

These results are analogous to the frequent but rarely successful challenges offered by the maturing young adults to their aging elders in the wild—a sporadic event which serves to reassure and reinforce the stability of the hierarchy. One can only assume that the electrically elicited subordinate-attacks must be of a radically different quality (more intense, longer duration, better directed, etc.) to have caused a dominance reversal so quickly. The suggestion that electrically-elicited upward aggression is unnatural (hyper-

threatening) is not difficult to accept. In the prestimulation state a subordinate ESB-S would not only rarely, if ever, attack the dominant male, but would regularly retreat or submit when threatened by him. Now, suddenly, under the influence of ESB, he is both attacking and not responding appropriately to threats. It is difficult to imagine a more confusing, stressful, and unnatural position for the dominant monkey to find himself in. Aggressive displacements, although they certainly occur in the wild, have a built-in period of adjustment so that the social structure and stability of the entire group are not jeopardized when two or even a few monkeys exchange positions. It is not surprising that forced attacks and displacements, such as with ESB, occurring within a few hours or even days produce some unexpected behavioral and social aspects.

One final point relates to the functional-neuroanatomical interplay between the various neural centers involved in emotional behavior. The wealth of affective symptoms resulting from ablation and stimulation of many subcortical centers, particularly limbic and thalamic, have largely been interpreted exclusive of cortical influence. Whether the descending cortical influence is ultimately best described as controlling, modulating, inhibiting, suppressing, releasing, exciting, or whatever, it is certain that all parts of the affective control network are always operating in the intact animal. As yet, no one has suggested a theory of emotional behavior in which the telencephalon is independently responsible for processing sensory input; selecting the appropriate response pattern; and controlling the intensity, direction, and duration of the motor output. The same cannot be said of many theories based on the results of lesion and

stimulation of exclusively subcortical structures. If the cortex is assumed to operate in the acquisition and performance of learned behavior and in the expression of emotion in the wild, it should become more and not less important to determine its role in an experimental preparation.

## Method

### Subjects

A group of four[1] male, adolescent, rhesus monkeys ranging in weight from 4.5 to 5.5 kg. and housed separately during the quarantine-conditioning period were simultaneously released into a group colony cage. These animals formed a permanent colony (matrix group). As indicated in Table 1, the social status in the matrix group of each of the experimental subjects was determined within weeks of either OF or sham surgery (last preoperative test), within a month after surgery (first postoperative test), and then for the OF Ss, at roughly bimonthly intervals for six months. Throughout these prolonged observations, the stable social group into which the surgical Ss were introduced (the matrix group) consisted solely of these four monkeys (Dax, Ed, Cal, and Abe) who were never separated (except for weekly cage cleaning) and who were handled only rarely (for TB tests).

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[1] The social colony was originally constituted of five members. During the introduction phase, Ben sustained severe injury and was removed from the group. Subsequently, Ben became an experimental S due to the unrelated death of another monkey and the social colony was fixed at four permanent members.

Apparatus

The colony cage measured 8 x 3 x 6 1/2 ft. and had top, sides, and back of heavy, galvanized wire mesh; front of two glass panels in shock-absorbing frames; and floor of steel grillwork. The long, narrow cage design produced unavoidable and frequent confrontations and physical interactions unless an animal retreated by climbing up and hanging on the wire mesh wall. One side of the cage consisted of a hinge-mounted door used to gain access for the introduction and removal of monkeys and for cleaning. In the center of the door above the floor was a vertically sliding panel with a hole through which monkeys could reach into a food hopper. The position of the hopper was such that a monkey had to climb up the wire-mesh wall and hang from the door and/or wall with at least an arm and leg while grabbing food. The reason for this design will be discussed below.

For food competition testing, a Foringer operant pellet dispenser mounted on a moveable platform was positioned over the food hopper and triggered by a remote switch manually operated by O. A small indicator light fastened to the edge of the glass front panel near the food bin flashed on and off as each banana pellet (190 mg.) dropped into the hopper.

At the end of the cage opposite the door was a perch made of four steel rods rigidly mounted from front to back and positioned 4 ft. above the floor. The perch provided the only elevated sitting-sleeping-grooming location and quickly became the preferred site for territorial-defensive behavior. The perch was placed as spatially distant from the feeder as possible to minimize possible confusion between agonistic territoriality and food-getting primacy.

Behind the perch was a solid metal sheet outside the wire mesh wall on which was mounted a platform for a five gallon water jug. Water, which was constantly available, was fed through metal tubing to two dispensers located approximately 2 ft. from both ends and set 1 ft. above the floor.

Throughout the entire testing period the cage was located along a wall in a large colony room in sight and sound of 12-15 other individually caged rhesus monkeys (including adolescent males and females, juveniles, and infants).

The observations were made from a darkened service hallway almost directly across from the group cage about 35 ft. away. O was seated well within the entrance to the hall and was concealed from the social colony by a masonite partition which was slid in front of the door and in which a viewing port was cut and covered with blue plastic. The beginning of a session, though, was delayed for 5-10 minutes until all disruption toward the doorway (O) had ceased. By using the visual barrier, human-inhibition of social interaction within the colony was avoided. As mentioned previously, there is reason to question any experiment in which social behavior was observed at close range by an experimenter who, in turn, was observed by his subjects.

Procedure

The determination of the matrix group hierarchy and social reordering that took place as each experimental S was introduced into the colony was accomplished by means of direct observation and written record of agonistic interactions (cf. Plutchik, 1964). Diary records

were kept of group interactions during spontaneous behavior and during food competition with special attention given to categories of agonistic behavior which relate to dominance-submission; threat-retreat; aggression-aversion similar to those utilized by Altmann (1962) and Bernstein (1964). Nonagonistic behaviors such as mounting, grooming, nestling, etc. which are not incorporated into the summary tables in the following section were included in the diary protocols and will be discussed where relevant to the lesion effects.

The food competition tests were interposed into a social behavior observation session as the O began remotely releasing banana pellets at either one every five or ten seconds. Records were kept of the order in which the Ss approached the food hopper, the number of pellets taken by each S, and the order in which the Ss supplanted or displaced each other at the food hopper.

Time passage was monitored and incorporated into the diary records at one minute intervals. Continuous social behavior was recorded for 2 - 3 hr. on the day of release and for 1 hr. per day for the succeeding week to ten days. In order to reduce the difficulty of simultaneously recording the behavior of five monkeys, emphasis was placed on the interactions between Ss with first attention directed toward the newly introduced animal (test S) and the alpha male of the matrix group. After a test S was removed, the colony was undisturbed for at least five days to allow for restabilization. Furthermore, the hierarchy of the matrix group was periodically checked for any internal changes before the next experimental S was introduced into the group.

In addition to the written notes, a 16 mm film record was made at the initial, preoperative introduction of each test S, at the postoperative reintroduction, and at selected retests of social status for the OF animals. The electrically driven movie camera in sight of the colony was remotely activated by O from behind the visual barrier.

Initially, two observers made concurrent diary records during all observation periods. After a total of 13 hours of combined data over three weeks the Os reached near perfect agreement in observed sequence, frequency, and kind of interactions occurring between all pairs of Ss in the matrix group. Thus, in subsequent sessions, the Os observed the colony independently.

## Results and Discussion

Analysis of the diary records from the matrix group prior to the introduction of the first test S indicated that a linear dominance hierarchy had indeed formed and that within two weeks of their simultaneous introduction nearly all aggression and submission was unidirectional and stable over nine weeks. The matrix group hierarchy from alpha to most subordinate was: Dax, Ed, Cal, and Abe. However, the agonistic relations within the matrix group did not follow the most often reported pattern whereby aggression is directed solely at the closest ranking subordinate. Second ranking Ed actively abstained from most aggressive episodes, while third ranking Cal formed a grooming and aggressive alliance with the boss monkey, Dax, which left fourth ranking Abe as the only regularly available target for aggression from everyone above him. Although he did not often

assert himself, there was no doubt that Ed was subordinate only to Dax in the matrix group which suggests that frequent agonistic behavior is not a requisite of high rank. Furthermore, Cal, in contrast to Ed, demonstrates that frequent agonistic behavior is also not an indicator of high rank. Throughout the course of conspecific behavior testing, the hierarchy of the matrix group in the absence of a test S remained stable, i.e., Dax, Ed, Cal, and Abe. During the periods that a dominant test S was in the group, Dax displayed the expected displaced-aggression directed downward through the hierarchy with Abe, the most submissive, receiving the greatest amount of punishment.

As each of the experimental Ss was introduced into the group, the hierarchy restabilized about him. Tables 6-13 are summaries of the frequencies of agonistic interactions recorded during all the observation periods between the four matrix group members and between each of them and the test Ss as they were introduced into the colony before and after surgery. The columns labelled aggression and aversion give the mean frequency per minute of aggressive and aversive behaviors. No distinction was made between agonistic and aversive gestures (e.g., threatening frown, mouth open, ear flatten, stare, or head thrust; fearful grimace and head or eye aversion) and whole-body movements (e.g., aggressive chase, hit, bite; aversive retreat, climb, or cower). AI refers to agonistic index which is based on the four basic agonistic interactions possible between any two animals: Monkey A can either dominate or submit to monkey B and, of course, the reverse is equally possible. The AI, then, is the sum of observed aggressive (dominating) behavior of S A toward

Table 6

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| First Month Pre or Post Sham Surgery | | Actors | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sham Op. S | | | Stable Colony Ss | | | | | | | | | | | | |
| | | Abba | | | Dax | | | Ed | | | Cal | | | Abe | | | |
| Ss | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | |
| Abba | Pre | | | | 0 | .35 | .01 | 0 | .20 | 0 | 0 | .23 | 0 | 0 | .29 | 0 | |
| | Post | | | | .01 | .11 | .11 | 0 | .05 | 0 | 0 | .04 | 0 | 0 | .06 | 0 | |
| Dax | Pre | .17 | .01 | .99 | | | | 0 | .20 | .02 | .01 | .24 | .03 | 0 | .32 | 0 | |
| | Post | .06 | .01 | .89 | | | | 0 | .19 | 0 | 0 | .21 | 0 | 0 | .17 | 0 | |
| Ed | Pre | .14 | 0 | 1.0 | .18 | .01 | .98 | | | | 0 | .04 | 0 | 0 | .04 | 0 | |
| | Post | 0 | 0 | 1.0 | .09 | 0 | 1.0 | | | | 0 | .09 | 0 | 0 | .14 | 0 | |
| Cal | Pre | .16 | 0 | 1.0 | .16 | 0 | .97 | .03 | 0 | 1.0 | | | | 0 | .07 | 0 | |
| | Post | .01 | 0 | 1.0 | .09 | 0 | 1.0 | .06 | 0 | 1.0 | | | | 0 | .05 | 0 | |
| Abe | Pre | .16 | 0 | 1.0 | .27 | 0 | 1.0 | .02 | 0 | 1.0 | .03 | 0 | 1.0 | | | | |
| | Post | .01 | 0 | 1.0 | .08 | 0 | 1.0 | .13 | 0 | 1.0 | .06 | 0 | 1.0 | | | | |

Recipients

[a] AI = Agonistic Index = Σ Aggression behavior directed toward another S + Σ Submissions received from that S/Total agonistic interactions between the two Ss.

Table 7

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| First Month Pre or Post Sham Surgery | | Actors | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sham Op. S | | | Stable Colony Ss | | | | | | | | | | | |
| | | Eban | | | Dax | | | Ed | | | Cal | | | Abe | | |
| Recipients Ss | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Eban | Pre | | | | .17 | .78 | .13 | 0 | .19 | 0 | .01 | .47 | .02 | 0 | .27 | 0 |
| | Post | | | | .17 | .51 | .24 | .02 | .16 | .08 | .04 | .26 | .08 | 0 | .28 | 0 |
| Dax | Pre | .54 | .03 | .87 | | | | .01 | .20 | .03 | .01 | .22 | .02 | 0 | .23 | 0 |
| | Post | .53 | .15 | .76 | | | | 0 | .17 | 0 | .01 | .20 | .05 | 0 | .26 | 0 |
| Ed | Pre | .04 | 0 | 1.0 | .08 | 0 | .97 | | | | 0 | .01 | 0 | 0 | .02 | 0 |
| | Post | .10 | 0 | .92 | .04 | 0 | 1.0 | | | | .02 | .04 | .30 | 0 | .05 | 0 |
| Cal | Pre | .08 | 0 | .98 | .15 | 0 | .98 | .01 | 0 | 1.0 | | | | 0 | .10 | 0 |
| | Post | .17 | 0 | .92 | .09 | .01 | .95 | .02 | .01 | .70 | | | | 0 | .14 | 0 |
| Abe | Pre | .09 | 0 | 1.0 | .16 | 0 | 1.0 | .10 | 0 | 1.0 | .12 | 0 | 1.0 | | | |
| | Post | .09 | 0 | 1.0 | .11 | 0 | 1.0 | .02 | 0 | 1.0 | .13 | 0 | 1.0 | | | |

[a] AI = Agonistic Index as defined below Table 6.

Table 8

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| First Month Pre or Post Sham Surgery | | Actors | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sham Op. S | | | Stable Colony Ss | | | | | | | | | | | |
| | | Ibid | | | Dax | | | Ed | | | Cal | | | Abe | | |
| Ss | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Recipients | | | | | | | | | | | | | | | | |
| Ibid | Pre | | | | .10 | .20 | .20 | 0 | .14 | .06 | .04 | .14 | .14 | 0 | .17 | 0 |
| | Post | | | | .36 | .43 | .34 | .01 | .17 | .04 | 0 | .17 | 0 | 0 | .21 | 0 |
| Dax | Pre | .22 | 0 | .80 | | | | 0 | .04 | .09 | .01 | .08 | .05 | 0 | .07 | 0 |
| | Post | .50 | .12 | .66 | | | | 0 | .06 | 0 | 0 | .12 | 0 | 0 | .15 | 0 |
| Ed | Pre | .07 | .01 | .94 | .06 | 0 | .91 | | | | 0 | .07 | 0 | 0 | .07 | 0 |
| | Post | .09 | 0 | .96 | .01 | 0 | 1.0 | | | | .01 | .04 | .09 | 0 | .03 | 0 |
| Cal | Pre | .14 | 0 | .86 | .10 | 0 | .95 | .02 | 0 | 1.0 | | | | 0 | .08 | 0 |
| | Post | .03 | 0 | 1.0 | .04 | 0 | 1.0 | .04 | 0 | .91 | | | | 0 | .01 | 0 |
| Abe | Pre | .08 | 0 | 1.0 | .06 | 0 | 1.0 | .08 | 0 | 1.0 | .06 | 0 | 1.0 | | | |
| | Post | .07 | 0 | 1.0 | .09 | 0 | 1.0 | .03 | 0 | 1.0 | 0 | 0 | 1.0 | | | |

[a] AI = Agonistic Index as defined below Table 6.

Table 9

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| First Month Pre or Post Sham Surgery | | Actors | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Sham Op. S | | | Stable Colony Ss | | | | | | | | | | | |
| | | Zeus | | | Dax | | | Ed | | | Cal | | | Abe | | |
| Recipients Ss | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Zeus | Pre | | | | .01 | .24 | .04 | 0 | .07 | 0 | .01 | .09 | .09 | 0 | .10 | 0 |
| | Post | | | | 0 | .51 | 0 | 0 | .27 | 0 | 0 | .25 | 0 | 0 | .34 | 0 |
| Dax | Pre | .17 | .01 | .96 | | | | .06 | .01 | .62 | .05 | .11 | .15 | 0 | .02 | 0 |
| | Post | .49 | 0 | 1.0 | | | | 0 | .11 | 0 | 0 | .11 | 0 | 0 | .30 | 0 |
| Ed | Pre | .05 | 0 | 1.0 | .04 | .04 | .38 | | | | 0 | .01 | 0 | 0 | .07 | 0 |
| | Post | .23 | 0 | 1.0 | .09 | 0 | 1.0 | | | | 0 | .04 | 0 | 0 | .10 | 0 |
| Cal | Pre | .06 | .01 | .91 | .18 | 0 | .85 | .01 | 0 | 1.0 | | | | .01 | .02 | 0 |
| | Post | .22 | 0 | 1.0 | .08 | 0 | 1.0 | .03 | 0 | 1.0 | | | | 0 | .05 | 0 |
| Abe | Pre | .09 | 0 | 1.0 | .01 | 0 | 1.0 | .07 | 0 | 1.0 | 0 | 0 | 1.0 | | | |
| | Post | .31 | 0 | 1.0 | .28 | 0 | 1.0 | .09 | 0 | 1.0 | .04 | 0 | 1.0 | | | |

[a] AI = Agonistic Index as defined below Table 6.

Table 10

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| Recipients: Months Pre and Post OF Surgery | | Actors: OF S | | | Stable Colony Ss | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Jim | | | Dax | | | Ed | | | Cal | | | Abe | | |
| Ss | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| | Pre 1 | | | | .44 | 1.19 | .18 | 0 | .38 | 0 | 0 | .52 | 0 | 0 | .37 | 0 |
| | Post 1 | | | | .42 | .73 | .29 | .01 | .18 | .02 | 0 | .22 | .02 | 0 | .29 | 0 |
| Jim | 3 | | | | 0 | 1.2 | .18 | 0 | 1.4 | 0 | 0 | 1.4 | 0 | 0 | 1.0 | 0 |
| OF | 5 | | | | 0 | .29 | 0 | 0 | .04 | 0 | 0 | .38 | 0 | 0 | 1.0 | 0 |
| | 6 | | | | .60 | 1.73 | .18 | 0 | .15 | 0 | 0 | .65 | 0 | 0 | .20 | 0 |
| | Pre 1 | 1.0 | .05 | .82 | | | | 0 | .21 | 0 | 0 | .25 | 0 | 0 | .24 | 0 |
| | Post 1 | .73 | .16 | .71 | | | | 0 | .24 | 0 | .01 | .27 | .01 | 0 | .35 | 0 |
| Dax | 3 | 1.60 | 0 | .82 | | | | INR | INR | - | INR | INR | - | INR | INR | - |
| | 5 | .40 | 0 | 1.0 | | | | 0 | .11 | 0 | 0 | .29 | 0 | 0 | .07 | 0 |
| | 6 | 1.50 | .10 | .82 | | | | 0 | .13 | 0 | 0 | .18 | 0 | 0 | .28 | 0 |
| | Pre 1 | .05 | 0 | 1.0 | .07 | 0 | 1.0 | | | | 0 | 0 | - | 0 | .04 | 0 |
| | Post 1 | .05 | 0 | .98 | .06 | 0 | 1.0 | | | | .01 | .01 | .25 | 0 | .01 | 0 |
| Ed | 3 | .60 | 0 | 1.0 | INR[b] | INR | - | | | | INR | INR | - | INR | INR | - |
| | 5 | 0 | 0 | 1.0 | 0 | 0 | 1.0 | | | | 0 | 0 | - | 0 | 0 | - |
| | 6 | .03 | 0 | 1.0 | .03 | 0 | 1.0 | | | | 0 | 0 | 0 | 0 | 0 | - |
| | Pre 1 | .16 | 0 | 1.0 | .10 | 0 | 1.0 | 0 | 0 | - | | | | 0 | .05 | 0 |
| | Post 1 | .05 | .01 | .98 | .11 | 0 | .99 | .01 | 0 | .75 | | | | 0 | .05 | 0 |
| Cal | 3 | .60 | 0 | 1.0 | INR | INR | - | INR | INR | - | | | | INR | INR | - |
| | 5 | 0 | 0 | 1.0 | 0 | 0 | 1.0 | 0 | 0 | - | | | | 0 | .11 | 0 |
| | 6 | .12 | 0 | 1.0 | .05 | 0 | 1.0 | 0 | .03 | 1.0 | | | | 0 | .75 | 0 |
| | Pre 1 | .17 | 0 | 1.0 | .18 | 0 | 1.0 | .01 | .01 | .89 | .02 | 0 | 1.0 | | | |
| | Post 1 | .05 | 0 | 1.0 | .08 | 0 | 1.0 | .01 | 0 | 1.0 | .01 | 0 | 1.0 | | | |
| Abe | 3 | .60 | 0 | 1.0 | .60 | 0 | 1.0 | INR | INR | - | INR | INR | - | | | |
| | 5 | 0 | 0 | 1.0 | .22 | 0 | 1.0 | 0 | 0 | - | .22 | 0 | 1.0 | | | |
| | 6 | .03 | 0 | 1.0 | .20 | 0 | 1.0 | 0 | 0 | - | .12 | 0 | 1.0 | | | |

[a] AI = Agonistic Index as defined below Table 6

[b] Interactions Not Recorded

Table 11

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| Recipients: Months Pre and Post OF Surgery | | | Actors: OF S | | | Stable Colony Ss | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | Willie | | | Dax | | | Ed | | | Cal | | | Abe | | |
| Ss | | | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Willie OF | Pre | 1 | | | | .49 | .58 | .31 | 0 | .11 | 0 | 0 | .22 | 0 | 0 | .55 | 0 |
| | Post | 1 | | | | .37 | .51 | .32 | 0 | .21 | .02 | .03 | .28 | .07 | 0 | .23 | 0 |
| | | 2 | | | | 4.6 | 1.4 | .44 | 0 | 2.2 | 0 | 0 | 2.2 | 0 | 0 | 2.4 | 0 |
| | | 6 | | | | (1.64) | (.42) | (.74) | (.43) | (.09) | (.99) | (.76) | (.07) | (.85) | (.03) | (0) | (1.0) |
| Dax | Pre | 1 | .68 | .08 | .69 | | | | 0 | .21 | 0 | .02 | .35 | .04 | 0 | .68 | 0 |
| | Post | 1 | .43 | .08 | .68 | | | | 0 | .16 | 0 | .02 | .23 | .08 | 0 | .21 | 0 |
| | | 2 | 4.6 | .2 | .56 | | | | 0 | 2.2 | 0 | 0 | 2.2 | 0 | 0 | 2.4 | 0 |
| | | 6 | (.35)[b] | (.56) | (.26) | | | | (0) | (0) | - | (0) | (.06) | (0) | (0) | (.07) | (0) |
| Ed | Pre | 1 | .03 | 0 | 1.0 | .04 | 0 | 1.0 | | | | .01 | .06 | .05 | 0 | .06 | 0 |
| | Post | 1 | .07 | .01 | .98 | .03 | 0 | 1.0 | | | | .02 | .02 | .44 | 0 | .03 | 0 |
| | | 2 | 0 | 0 | 1.0 | 0 | 0 | 1.0 | | | | 0 | 0 | - | 0 | 0 | - |
| | | 6 | (0) | (.29) | (.01) | (0) | (0) | - | | | | (0) | (0) | - | (0) | (.04) | (0) |
| Cal | Pre | 1 | .04 | 0 | 1.0 | .19 | .01 | .96 | .07 | 0 | .95 | | | | 0 | .02 | 0 |
| | Post | 1 | .16 | .01 | .93 | .10 | .01 | .92 | .01 | .01 | .56 | | | | 0 | .01 | 0 |
| | | 2 | 0 | 0 | 1.0 | 0 | 0 | 1.0 | 0 | 0 | - | | | | 0 | 0 | - |
| | | 6 | (.09) | (.20) | (.15) | (.01) | (0) | (1.0) | (0) | (0) | - | | | | (0) | (.04) | (0) |
| Abe | Pre | 1 | .02 | 0 | 1.0 | .09 | 0 | 1.0 | .06 | 0 | 1.0 | .01 | 0 | 1.0 | | | |
| | Post | 1 | .06 | 0 | 1.0 | .02 | 0 | 1.0 | .03 | 0 | 1.0 | .01 | 0 | 1.0 | | | |
| | | 2 | 0 | 0 | 1.0 | 0 | 0 | 1.0 | 0 | 0 | - | 0 | 0 | - | | | |
| | | 6 | (0) | (0) | (0) | (.03) | (0) | (1.0) | (.02) | (0) | (1.0) | (.02) | (0) | (1.0) | | | |

[a] AI = Agonistic Index as defined below Table 6

[b] Interactions Not Recorded.

Footnotes for Table 12

a AI = Agonistic Index as defined below Table 6.

b Parentheses indicate observations made after OF S had fallen from most dominant to most submissive social rank.

c Walt tested at 7 months postoperatively with 3 normal, juvenile females:

| | Walt | | Juveniles | |
|---|---|---|---|---|
| | Agg. | Aver. | Agg. | Aver. |
| Walt | | | (2.3) | (.03) |
| Juveniles | (0) | (.57) | | |

d Interactions Not Recorded

Table 12

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| Recipients | Months Pre and Post OF Surgery | Actors | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | OF Ss | | | Stable Colony Ss | | | | | | | | | | | |
| | | Walt | | | Dax | | | Ed | | | Cal | | | Abe | | |
| | Ss | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Walt OF | Pre 1 | | | | .11 | .35 | .15 | 0 | .19 | 0 | .06 | .27 | .12 | 0 | .10 | 0 |
| | Post 1/2 | | | | 1.01 | .67 | .49 | 0 | .24 | .08 | 0 | .23 | 0 | 0 | .30 | 0 |
| | 1 | | | | (.16) | (0) | (1.0) | (.24) | (0) | (1.0) | (.07) | (0) | (1.0) | (.55) | (0) | (1.0) |
| | 4 | | | | (1.67) | (0) | (1.0) | (1.17) | (0) | (1.0) | (1.5) | (0) | (1.0) | (0) | (0) | - |
| | 5[c] | | | | INR[d] | (0) | (1.0) | INR | INR | (1.0) | INR | INR | (1.0) | INR | INR | (1.0) |
| | 7 | | | | | | | | | | | | | | | |
| Dax | Pre 1 | .36 | .02 | .85 | | | | 0 | .10 | 0 | 0 | .23 | .01 | 0 | .13 | 0 |
| | Post 1/2 | .61 | .21 | .51 | | | | .01 | .10 | .06 | .02 | .17 | .11 | 0 | .11 | 0 |
| | 1 | (0)[b] | (.20) | (0) | | | | (0) | (.33) | (0) | (0) | (.35) | (0) | (0) | (.24) | (0) |
| | 4 | (0) | (1.3) | (0) | | | | (0) | (.17) | (0) | (0) | (.50) | (0) | (0) | (.50) | (0) |
| | 5 | (0) | (Con't) | (0) | | | | INR | INR | - | INR | INR | - | INR | INR | - |
| Ed | Pre 1 | .18 | 0 | 1.0 | .08 | 0 | 1.0 | | | | 0 | .06 | 0 | 0 | .08 | 0 |
| | Post 1/2 | .09 | .03 | .92 | .05 | 0 | .94 | | | | 0 | .01 | 0 | 0 | .01 | 0 |
| | 1 | (0) | (.31) | (0) | (.13) | (0) | (1.0) | | | | (.06) | (.27) | (.09) | (0) | (.04) | (0) |
| | 4 | (0) | (0) | (0) | (0) | (0) | (1.0) | | | | (0) | (0) | (0) | (0) | (0) | (0) |
| | 5 | (0) | (Con't) | (0) | INR | INR | - | | | | INR | INR | - | INR | INR | - |
| Cal | Pre 1 | .26 | .01 | .88 | .20 | 0 | .99 | .06 | 0 | 1.0 | | | | 0 | .02 | 0 |
| | Post 1/2 | .09 | 0 | 1.0 | .06 | .01 | .89 | .01 | 0 | 1.0 | | | | 0 | 0 | 0 |
| | 1 | (0) | (.09) | (0) | (.24) | (0) | (1.0) | (.31) | (0) | (.91) | | | | (0) | (.09) | (0) |
| | 4 | (0) | (1.0) | (0) | (.50) | (0) | (1.0) | (0) | (0) | (0) | | | | (0) | (0) | (0) |
| | 5 | (0) | (Con't) | (0) | INR | INR | - | INR | INR | - | | | | INR | INR | - |
| Abe | Pre 1 | .08 | 0 | 1.0 | .16 | 0 | 1.0 | .08 | 0 | 1.0 | .02 | 0 | 1.0 | | | |
| | Post 1/2 | .07 | 0 | 1.0 | .03 | 0 | 1.0 | .01 | 0 | 1.0 | 0 | 0 | 0 | | | |
| | 1 | (0) | (.18) | (0) | (.05) | (0) | (1.0) | (.02) | (0) | (1.0) | (.06) | (0) | (1.0) | | | |
| | 4 | (0) | (0) | - | (.50) | (0) | (1.0) | (0) | (0) | (1.0) | (0) | (0) | (0) | | | |
| | 5 | (0) | (Con't) | (0) | INR | INR | - | INR | INR | - | INR | INR | - | | | |

See Footnotes on facing page.

Table 13

Mean Aggression and Aversion Frequencies Per Minute and Agonistic Indices (AI)

| Recipients | Months Pre and Post OF Surgery | Actors | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | OF S | | | Stable Colony Ss | | | | | | | | | | | |
| | | Ben | | | Dax | | | Ed | | | Cal | | | Abe | | |
| | Ss | Agg. | Aver. | AI[a] | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI | Agg. | Aver. | AI |
| Ben OF | Pre 1 | | | | .69 | .26 | .17 | 0 | .10 | 0 | 0 | .15 | 0 | 0 | .14 | 0 |
| | Post 1 | | | | .02 | 1.09 | .02 | 0 | .21 | 0 | 0 | .25 | 0 | 0 | .17 | 0 |
| | 2 | | | | 0 | .40 | 0 | 0 | .20 | 0 | 0 | .40 | 0 | 0 | .40 | 0 |
| | 4 | | | | (.42) | (0) | (1.0) | (.17) | (0) | (1.0) | (.33) | (0) | (1.0) | (0) | (0) | (1.0) |
| | 6 | | | | (1.4) | (0) | (1.0) | (.73) | (0) | (1.0) | (.87) | (0) | (1.0) | (0) | (0) | - |
| Dax | Pre 1 | .19 | .02 | .83 | | | | 0 | .29 | 0 | .01 | .36 | .02 | 0 | .31 | 0 |
| | Post 1 | .10 | 0 | .98 | | | | 0 | .09 | 0 | .01 | .22 | 0 | 0 | .13 | 0 |
| | 2 | .20 | 0 | 1.0 | | | | INR | INR | - | INR | INR | - | INR | INR | - |
| | 4 | (0)[b] | (.42) | (0) | | | | INR | INR | - | INR | INR | - | INR | INR | - |
| | 6 | (0) | (1.47) | (0) | | | | (.03) | (.13) | (.20) | (0) | (.33) | (0) | (0) | (.03) | (0) |
| Ed | Pre 1 | .69 | 0 | 1.0 | .65 | 0 | 1.0 | | | | 0 | .03 | 0 | 0 | .07 | 0 |
| | Post 1 | .06 | 0 | 1.0 | .01 | 0 | .99 | | | | 0 | .07 | 0 | 0 | .02 | 0 |
| | 2 | .20 | 0 | 1.0 | INR[c] | INR | - | | | | INR | INR | - | INR | INR | - |
| | 4 | (0) | (.17) | (0) | INR | INR | - | | | | INR | INR | - | INR | INR | - |
| | 6 | (0) | (.63) | (0) | (0) | (0) | (.80) | | | | (0) | (0) | - | (0) | (0) | - |
| Cal | Pre 1 | .08 | 0 | 1.0 | .10 | 0 | .98 | .03 | 0 | 1.0 | | | | 0 | .07 | 0 |
| | Post 1 | .03 | 0 | 1.0 | .13 | 0 | 1.0 | .02 | 0 | 1.0 | | | | 0 | .04 | 0 |
| | 2 | .40 | 0 | 1.0 | INR | INR | - | INR | INR | - | | | | INR | INR | - |
| | 4 | (0) | (.33) | (0) | INR | INR | - | INR | INR | - | | | | INR | INR | - |
| | 6 | (0) | (.47) | (0) | (.06) | (0) | (1.0) | (0) | (0) | - | | | | (0) | (0) | - |
| Abe | Pre 1 | .10 | 0 | 1.0 | .11 | 0 | 1.0 | .04 | 0 | 1.0 | .03 | 0 | 1.0 | | | |
| | Post 1 | .03 | 0 | 1.0 | .01 | 0 | 1.0 | 0 | 0 | 1.0 | .02 | 0 | 1.0 | | | |
| | 2 | .40 | 0 | 1.0 | INR | INR | - | INR | INR | - | INR | INR | - | | | |
| | 4 | (0) | (.01) | (0) | INR | INR | - | INR | INR | - | INR | INR | - | | | |
| | 6 | (0) | (0) | - | (0) | (0) | (1.0) | (0) | (0) | - | (0) | (0) | - | | | |

a AI = Agonistic Index as defined below Table 6.
b Parentheses indicate observations made after OF S had fallen from most dominant to most submissive social rank.
c Interactions Not Recorded

another S B plus the sum of observed aversive (submitting) behaviors of B toward A divided by the total number of observed agonistic interactions between A and B. To say, therefore, that S A had an AI of 1.0 over S B means that A was observed to completely dominate over B; that A was always observed to aggress B and B always observed to submit to A when A and B interacted. Of course, S B would have the complimentary AI of 0.0 over S A. The information in these tables not only established the agonistic hierarchy at each of the testing stages by simply rank-ordering the relative AIs between all pairs, but describes the intensity of the social interplay between each of the Ss by the rates at which they aggressed and submitted to each other.

Because of their greater age and weight, each of the sham operates achieved immediate preoperative dominance in the social colony supplanting Dax as the alpha male. Surgery had no effect on their observed frequencies of agonistic social behavior or hierarchical position following postoperative introduction. Additionally, casual observations of two sham Ss (Abba and Zeus) retested with the colony three and four months after surgery did not suggest any decline in social dominance.

The social behavior summaries of the four OF monkeys (Tables 10-13) are somewhat more lengthy than for the sham operates because of the retesting for permanence of the social behavior changes. Each of the OF monkeys replaced Dax as the alpha male when they were introduced into the colony preoperatively, as did the four sham operates. Following OF surgery, three of the Ss retained their dominant position one, four, and six months, respectively, at which

time they rapidly fell to the bottom of the dominance hierarchy. The other OF monkey, Jim, retained his position of dominance through the conclusion of the experiment nearly eight months after his operation (Table 10). A possible histological reason for Jim's atypical behavior was suggested in Chapter II and will be discussed further in Chapter VII. In Tables 11-13, the aggression and aversion rates and the aggression indices in parantheses are based on observations taken after the previously dominant OF operate had fallen to the most submissive position.

The third footnote in Table 12 briefly summarizes the results of an attempt to sample the completeness of one OF monkey's loss of conspecific aggression. Seven months after Walt's operation, the matrix group was removed from the colony cage and Walt, along with three, unoperated, juvenile female rhesus monkeys were simultaneously introduced. In agreement with Bernstein and Mason (1963), there were frequent, agonistic encounters between the juveniles and Walt which demonstrated immediate recognition of relative status. The juveniles immediately formed an aggressive alliance against Walt and during the two hours immediately following release and two hours of recorded interactions the following day they maintained an extremely high rate of 2.3 threats of attacks per minute. Walt's .57 aversions per minute were mostly fleeting grimaces as he continually paced back and forth. Walt's reaction to the young females were indistinguishable from this behavior with the matrix group over the prior 6 1/2 months: facial and vocal aversion, continual pacing and total lack of aggression. The behavior of the juveniles was, in fact, more interesting than Walt's. Within one minute of being released

into the colony cage with him, they reacted as though this male monkey who was nearly three times their size, outweighing them by 10-15 pounds, presented no threat whatsoever. For the two days they were caged with Walt, they spent very little time playing, grooming, or nestling among themselves. Instead, acting either independently or in combination, they kept up an almost continual harassment of Walt even to the point of hitting him or trying to bite his legs as he paced past them. It would be interesting to see if OF monkeys housed with easily dominated animals (i.e., juveniles) immediately after surgery show the same tendency towards retention of aggression and social rank as did Mirsky's (1960) amygdalectomized monkeys.

The preoperative integration of the OF monkeys into the colony showed the same pattern as did the sham operated monkeys: initially high and rapidly declining aggression frequencies against the displaced alpha male (Dax) and uniformly low rates of submission towards Dax while Dax showed decreasing aggression and initially high and slowly decreasing submission rates (Tables 6-13). In summary, all the OF and sham monkeys assumed the alpha position over Dax in a manner which substantiates Bernstein's (1964) observation that the highest frequencies of aggression and submission occur immediately after introduction and then decline rapidly.

The social interactions immediately following surgery gave no indication that the OF damage had affected the dominance ranks. In light of the profound loss of aggression toward humans (see Chapter IV), this was indeed an unexpected result. Nevertheless, when re-introduced into the matrix group, the OF monkeys displayed high levels

of aggression toward Dax and minimal rates of submission. Dax, on the other hand, also frequently threatened or attacked but regularly submitted more often than the OF monkeys. The absolute frequencies of agonistic encounters indicates, in fact, that Dax was more frequently aggressive towards Jim, Willie, and Walt when they were first replaced into the colony than the same OF monkeys were toward Dax. The real difference in social power lies not in who initiates how many threats toward whom; but in what happens after a threat is signaled, i.e., who submits to whom. In this case, the OF monkeys maintained low rates of submission toward Dax while Dax frequently submitted or retreated from an agonistic encounter. It was the nature of this exhuberant, young monkey to initiate many exchanges ("wrestling matches"), particularly with the test Ss, which should properly be classified as play. Nevertheless, if the alpha-test S did not "want to play" and responded to Dax's overtures with threats from which Dax retreated, the interaction was scored as a dominant act from the test S and a submission from Dax. The point is that whether or not one is dealing with playful adolescents, it is equally as misleading to base a presumed dominance ranking on the relative frequency of solely aggressive behaviors as it is to base it, for example, solely on primacy in food-getting. Agonistic interactions are just that--interactions--and the frequency and form of the submissive acts are potentially more important than overt aggression in determining the linear order of dominance hierarchy; a conclusion supported by Bernstein (1969) and by Rowell (1967).

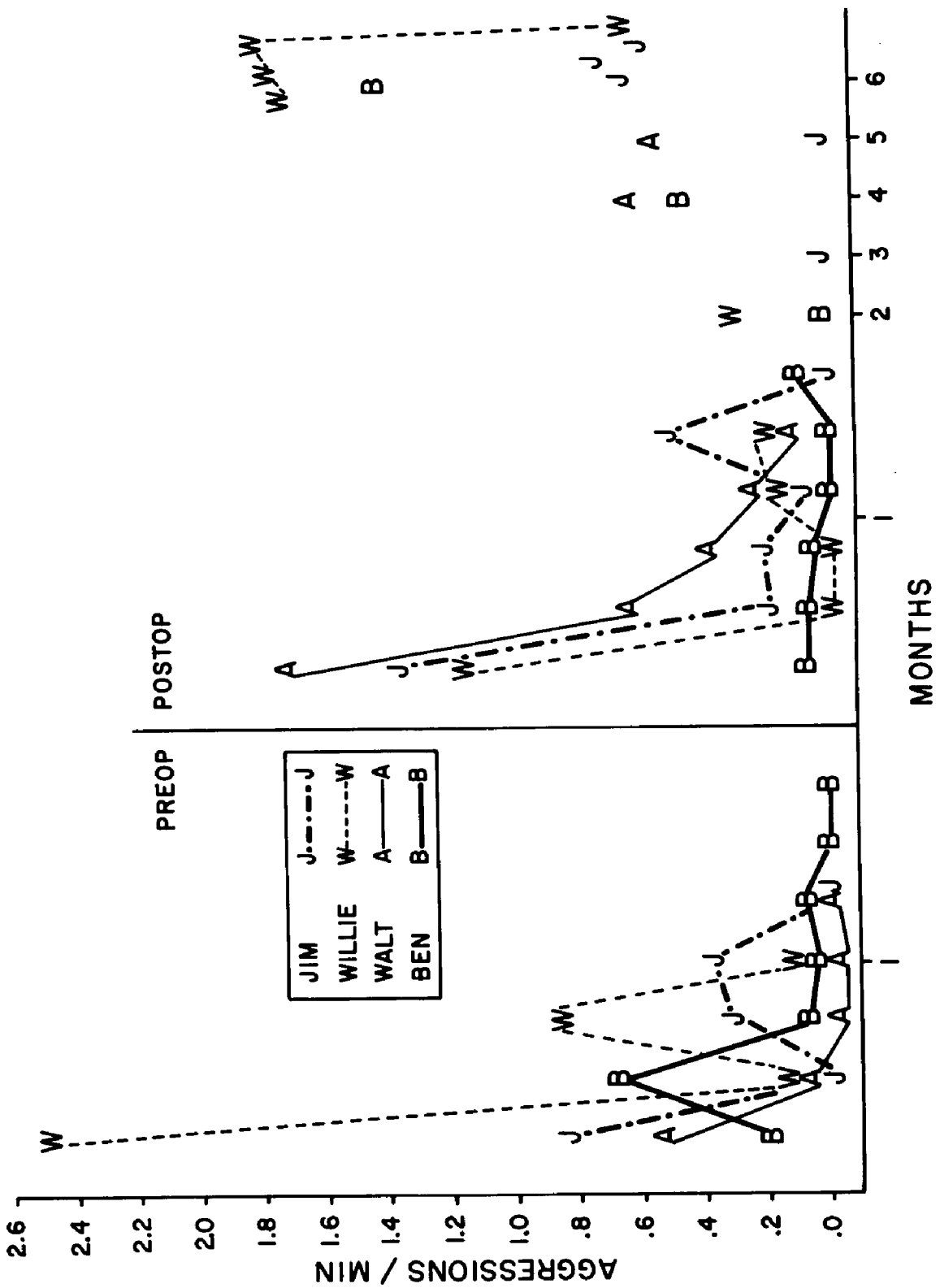
As stated earlier, the apparent lack of effect of OF ablation on social behavior was short lived. For on the eleventh day after

he was returned to the colony (about three weeks after surgery), Walt dropped abruptly in rank and commenced pacing. His sole reaction to commotion within or without the colony was forced-pacing identical to that observed in the home-cage stare test (Chapter IV) in addition to the OF hyperreactivity and bulimia described before (Chapters I and II).

Walt's aggression toward Dax began to decline from the first post-operative session falling permanently to zero by the fourth observation period (see Table 12). At the four month retest Walt was submitting at a 1.3/min. rate and one month later his behavior was that of continuous, complete submission to Dax as well as to the other members of the colony. Even lowest-ranking Abe bit and stole food from Walt when he was devoid of all but aversive, pacing behavior. During these retests, Walt received several vicious attacks from all four of the matrix group members during which he cowered and screeched but made no attempts to escape. In summary, Walt maintained a position of social dominance for a few days after surgery at which time he abruptly ceased behaving aggressively, fell to the bottom of the hierarchy, and displayed many of the same behaviors shown toward humans earlier in his home cage.

Figure 2 shows the frequency per minute of aggression by Dax against the OF monkeys during all observation periods throughout the course of social dominance testing. The return of aggression toward Walt, Jim, and Willie immediately after the postsurgical reintroduction is apparent. While Jim and Willie (and, of course, Ben) were able to quickly reassert complete dominance over Dax, Walt was not able to do the same and received continual harassment and aggressive challenges

Fig. 2 Frequency per minute of aggression by the matrix group alpha male (Dax) against OF monkeys before and after surgery.


AGGRESSIONS / MIN
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
.8
.6
.4
.2
.0
PREOP
POSTOP
JIM J
WILLIE W
WALT A
BEN B
MONTHS
1
2
3
4
5
6

until he fell. It is possible that the heightened, persistent aggression Dax directed toward Walt compared to the other OF monkeys was correlated with his earlier fall.

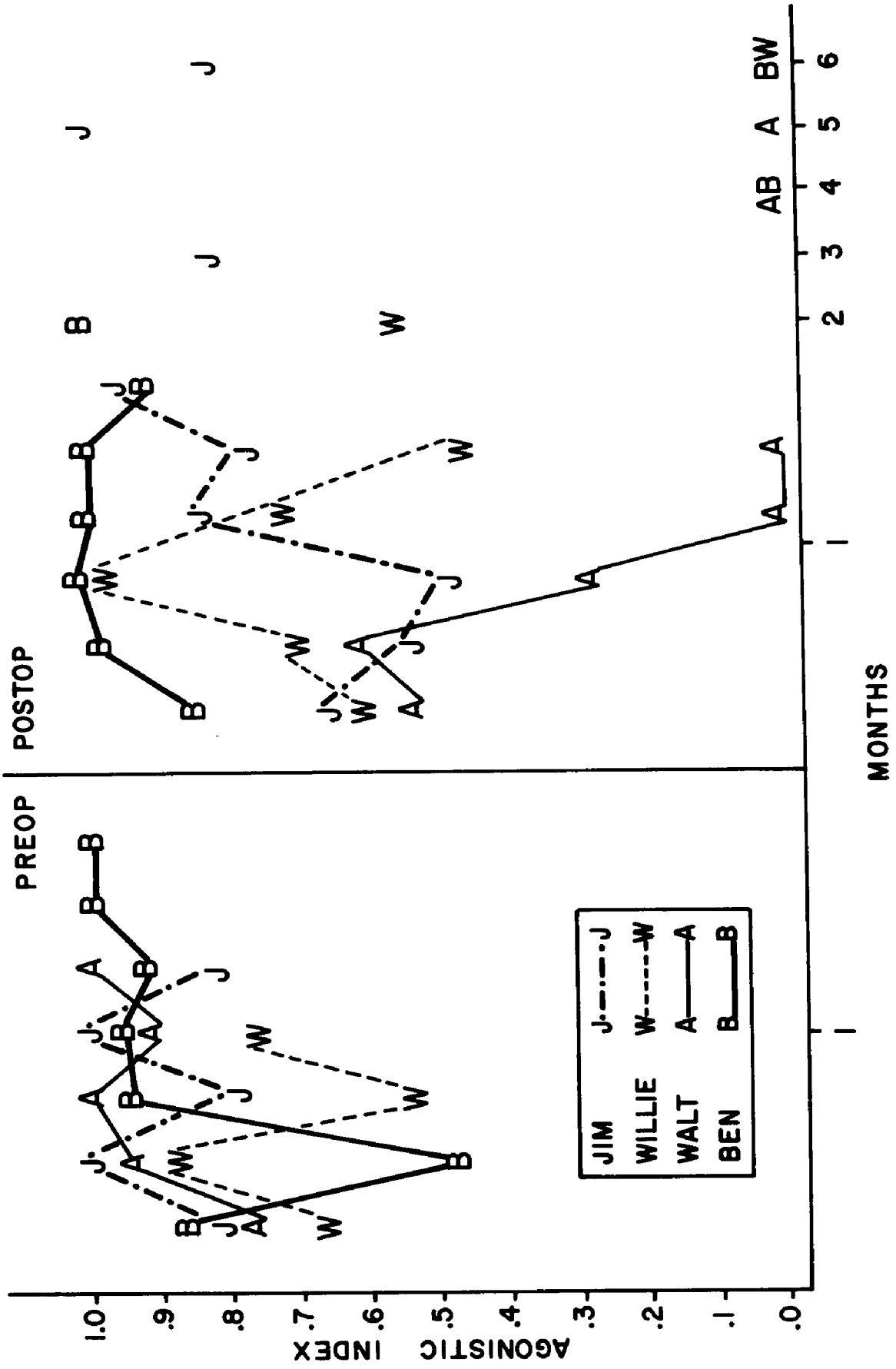
Throughout the first postoperative month of social behavior observations, the three remaining OF monkeys: Jim, Willie, and Ben maintained their dominant positions in the colony. As listed in Table 1 (Chapter I), these subjects were involved in a series of other experiments which necessitated their removal from the matrix group. At regular intervals, however, they were replaced into the matrix group to evaluate their social status. It was during the course of this dominance retesting that Ben and Willie were found to have also fallen to the bottom of the hierarchy at four and six months after surgery, respectively (Tables 11 and 13). There were no prior changes in their gross behavior either in the concurrent experimental situations or in their home cages which suggested the abrupt social alterations which had occured. If Ben and Willie had been allowed to remain in the colony for six months it is likely that the loss of rank associated with decreased aggressiveness and increased submissiveness would have been documented for them as it was for Walt. However, as soon as they entered the cage it was apparent that their relationship with the matrix group members (especially Dax) had changed. Dax's threats toward Ben had remained near or at zero through two months of postoperative testing (Figure 2). At the four month re-entry there was an abrupt rise coincidental with Ben's fall and at six months the interactions peaked at 1.4 attacks/min. Similarly for Willie, there occurred an enormous increase in the frequency at which Dax threatened and attacked him at

the six month retest (Figure 2) which declined within 24 hours as Willie became progressively submissive. This suggests that the fall in social dominance observed in Walt, Ben, and Willie was associated with, although not necessarily instigated by, an inability of the OF monkeys to cope with increased stress (threat) as reflected in Dax's heightened aggression toward them.

At the conclusion of the retest period, only Jim remained dominant in the hierarchy, and became increasingly aggressive. As described in Chapter IV, Jim had also displayed a return of aggression toward humans in the home-cage stare test. Because of the corroborating evidence from other experimental situations and the stare test, it was concluded that Jim was an "atypical" OF subject and the social colony experiment was terminated with only Jim of the four OF monkeys remaining dominant.

Figure 3 is a graphic display of the dramatic changes which occurred in Walt, Ben, and Willie: the AI levels (from which the mean values listed in Tables 10-13 were derived) are plotted session by session for each of the OF monkeys versus Dax, the displaced alpha male. As described earlier, a subject need not maintain an AI of 1.0 to be clearly dominant. Preoperatively, all of the OF monkeys showed consistently high AI scores, and Jim, Walt, and Ben repeatedly reached maximal dominance. Immediately after the postoperative reintroductions, each of the OF animals successfully reasserted their dominance over Dax (and, of course, the other matrix group members) although the mastery exerted by Jim and Willie over Dax was not as complete as before while Walt's mastery was markedly reduced and temporary. After they fell from dominance, Willie, Walt, and Ben

Fig. 3 Agonistic indices of OF monkeys over the matrix group alpha male (Dax) before and after surgery.


AGONISTIC INDEX
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
.0
PREOP
POSTOP
JIM
WILLIE
WALT
BEN
MONTHS
AB
A
BW
1
2
3
4
5
6

were threatened and attacked by each member of the group; they paced, occasionally grimaced, cowered, and submitted to punishment from all—even lowest ranking Abe; and they were never again observed to display any aggressive behavior.

There was no evidence that Willie, Walt, and Ben were in any way strange or socially aberrent until the fall in dominance actually occurred. They appeared to transmit and respond to facial and postural social communication signals as they had before surgery. After reintroduction and for as long as they held the alpha position, the OF monkeys were not observed to continue an attack after the subordinate signalled submission and they often intervened between squabbling group members "keeping the peace" as leaders have often been observed to do in the wild. In light of this lack of hyper-aggression as the alpha males, the severe attacks suffered by the OF monkeys after they fell to the bottom of the hierarchy was most surprising. Whenever observed, they continually exhibited submissive gestures (e.g., head and eye aversion and grimacing) while the other monkeys hit, bit, and chased them. Within a few days, the OF monkeys had multiple open wounds and hairless patches of skin about the head, neck, back, and legs. Once begun, no amount of cowering or screeching stemmed the frequent group attacks. The typically blank face (save for infrequent grimacing) plus the continual forced-pacing of the OF monkey under stress suggests that the normal mechanisms of macaque social communication were severely and detrimentally affected. After surgery but <u>before</u> the fall, the OF monkeys ceased aggressing subordinates who properly signalled submission and often responded to the submissive monkey's grooming invitations—a normal

macaque method of diverting aggression. After the fall, however, the OF monkeys appeared to be incapable of properly signalling submission in their own behalfs. At the very least, it appeared that the pacing OF monkey had very little control over when the attacks against him commenced and ceased. One possible reason is that the socially-fallen OF monkey very rarely showed perineal presenting, and on the few occasions when they did seem to raise their hindquarters, it was in the process of turning a corner during a pacing circuit and even then the tail position was as often down as up. Thus, the posture of abject submission was either never or poorly transmitted by the OF monkeys who fell. It is reasonable that inappropriate social communication on the part of the lesioned animals rather than "sadistic retribution" on the part of the matrix group explains the aggression received by the OF monkeys. Nevertheless, deposed leaders in the field often suffer total expulsion from the group, usually preceded by one or more attacks by the younger challengers (e.g., Kaufmann, 1967). Perhaps if the feral ex-leaders also had no escape route they too might receive the kind of repeated punishment our captive, ex-leader, OF monkeys received. In short, the interrelations between the effects of captivity, emotional stress, areal restriction, and brain damage are far from distinct. It should be noted, in addition, that the amygdalectomized monkeys that fell to the bottom of the dominance hierarchy in captivity (Rosvold et al., 1954) and rhesus monkeys released back into their feral group in the wild after ablation of the amygdaloid nuclei and uncinate cortex (Dicks, Myers, & Kling, 1969) also received repeated, intense, directed attacks from their conspecifics.

Earlier in the Apparatus section of this chapter the operant pellet dispenser outside the colony cage over the food hopper was described. At any time during a social behavior observation session O could remotely release banana-flavored pellets under manual control. During these competitive feeding sessions pellets were released at either one every five or ten seconds. Records were kept of the order at which the Ss approached the food hopper, the number of pellets taken by each S, and the order in which the Ss supplanted or displaced each other at the food hopper. A more important finding is that only the latter measure was found to correlate perfectly with the dominance hierarchy. It is for this reason that the earlier criticisms of the primacy-in-food-getting and several other competitive situations were offered. Once again, a major difference between the present method and many earlier reports is that the O was totally hidden from sight of the colony: the dominant Ss were not preoccupied with threatening a visible danger; they were free to socially interact with the group. The results indicated that if an S was approached by another S at the feeder whose AI was higher, the lower ranking S would either submit (i.e., body turn allowing the more dominant to remain in control as long as he wished) or retreat. The supplanted S would reapproach the feeder again only after the more dominant one had left or if an even lower ranking S was retrieving pellets. This simply indicates that control of a food-hooper followed the same rules as control of the perch or, for that matter, all other macaque behavior; however, the importance is that other commonly used measures of dominance such as order of food-getting and number of pellets eaten did not correlate nearly

as highly with the agonistic hierarchy as did the ability of one S to supplant another at the feeder. There were sessions during which the alpha male allowed more than 125 pellets to be consumed by his subordinates before he made his first approach to the feeder whereas on another day the same alpha might leap across the cage to the hopper at the first click of the dispenser relay. Similarly, on some days the alpha might consume more than 500 of the 720 pellets provided during a one hour test while on other days he might take 15-20 and show no further interest for the remainder of the session.

Some possible reasons for this variability have been listed. In any case, whenever a monkey approached the feeder all other of lower rank stayed clear. When the OF monkeys fell from dominance all further attempts at pellet retrieval permanently ceased even after all the others were fully satiated and the hopper remained unclaimed with pellets dropping into it.

Support for the position that the ability to supplant another monkey at the feeder is more indicative of social rank than either number or order of pellets received comes from Kaufmann's (1967) observations of free-ranging rhesus monkeys. He reported that the most common of all social interactions was displacement, either active (overt threat) or passive, of which 75% occurred at the feeders.... "Displacements were highly reliable indicators of rank; alternation of the dominant role occurred only when social rank was changing or not yet established."

In summary, the effect of OF ablation in this experiment are similar to the effects of amygdala lesions in the rat (Bunnell, 1966), dog (Fuller, Rosvold, & Pribram, 1957), squirrel monkey (Plotnik, 1968),

and rhesus monkey (Rosvold et al., 1954). In these studies the dominant S, after temporal lobe (amygdala) lesion, showed a decrease in aggression and social rank. The anatomical relation between orbitofrontal cortex and the amygdala as well as functional processes which may explain the commonality in the effects of damage to these structures will be discussed in Chapter VII.

## Chapter IV

## ALTERATIONS IN EMOTIONAL BEHAVIOR DIRECTED TOWARD HUMANS

As suggested in the introduction, the changes in emotional reactivity observed following OF injury may be due to an inability to suppress earlier response tendencies which consequently become dominant. Alternatively, it is possible that these changes are related to an inability to cope with stress; to modify emotional behavior according to the degree of threat present. Such a deficit would produce variable behaviors depending on the stimuli confronting the monkey as opposed to a capacitive loss which, presumably, would produce a uniform, postoperative change across many situations. The entire test series, then, was designed to place the animals in a variety of environmental situations containing varying degrees of threat or stress. We have observed that juvenile or adolescent rhesus monkeys are likely to retreat in fear if approached by a human. As they near puberty, however, the characteristic running away-climbing-escape pattern begins to progressively weaken as the animals show a mixture of aversion and aggression. Finally, one sees purer and increasingly aggressive threats from sexually maturing rhesus of both sexes.

When approached and stared at by humans, rhesus monkeys react emotionally. This is understandable both because human approach to an individual animal usually means disruption, transference to a testing chamber or another cage, or physical handling and because the act of directly looking into the eyes of another animal (at least

between conspecifics) is an aggressive facial threat (e.g., Altmann, 1962; Chance, 1956; Hinde & Rowell, 1962; Varley & Symmes, 1966).

These emotional reactions to staring confrontations have previously been used to establish sex differences in affective behavior (Mason, Green, & Posepanko, 1960) and changes in emotional behavior after OF lesions described as decreased aggression but increased aversion toward humans (Butter, Mishkin, & Mirsky, 1968) and markedly decreased aggression with no consistent effects on aversion (Butter, Snyder, & McDonald, 1970). Unfortunately, the two earlier studies suffer from the brevity of the total behavior samples taken from each animal: 60 seconds per observer in Butter et al. (1968) and 200 seconds per observer in Mason et al. (1960). Subsequently, it was established that an individual monkeys' responses to a human are quite labile and may show unexpected increases or decreases in both aversion and aggression from one day to the next (Butter et al., 1970).

A more reliable procedure, then, is one which regularly samples the S's behavior for as long a time as possible in as constant an environment as possible. In this way the early patterns of aversion and the development of aggression can be documented providing a behavioral baseline against which one can test the possible return of the initial emotional response profile after surgery.

Procedure

The emotional behaviors were elicited and judged by two experimenters (C.M.B. and D.R.S.) acting alone and independently as both stimulus object and observer. An effort was made to observe the animals

near the noon hour when a regular interruption in concurrent testing occurred and before the animals became increasingly active and responsive prior to feeding in the later afternoon. Both Os had frequent contact with all the animals in a variety of situations.

The Ss[1] were observed in their home cages from 60 to 80 times preoperatively, and from 40 to 60 times postoperatively. Observations were begun immediately upon arrival from the importer, while in quarantine, and continued through surgery to a few days prior to sacrifice. At the rate of two to three sessions per week, this represents nearly 16 months of testing. By weight and dentition, the Ss were estimated to be two years of age at arrival. Over 16 months, therefore, one would have expected a progressive weakening of aversion and strengthening of aggression in the absence of any confounding lesion effects as the monkeys entered puberty.

The observational method is adapted from the one described by Mason et al. (1960) and is identical to that used by Butter et al. (1968, 1970). The experimenters entered the colony area alone wearing laboratory coats and stood in front of the animal's cage for 20 seconds. The observers stared impassively and directly into the monkey's eyes for 20 seconds since monkeys are sensitive to

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[1] One S, Ben, arrived in the laboratory seven months after stare testing had begun as a member of a permanent social colony (see Chapter III). Because of injuries he received during the early dominance hierarchy stabilization period and because of the prior death of a possible experimental animal, Ben was removed from the stable colony (which was left at four members) and became an experimental subject. (It was months later after numerous preoperative tests that a decision was reached as to which monkeys, including Ben, should be assigned to the OF or S groups.)

slight changes in O's facial expression and movement. After each 20 second stare test, O recorded the frequency of the behaviors listed in Table 14.

In Table 14, the abbreviations in parentheses are those used in the following figures and the numbers are the relative weights assigned (where indicated in the figures) to each behavior in determining overall aversion and aggression scores. The weighting factors were assigned from one to three by relative intensity of the response and were patterned after similar systems described elsewhere (Butter et al., 1970; Mason et al., 1960; Mirsky, Rosvold, & Pribram, 1957; Mirsky, 1960; Rosvold, Mirsky, & Pribram, 1954).

Results and Discussion

As had been previously observed (Butter et al., 1970), there was considerable variance between the animals in both kind and frequency of aversive and aggressive behaviors directed at the two Os. Similarly, a majority of the animals showed differential behavior to the two Os although these individual differences were most often in frequency and not in the kind of responses displayed. In order to be certain that there was complete agreement between the Os as to behavioral categories and judgmental criteria, a series of stare tests was run in the standard manner with hidden observers behind a one-way mirror. Over several such reliability tests, the records of the O confronting the S and of the hidden O were typically identical although most of the animals did show variable frequencies of aversive and agonistic behaviors depending on which person confronted them.

Table 14

Behavioral Reactions Scored in Stare Testing

| Aversion | Aggression | Neutral or Approach |
|---|---|---|
| Head and/or eye aversion (HE-1) | Stare at O (ST-1) | Pace (locomote) |
| Grimace (GR-1) | Frown (FR-1) | Eat feces |
| Chew or lick lips (CH-1) | Mouth open (MO-1) | Climb cage to approach O |
| Move to back of cage (MB-2) | Ear flatten (EF-1) | Approach O (locomotion toward) |
| Body turn away from O (BT-2) | Vocalize; bark (VO-1) | Lie down (approach) |
| Cower (CO-3) | Head thrust forward or lateral (HT-2) | Yawn |
| Run across back of cage (RU-3) | Arm thrust or reach for O (AT-2) | Lipsmack |
| Climb up cage away from O (CL-3) | Shake cage (SC-3) | Stand near O at cage door |
| Present hindquarters with tail raised (PRE-3) | Attack or body lunge at O (Att-3) | Invite grooming |
| | | Absence of response |

The course of emotional reactivity over time is illustrated separately for the two Os: Figures 4 and 6 D.R.S. and Figures 5 and 7 C.M.B.. The points plotted in these figures are the frequencies of aversive and aggressive behaviors weighted according to the values listed in Table 14, grouped into units of five successive observations. These curves, then, chart the changes in emotional behavior to two human observers over approximately eight months preceding and eight months following surgery.

As previously described, seven of the eight Ss were feral adolescents at the beginning of the present experiment and were expected to be initially fearful, highly aversive to humans, and nonaggressive. Contrary to expectations, only two monkeys (Abba and Willie) were initially without aggression, the more common response being a mixture of fear (MB, RU, BT, CL, HE) and agonistic facial threats (MO, FR, EF, HT) beginning from the very first approach. However, of the seven animals whose emotional development in the laboratory was recorded from arrival, only Eban (Figures 4 and 5) did not show a steady increase in the overall level of aggression elicited by both Os. Eban was atypical in that his initial levels of fear and aggression were two or three times higher than the others for one O (C.M.B.) producing a "ceiling effect" or uninterrupted reactions for the full 20 seconds of observation. His singular, progressive decline in both aversion and aggression is unexplained. The other animals displayed, for the most part, a steady increase in aggression and rather stable or slightly declining aversion prior to surgery.

There were no discernable effects of sham surgery on either aversive or aggressive behavior. The kinds of behaviors displayed

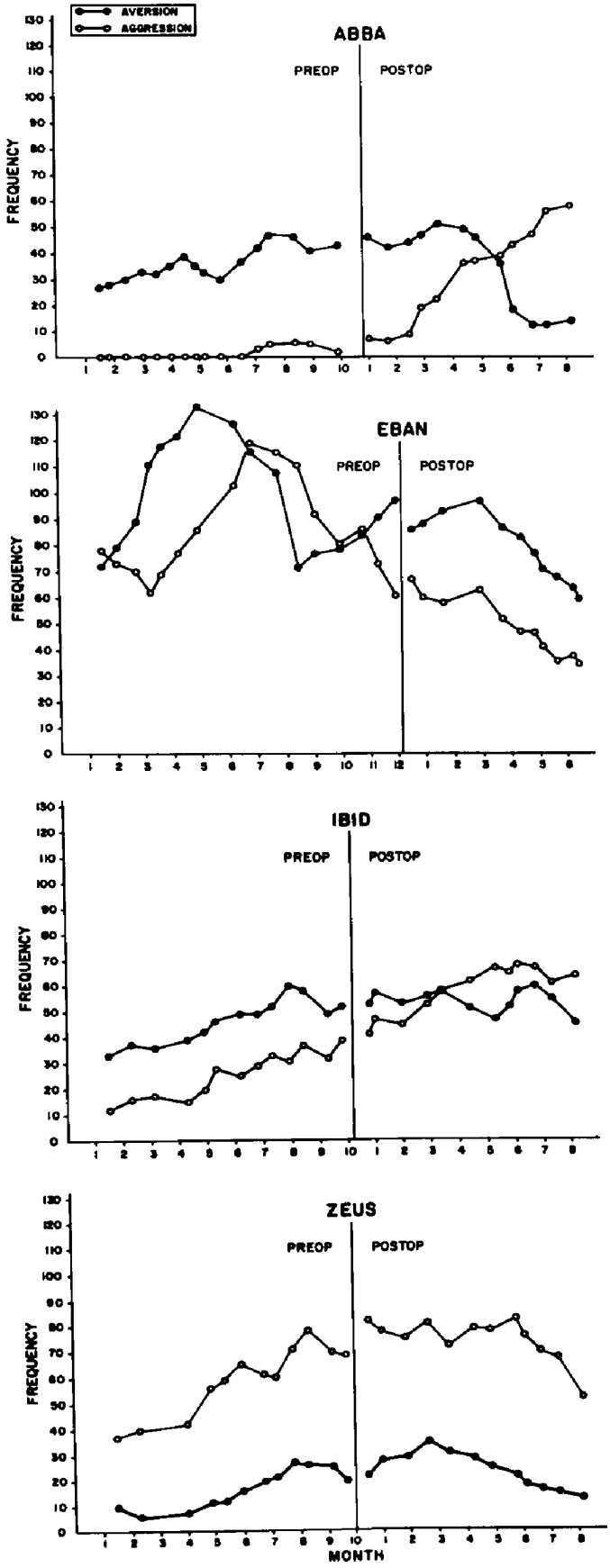
were not altered either immediately after surgery or in the following months. Likewise, OF surgery had no consistent effect on aversive behavior (Figures 6 and 7).

Three OF animals, Jim, Willie, and Ben, showed slight increases in aversion to one O (D.R.S.) within the first postoperative month; Walt, on the other hand, declined. A similar pattern was observed by the other O except for Jim, who displayed less aversion toward C.M.B. after surgery. Furthermore, since there were no consistent changes in frequency of particular behavior categories following OF surgery, no effects on aversive behavior toward humans can be claimed.

As stated before, all of the OF monkeys, as well as three of the shams, preoperatively became more and more aggressive over time. The OF ablations, however, had a profound effect on aggression. Immediately after surgery, all OF animals showed a total abolition of all aggressive behavior to one O (D.R.S.) while to the other O (C.M.B.) only Willie and, to a negligible degree, Jim retained any vestige of their former behavior. Within three months, Willie ceased threatening C.M.B. and from then on he, along with Walt and Ben, never again displayed agonistic behavior toward humans. Jim, on the other hand, began to show a partial recovery of aggression about two months following surgery and, as seen in Figures 6 and 7, quickly reached his preoperative level of agonistic behavior.

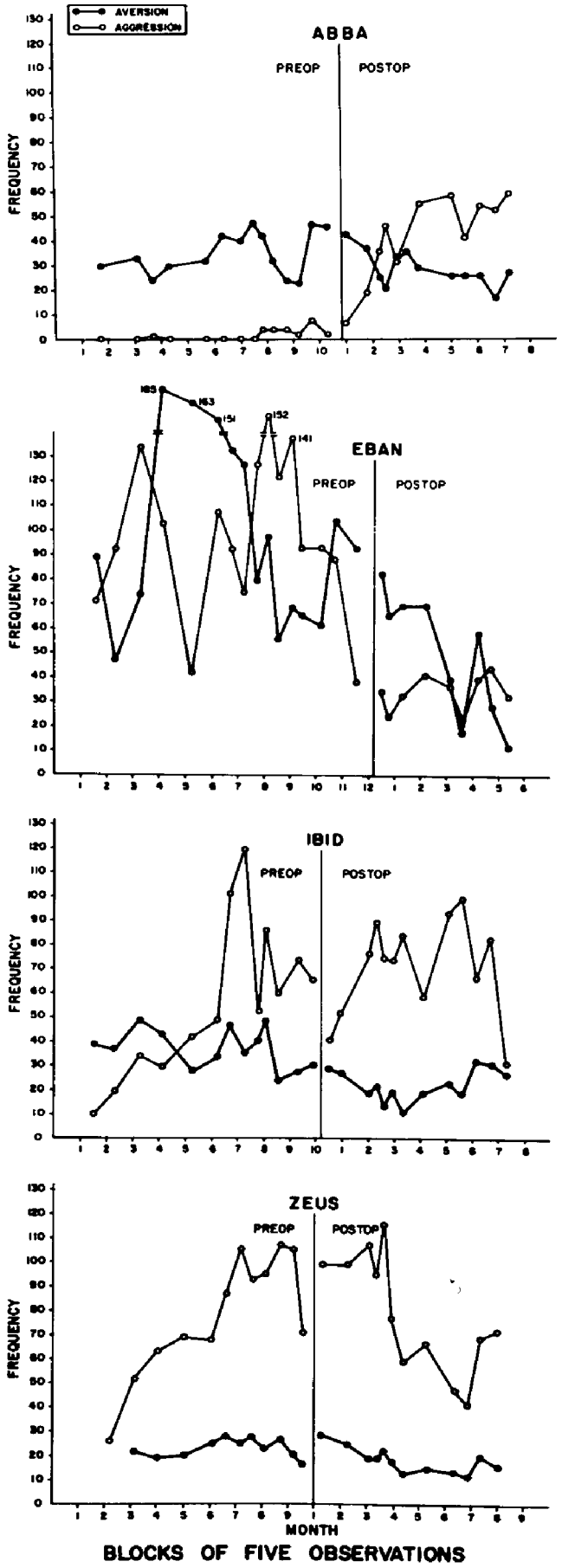
Concurrent with the decrements in aggression in OF monkeys was the onset of persistent forced pacing (beginning, of course, at the conclusion of the hypoactive phase). Locomotor pacing (Table 15) was observed in all OF monkeys but ceased abruptly in Jim as his

Fig. 4 Mean weighted frequencies of aversive and aggressive reactions of sham operated monkeys to D.R.S. before and after surgery.



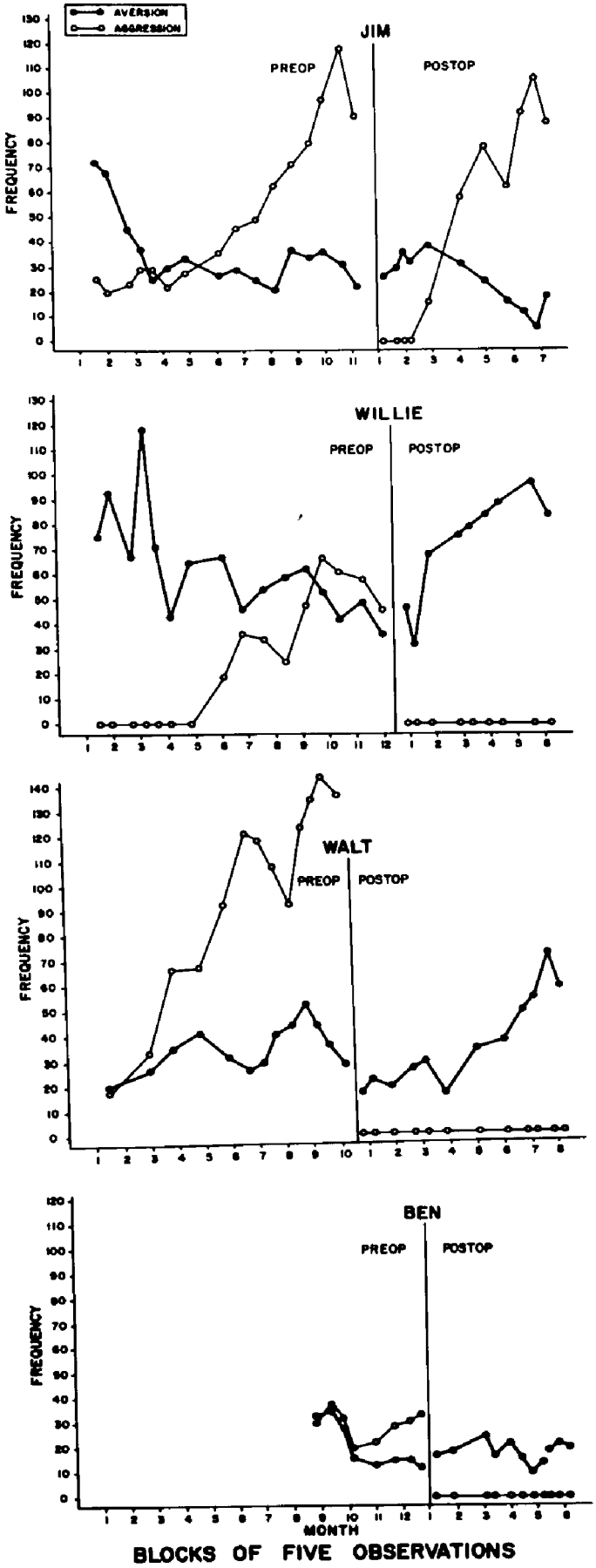

BLOCKS OF FIVE OBSERVATIONS

Fig. 5 Mean weighted frequencies of aversive and aggressive reactions of sham operated monkeys to C.M.B. before and after surgery.



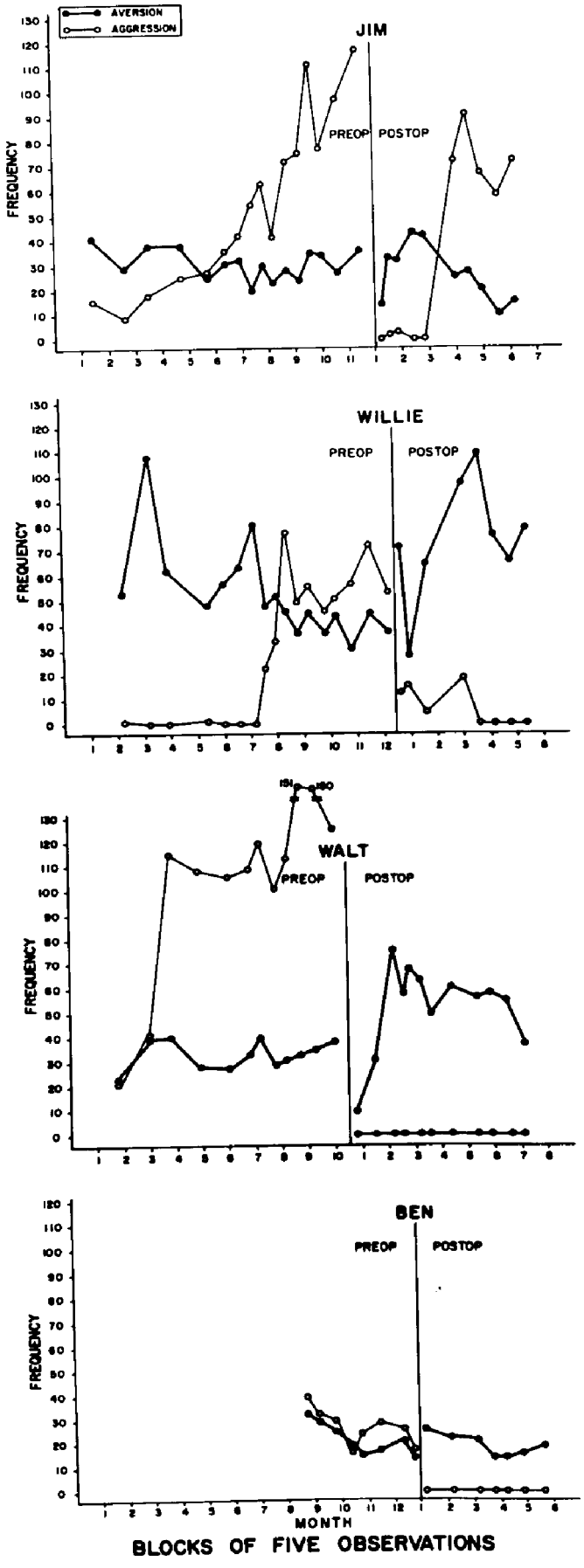

BLOCKS OF FIVE OBSERVATIONS

Fig. 6 Mean weighted frequencies of aversive and aggressive reactions of OF monkeys to D.R.S. before and after surgery.




BLOCKS OF FIVE OBSERVATIONS

Fig. 7 Mean weighted frequencies of aversive and aggressive reactions of OF monkeys to C.M.B. before and after surgery.




BLOCKS OF FIVE OBSERVATIONS

aggression began to return. Similarly, Willie was only rarely observed to pace for the first three postoperative months until his aggression was totally abolished.

Table 15

Occurrence of Orbital Frontal Locomotion

| S | Total No. Postop. Observations | Total No. Onset of Locomotion | Percent of Postop. Observations in Which Locomotion Occurred |
|---|---|---|---|
| Jim | 50 | 8 | 16 |
| Willie | 40 | 26 | 65 |
| Walt | 60 | 54 | 90 |
| Ben | 35 | 31 | 89 |

There did not appear to be any features about Jim's behavior toward human Os, either pre- or postoperative, which would have forecasted the unexpectedly delayed rise in aggression and fall in aversion after surgery. Jim exhibited a strong tendency to persist in those behaviors which characterized his emotional reactivity just prior to surgery. Notably, the fearful responses of moving to the back of the cage (MB) and head and eye aversion (HE), the only two aversive behaviors present just before OF surgery, reappeared immediately and were the only ones to remain as aversion declined in the midst of rising aggression. Subsequent to the return of aggression, the behavioral profile was indistinguishable from the immediately preoperative profile and did not reflect his earlier response pattern. Specifically, the behaviors that returned when Jim regained his aggression: lunging attacks at O (ATT), mouth

opening (MO), staring (ST), and cage shaking (SC), accounted for 98% of his agonistic behaviors before surgery.

In order to more directly test the "reversion hypothesis" (see Research Plan, Chapter I), the behavioral profiles for all Ss were drawn for the ten initial tests of emotional reactions to humans taken within the first two weeks in the laboratory, the ten observations immediately preceding surgery (either sham or OF), and the ten observations immediately following surgery which were begun at the conclusion of the hypoactive phase (see Chapter I). Figures 8 and 9 show the absolute frequency of each aversive and aggressive behavior plotted separately for each of the sham operates and Figures 10 and 11 are identical presentations for the OF groups. According to the "reversion hypothesis," one would predict that those behaviors which were present initially and decreased with maturation or experience in the laboratory would reappear following OF damage. Conversely, those behaviors which increased preoperatively (e.g., aggression) would tend to decrease postoperatively. Since subadult rhesus macaques initially show little aggression toward human Os and since one of the effects of OF damage is to abolish aggression toward humans, it may be that there is an artifactual bias toward support of the "reversion hypothesis" as presently formulated. At least one may assume that the shifts in frequency of aversive rather than aggressive behaviors from the initial to the preoperative to the postoperative periods is a more critical test for the return to previously dominant behaviors.

Fig. 8 Summed frequencies of aversive reactions of sham operated monkeys to human in ten intial observations, ten observations immediately preceding surgery, and ten observations immediately following surgery. (HE) head and eye aversion; (GR) grimace; (CH) chew; (MB) move to back of cage; (BT) body turn; (CO) cower; (RU) run across back of cage; (CL) climb up.

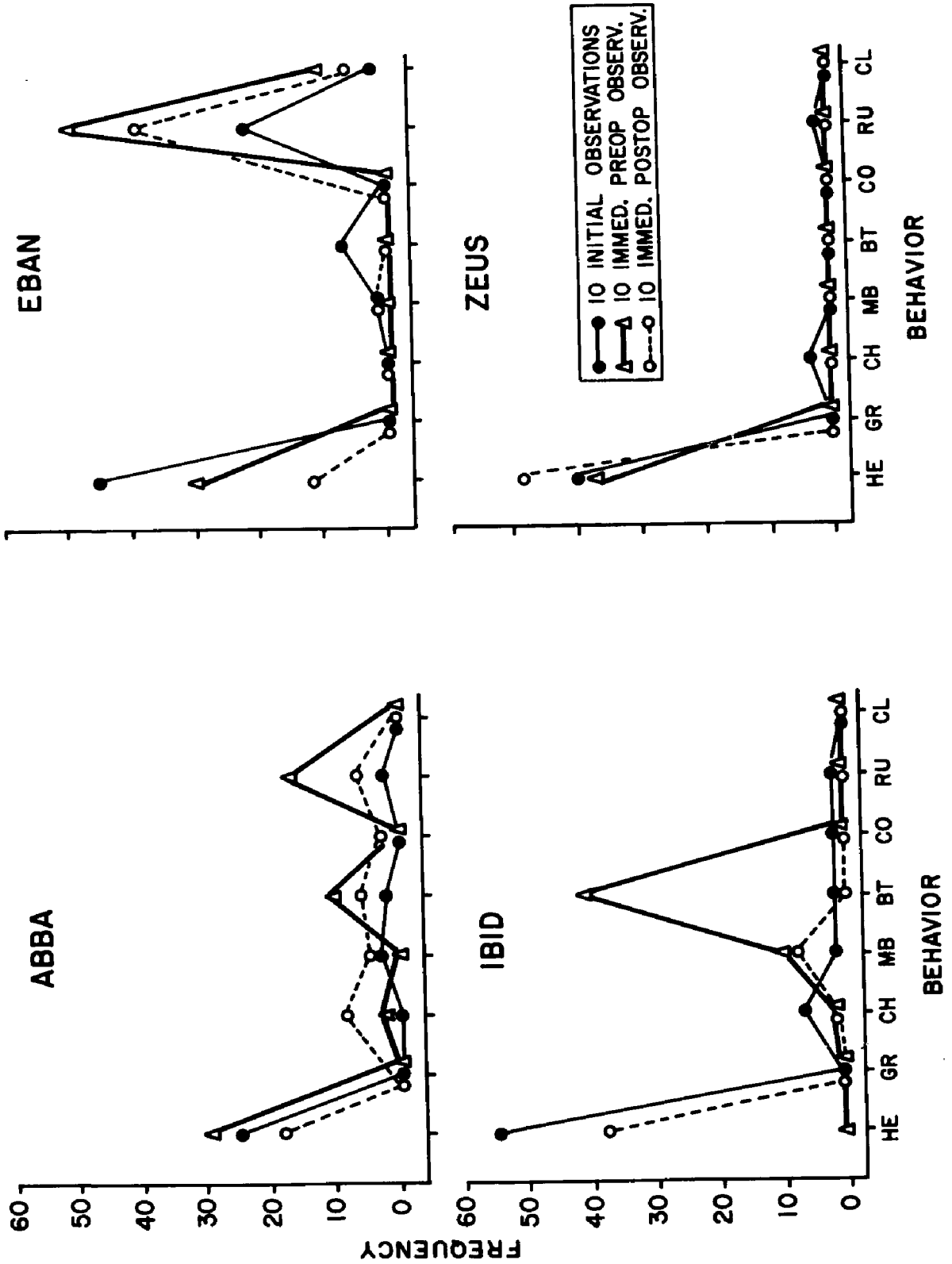

EBAN
ZEUS
ABBA
IBID
10 INITIAL OBSERVATIONS
10 IMMED. PREOP OBSERV.
10 IMMED. POSTOP OBSERV.
FREQUENCY
0
10
20
30
40
50
60
HE
GR
CH
MB
BT
CO
RU
CL
BEHAVIOR

Fig. 9 Summed frequencies of aggressive reactions of sham operated monkeys to human in ten initial observations, ten observations immediately preceding surgery, and ten observations immediately following surgery. (ST) stare; (FR) frown; (MO) mouth open; (EF) ear flatten; (VO) vocalize or bark; (HT) head thrust; (AT) arm thrust; (SC) shake cage; (ATT) attack.

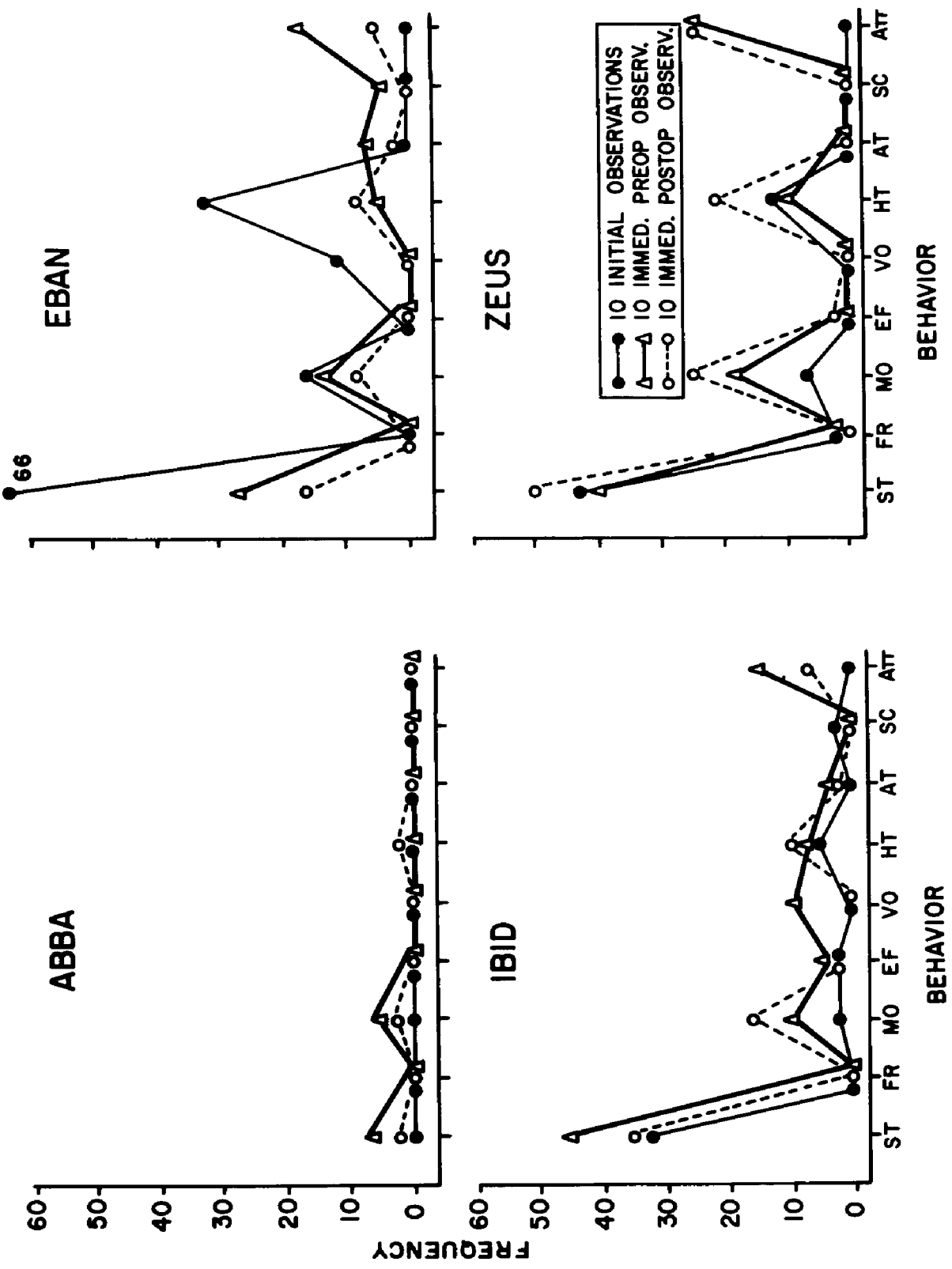

ABBA
EBAN
IBID
ZEUS
66
10 INITIAL OBSERVATIONS
10 IMMED. PREOP OBSERV.
10 IMMED. POSTOP OBSERV.
FREQUENCY
0
10
20
30
40
50
60
ST
FR
MO
EF
VO
HT
AT
SC
ATT
BEHAVIOR

Fig. 10 Summed frequencies of aversive reactions of OF monkeys to human in ten initial observations, ten observations immediately preceding surgery, and ten observations immediately following surgery. (HE) head and eye aversion; (GR) grimace; (CH) chew; (MB) move to back of cage; (BT) body turn; (CO) cower; (RU) run across back of cage; (CL) climb up.

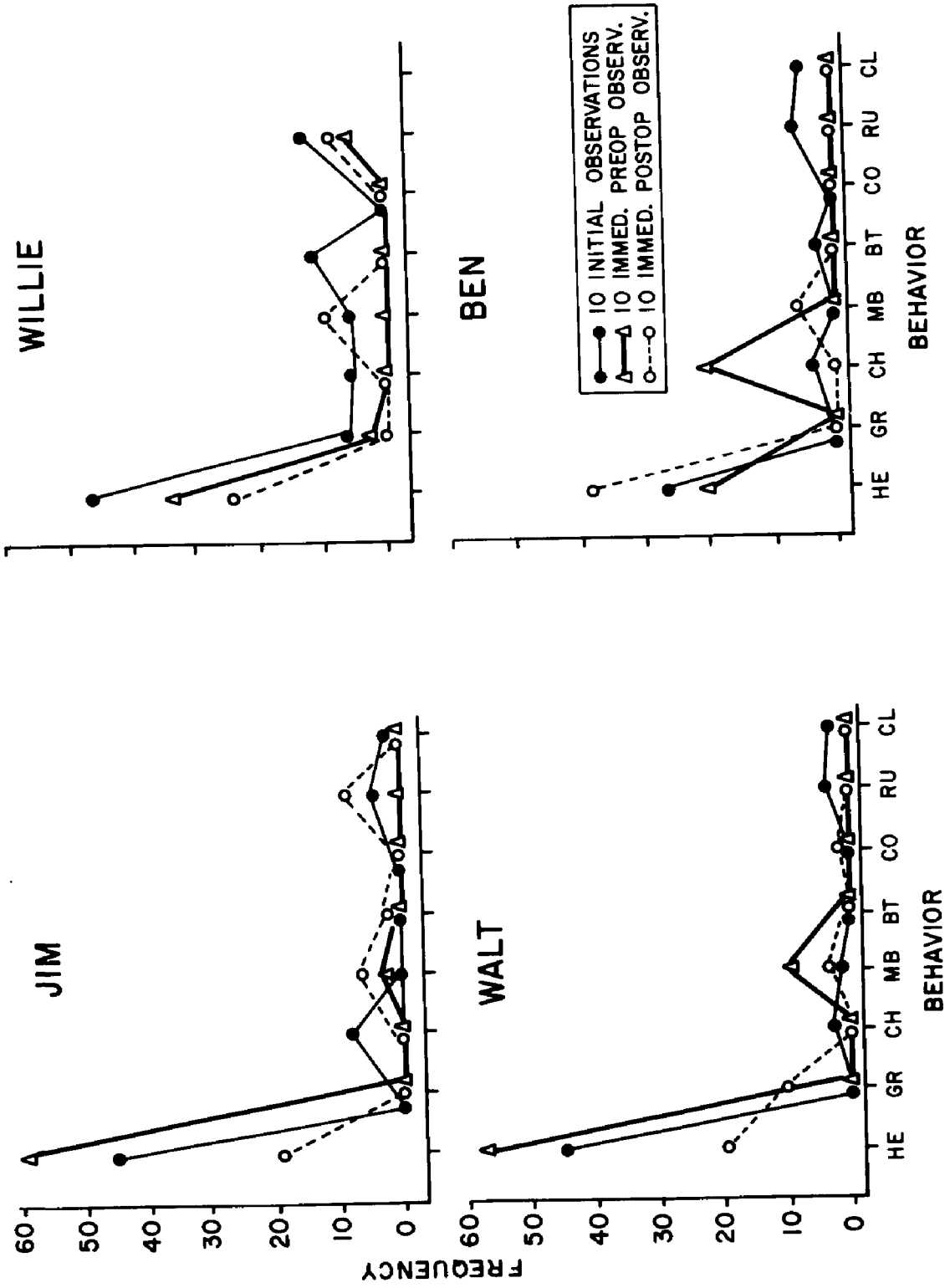
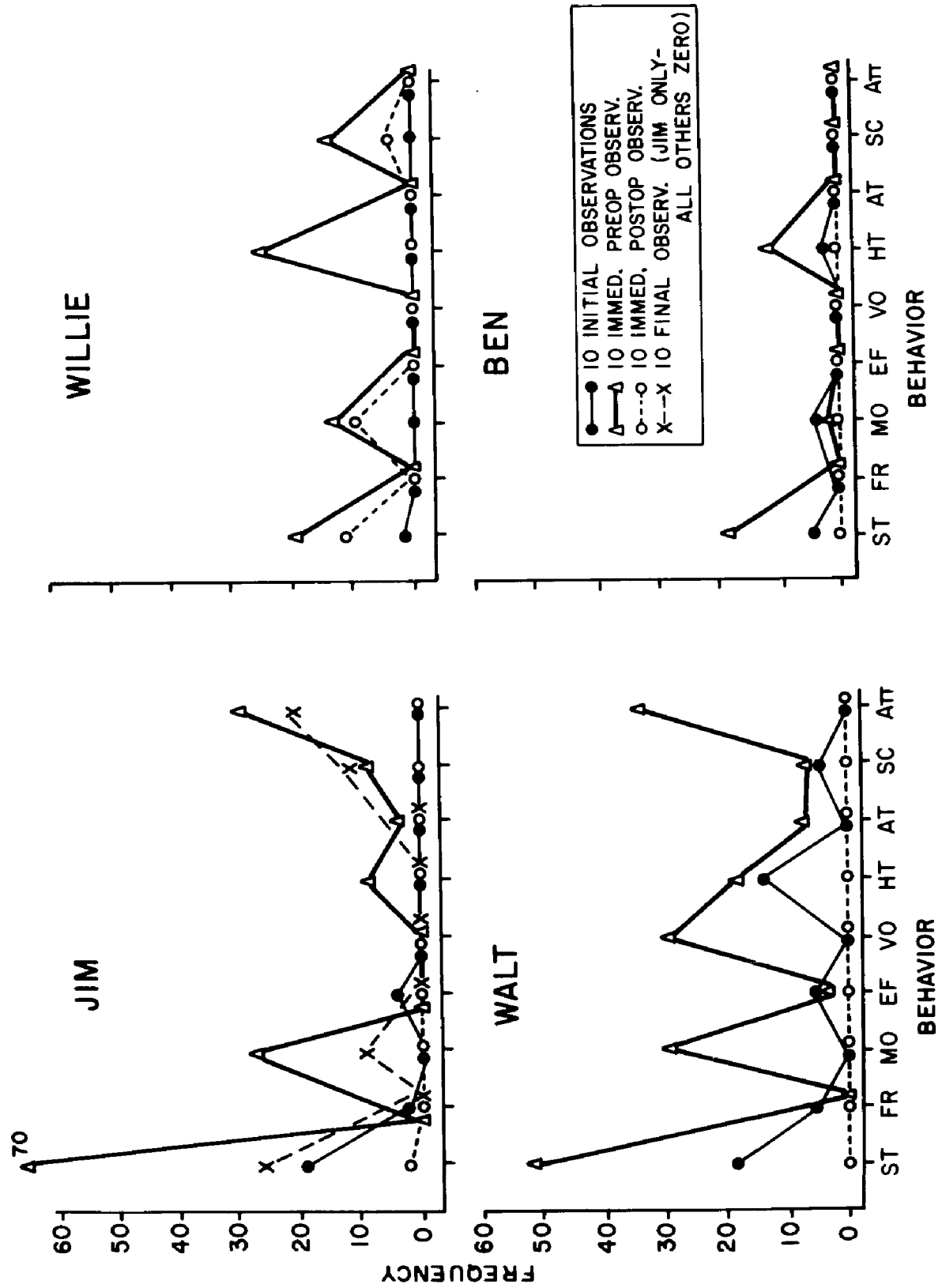

JIM
WILLIE
WALT
BEN
FREQUENCY
60
50
40
30
20
10
0
HE GR CH MB BT CO RU CL
BEHAVIOR
10 INITIAL OBSERVATIONS
10 IMMED. PREOP OBSERV.
10 IMMED. POSTOP OBSERV.

Fig. 11 Summed frequencies of aggressive reactions of OF monkeys to human in ten initial observations, ten observations immediately preceding surgery, ten observations immediately following surgery, and, for Jim only, ten final observations. (ST) stare; (FR) frown; (MO) mouth open; (EF) ear flatten; (VO) vocalize or bark; (HT) head thrust; (AT) arm thrust; (SC) shake cage; (ATT) attack.


JIM
WILLIE
WALT
BEN
70
60
50
40
30
20
10
0
FREQUENCY
ST FR MO EF VO HT AT SC ATT
BEHAVIOR
10 INITIAL OBSERVATIONS
10 IMMED. PREOP OBSERV.
10 IMMED. POSTOP OBSERV.
10 FINAL OBSERV. (JIM ONLY-
ALL OTHERS ZERO)

Inspection of Figures 8 and 10 reveals relatively few behaviors which shifted in the direction of their initial values after surgery. Those behaviors which did show a postoperative "reversion" shift are listed in Table 16 along with the proportion that they represent of the total of only those behaviors which were observed to have occurred at least four times in either the ten initial or ten immediately preoperative tests.

The sham and OF groups showed a similar effect on the aversion measure in that each had a mean of less than 1/2 of all the aversive behaviors tending to revert to the initial levels after surgery. For aggression, the sham group showed 1/5th of all observed behaviors tending toward reversion as opposed to more than 3/4ths for the OF animals which may be partially explained by the bias mentioned above. In any case, these results indicate that little support for the "reversion hypothesis" may be found in the emotional responsivity toward humans before and after OF ablation.

The differences between the present results and those of the only other long-term study of rhesus reactions to humans (Butter, Snyder, & McDonald, 1970) are likely due to differences between the subjects since both the observational methods and the Os were identical. The former experiment used monkeys of both sexes ranging in approximate age from two to five years with the larger males approaching 20 kg. while the present experiment involved a homogenous group of adolescent males. As Mason, Green, and Posepanko (1960) and Rosvold (1968) pointed out, rhesus macaques show large sex differences in both frequency and kind of affective responses toward humans and the inclusion of both sexes suggests an additional

Table 16

Behaviors Appearing Immediately Postoperatively

Shifted Toward Initial Level

| | Aversion | | Aggression | |
|---|---|---|---|---|
| Ss | Behaviors | % of Total Observed Behaviors | Behaviors | % of Total Observed Behaviors |
| S Group | | | | |
| Abba | HE, BT, RU | 75 | None | 0 |
| Eban | RU, CL | 50 | ATT | 20 |
| Ibid | HE, BT | 50 | ST, VO, ATT | 60 |
| Zeus | None | 0 | None | 0 |
| Sham Group Mean %: | | 44% | | 20% |
| OF Group | | | | |
| Jim | HE, RU | 50 | ST, MO, HT, SC, ATT | 83 |
| Willie | MB | 17 | ST, MO, HT, SC | 100 |
| Walt | HE, MB | 67 | ST, MO, VO, HT, AT, ATT | 67 |
| Ben | HE, CH | 40 | ST, HT | 67 |
| OF Group Mean %: | | 44% | | 80% |

variable capable of masking or artificially enhancing any lesion effects. The fact that some of the animals in the earlier work were sexually mature while others were not, plus the male-female split in both the orbital and control lesion groups, suggests two possible sources of behavioral artifacts. Nevertheless, there is much agreement between these studies which strongly indicates an effect of OF surgery on emotional behavior. Specifically, both studies failed to show any consistent effect of OF damage on either frequency or individual categories of aversive reactions. Both experiments produced marked decrements in postoperative aggression which proved permanent in 75% of the animals involved. In the earlier work, though, the OF monkey that regained his aggression towards humans did show a difference in kind of threat behavior in that he never made any attack-lunges at the Os, a preoperatively high frequency behavior. In contrast, the OF monkey who displayed postoperative aggression in the present study, Jim, recovered all behavioral categories equally, leaving no pre- to post differences.

With regard to pacing, the present work does suggest a correspondence between the onset of stereotyped, forced pacing and reduction of aggression (see Table 15 and Figures 6 and 7): the two animals who initially lost all aggression (Walt and Ben) began to pace as soon as postsurgical depression abated; Willie paced only after his lingering, low level of aggression fell to zero; and Jim abruptly ceased pacing when his aggression returned. This selective relationship between agonistic behavior and pacing is not consistent with the earlier work of Butter et al. (1970) and whether this is due to age, sex, fine lesion differences, or another unknown variable is presently unclear.

Chapter V

# ALTERATIONS IN A CONDITIONED AVERSION RESPONSE

Brutkowski (1965) has commented on the need for evaluative procedures to establish and interpret changes in emotional behavior after frontal lobe damage. Certainly this need increases as more and more data accumulate from lesion (both surgical and chemical) and stimulation (both electrical and chemical) experiments in an expanding variety of socially and emotionally provoking situations. It is, therefore, surprising that experimental methods like classically conditioned aversion or aggression which enjoy wide agreement as to training and testing procedures, data format, etc. have not been used much more often as regular screening measures in the assessment of primate emotional behavior.

Pribram and Weiskrantz (1957) reported that monkeys with bilateral lesions of the posterior orbital, insular, and temporal polar cortex plus the amygdaloid complex (Pribram's neuronographically defined frontotemporal region) show a severe postoperative impairment in relearning a preoperatively acquired conditioned avoidance response. These monkeys also showed rapid extinction and a negative savings in relearning after postoperative extinction. Furthermore, if the conditioned avoidance response was acquired postoperatively, they showed abnormally delayed acquisition and, subsequently, rapid extinction. Damage restricted to the amygdaloid complex (Weiskrantz, 1956) also produced retarded acquisition and hastened extinction of the shock avoidance response in the same situation. In an instrumental task

involving a positive reinforcer, Butter, Mishkin, and Rosvold (1963) reported that monkeys with ablations restricted to OF or lateral frontal cortex also showed significant but temporary response rate decrements postoperatively. In extinction testing, however, the OF monkeys' response rates markedly increased and remained consistently high throughout the duration of the extinction sessions. Whether these opposite effects on extinction reported by Pribram and Weiskrantz and by Butter, Mishkin, and Rosvold are due to the involvement of temporal lobe-limbic structures in the former study or due to the use of positive versus negative reinforcement is unclear.

It is possible, as suggested by Brutkowski (1965), that the reported impairments or depressions in conditioned response performance levels (such as those in Butter et al., 1963) appeared because the Ss were tested too soon (10-20 days) after surgery when they might still have been hyporesponsive to environmental stimulation (see Chapter I). Since this phase is particularly likely to occur after OF ablation, this is a factor which should be controlled in future studies.

According to the drive disinhibition view (Brutkowski, 1964, 1965), OF lesions remove the inhibitory influences over hypothalamic drive centers which regulate "motivational behavior patterns." It is reasonable to assume that these more primitive behaviors compete with the more recently learned, complex, conditioned response. Thus, one would predict that following OF lesions, recently acquired CRs would be reduced or abolished and undergo rapid extinction. However, this prediction is at variance with the retarded instrumental extinction reported following OF ablation (Butter et al., 1963). A corollary

explanation, derived from the drive disinhibition view, for postoperative deficits in conditioned avoidance might be that the simpler, competing behaviors represent a return to the reactions which dominated before the S acquired the CR, in which case the reversion hypothesis (see Chapter I) could also account for a CR decline. Moreover, once the CR became re-established in the situation postoperatively, it should perseverate in extinction.

The present experiment tests the drive disinhibition/reversion hypotheses in an aversive situation at a time when the Ss were well beyond any hyporesponsive after effects of surgery in order to determine if recently acquired emotional responses are impaired following OF lesions as anticipated by these hypotheses. An inescapable shock situation was chosen as an ideal conclusion to the test series discussed in the preceding chapters. In overall design, each of the experiments in this series was designed to differentially threaten or stress the Ss. The present experiment was assumed to be highly aversive (motivating); placing the Ss under maximal stress short of physical abuse.

## Method

### Apparatus

The test cage measures 30 x 30 x 30 in. and was formed of 1/2 in. steel bars set into a wood frame 4 in. apart on all six sides. Leads from each bar were connected to a Foringer A.C. shock source and scrambler in groups of six so that each contact point in the shock scrambler simultaneously electified one bar on each side of the cage. Input voltage and impedance were variable between 0-100 V. and 0-100,000 ohms and the shock level which induced rapid limb withdrawal

was determined individually for each S. The test cage was mounted atop a wheeled platform to facilitate transport between the home cage area and the testing room.

As an object for elicited aggression, a young female monkey was placed into a metal transport cage of identical dimensions as the shock cage, one side of which was made of 1/4 in. steel bars about 4 in. apart. This cage was also mounted on a mobile platform and was strapped alongside the shock cage throughout the course of the conditioned aversion experiment. These two cages were close enough together and sufficiently small for either monkey to reach between the bars and strike the other as he (she) moved about.

The CS was a standard doorbell activated manually by one of the Os. The UCS (electric shock) equipment, also under manual control, was in the same room with the test cage but out of sight of the Ss so that the scrambler and relays produced a loud noise while operating.

Procedure

The Ss were tested on alternate days for four sessions preoperatively and again 3-4 months postoperatively for four sessions followed immediately by one sensitization session and up to eight extinction sessions. These tests occurred in the same sequence with the other experimental procedures for all Ss (see Table 1, Chapter I). Throughout each session, which was 25 min. in duration, two Os, seated behind a one-way mirror, time-sampled the animal's emotional reactions (e.g., see Table 14, Chapter IV) and other behaviors in successive 5 sec. periods.

To avoid the possibility of temporal conditioning, 12 CS-UCS trials with one, two, or three min. inter-trial intervals (ITIs) were

randomly distributed over each 25 min. session. Thus, four 10 sec. shocks were administered with a 1 min. ITI, four shocks with a 2 min. ITI, and four shocks with a 3 min. ITI in random sequence in each 25 min. session. The CS and CS + UCS intervals each lasted 10 sec. coinciding with two 5 sec. observational periods. The CS was on continuously to the end of the UCS interval.

The single sensitization test was the first extinction session run on the day following completion of the four postoperative sessions. An 800 Hz. tone, judged by three Os as very near the dominant frequency and intensity of the CS-doorbell, was substituted for the CS and CS + UCS (20 sec) on half the trials. On the other half of the trials, the CS and CS + shock scrambler sounded at the appropriate times, but the shock leads to the cage were disconnected.

Extinction testing was initiated immediately after the sensitization test. Each session consisted of the standard 12 CS (10 sec.) and the 12 CS + scrambler noise (10 sec.) intervals with the shock disconnected.

## Results and Discussion

During the first preoperative session each of the Ss frequently interacted with the young female in the adjoining cage. Not surprisingly, the initial shocks disrupted ongoing activity and greatly upset the test Ss. Most of them directed at least a few facial threats; barks; cage shaking; and, if they could reach her, arm thrusts and blows at the submissive female while they were being shocked. In response, the female quickly learned (within the first session) to retreat across her cage and cower or present her hindquarters at the onset of the scrambler noise. (If she retreated completely across her cage and stood quietly

she was out of reach of the largest test S.) In other words, the female, originally intended as a target for elicited aggression, effectively suppressed all aggression directed at her by submitting to each male test S while and only while he was being shocked. It appears that peripheral, shock-elicited aggression is best accomplished with all Ss in one cage where (social) escape is more difficult (Azrin, Hutchison, & Hake, 1963; Plotnik, 1968 ; Plotnik, Mir, & Delgado, 1970).

The occurrence of agonistic behavior, UCRs, and CRs recorded by the two Os were highly correlated in all sessions (rs ranged from .90 to .97) as were the behaviors recorded in all the other observational experiments (e.g., Chapter III). Since there were no intraobserver differences like those in the monkey's responses to direct, human confrontation (Chapter IV), the data from only one O who was present at all sessions (D.R.S.) will be reported.

The scores presented in Figures 12 and 13 represent frequencies of 5 sec. periods in which O recorded the occurrence of a CR, UCR or locomotion. Multiple occurrences were not included in the score unless the Ss clearly ceased one behavior and then reinitiated it in the same 5 sec. period. The conditioned avoidance response adopted sooner or later by all the Ss was a "rock back" (RB) sitting posture in which the monkey literally balanced himself on his ischial callosities across one or two bars with all four limbs in the air. Since the macaque's seat-pads have the highest resistance of any skin, including fur, sitting RB is the optimal position to reduce or eliminate the shock.

Emotional reactions to the UCS or CS are not included in these analyses because neither the OF monkeys nor the sham monkeys persisted

in any unambiguous aversive or aggressive behaviors longer than the second or third preoperative sessions. Aversive responses were particularly ambiguous because it was difficult to judge if body, arm, and leg jerks; flinching; etc. were emotional behaviors or simply motor reflexes to electric shock. By the time most of the Ss began making anticipatory emotional responses during the CS period, they were proficient at the UCR-escape posture which replaced other agonistic reactions.

Figures 12 and 13 present the frequency (number of 5 sec. periods) of observed RB responses or locomotion during the CS (CR) and CS + UCS (UCR) periods through the course of conditioned aversion testing for the sham and OF monkeys. In order to more easily trace each S's performance, each session was arbitrarily divided in half. Each half included six CS and six UCS presentations. Thus, a frequency of 12 CRs or UCRs indicates that an S assumed the RB position during each of the twelve 5 sec. CS or twelve 5 sec. CS + UCS periods comprising a half of the 24 5 sec. periods in a single day's session. Similarly, the total onsets of locomotion in the combined CS and CS + UCS intervals are indicated for each half of a single day's session.

Six of the Ss performed the RB as a UCR by the second preoperative session. The two remaining Ss (Eban and Walt) appeared to be more intensely upset by the shock and rarely remained still long enough to properly assume the RB posture. The CR was acquired and consistently present during more than 50% of the 5 sec. CS intervals by the end of the second preoperative session for all Ss except Eban, Walt, and Jim.

Sham surgery (Figure 12) did not appear to have any effect on the UCR nor any consistent effect on the CR. Abba's CR frequency initially declined and then increased by the middle of the second postoperative session. Ibid showed increasingly consistent UCRs and no change in his CR performance, while Zeus' CR and UCR performance became stable postsurgically. Eban's high level of locomotion, which impaired his performance of the RB response before surgery, abated during postoperative testing and he successfully avoided all shocks by remaining fixed in the RB posture during the UCS periods and showed a clear increase in CR performance.

The UCR levels of the OF monkeys (Figure 13) were also unaffected by surgery. Jim and Ben, who had performed the RB response in at least one session before surgery, continued responding after OF surgery. Walt showed a decline in UCR frequency for only the first postoperative session and then, like Willie, quickly returned to his preoperative performance level. However, the CR levels for three OF monkeys (Willie, Walt, and Ben) were significantly and consistently reduced by OF damage. There was no overlap between the CR frequencies in the third and fourth preoperative sessions and the CR frequencies in postoperative sessions: i.e., OF ablation either selectively abolished the CR (Walt) or depressed it below the preoperative postacquisition performance level (Willie and Ben) while not impairing the UCR. To re-emphasize an earlier point, this CR impairment after OF ablation cannot be due to hyporeactivity since testing took place three to four months following surgery, long after the hyporeactive period had passed.

Disruption of the RB-CRs in the OF monkeys postoperatively was not due to any stereotyped, competing motor response such as locomotion.

Fig. 12 Frequencies of RB responses as a CR and as a UCR and frequency of locomotion of sham operated monkeys during preoperative, postoperative, and extinction testing. Each half of a day's trials is plotted separately. The first extinction session was a test for sensitization (ST). (CS) standard CS-doorbell used throughout; (T) 800 Hz. tone.

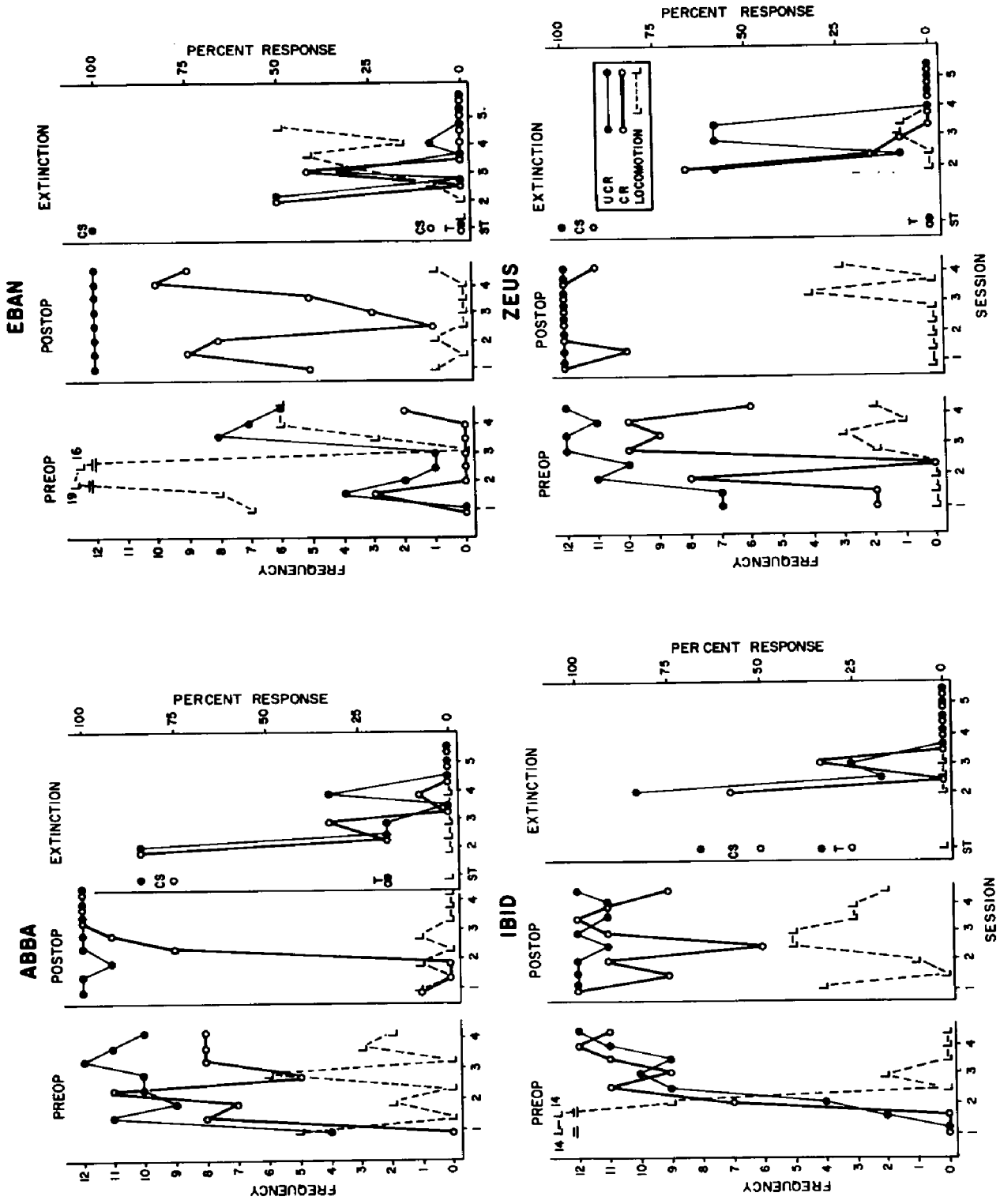
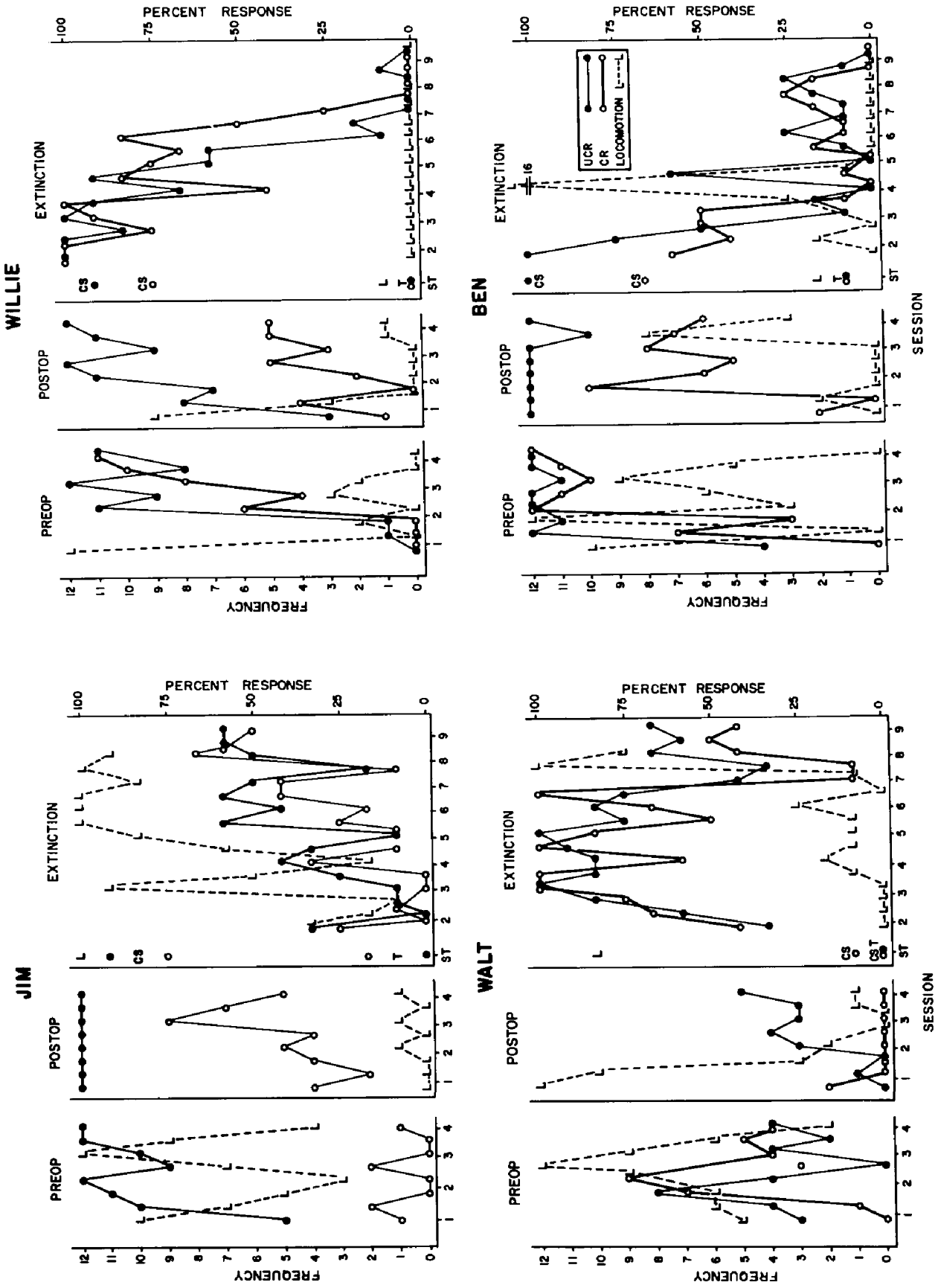

EBAN
ZEUS
ABBA
IBID
PERCENT RESPONSE
PER CENT RESPONSE
EXTINCTION
POSTOP
PREOP
FREQUENCY
SESSION
UCR
CR
LOCOMOTION
CS
ST

Fig. 13 Frequencies of RB responses as a CR and as a UCR and frequency of locomotion of OF monkeys during preoperative, postoperative, and extinction testing. Each half of a day's trials is plotted separately. The first extinction session was a test for sensitization (ST). (CS) standard CS-doorbell used throughout; (T) 800 Hz. tone.


WILLIE
BEN
JIM
WALT
PERCENT RESPONSE
EXTINCTION
POSTOP
PREOP
FREQUENCY
SESSION
UCR
CR
LOCOMOTION
CS
ST

Ben and Jim showed reduced frequency of 5 sec. periods in which locomotion was observed immediately after OF surgery while Willie and Walt showed a reduction after an initial increase during the first postoperative session only (Figure 13).

As in prior experiments (Chapters III and IV), Jim responded differently from the other OF monkeys. He, like Eban, performed relatively few UCRs and did not learn the CR preoperatively due to a relatively high degree of locomotor activity. Unlike the other OF Ss and in a pattern nearly identical to Eban's, his UCR level was unimpaired and his CR performance continually improved after surgery. It is suggested that posteromedial OF cortex, already implicated as a focus for aggressive behavior (Butter, Snyder, & McDonald, 1970), might also be involved in mediating learned reactions to emotional (painful) stimulation and, furthermore, that the critical portion might be in the medial half where Jim's selective sparing occurred (see Chapter II).

The sensitization test (ST) indicated that the CR frequencies in response to the CS alone or CS + scrambler on one hand and 800 Hz. tone (T) on the other were quite divergent. There is no evidence that any of the conditioned behavior or the CR changes after OF ablation can be explained on the basis of a pseudo-conditioning effect.

The effects of sham (S) and OF surgery on extinction are illustrated in Table 17 which shows the total number of RBs observed to an extinction criterion of not more than one CR during two consecutive sessions.

Table 17

Total CRs to Extinction or to Termination of Extinction Testing (parentheses)

| Ss | CRs to CS-doorbell | CRs to shock scrambler sound onset |
|---|---|---|
| S Group | | |
| Abba | 17 | 18 |
| Eban | 11 | 11 |
| Ibid | 11 | 15 |
| Zeus | 11 | 22 |
| S Group Mean: | 12.5 | 16.5 |
| OF Group | | |
| Jim | NE[a](47) | NE (66) |
| Willie | 107 | 93 |
| Walt | NE(119) | NE(136) |
| Ben | NE (37) | NE (49) |
| OF Group Mean Through Eighth Extinction Session: | 77.5 | 86.3 |

[a] NE = No extinction through eight sessions (Σ 192 5 sec. observation periods).

All the sham Ss (Figure 12) extinguished their responding to the CS by the third session, but the OF monkeys (Figure 13) extinguished far more slowly. Jim's CR frequencies declined in the first extinction session and Ben's declined in the second session. However, neither Jim nor Ben completely ceased responding and their responses to the CS and the scrambler became more frequent as the extinction sessions continued. Furthermore, Willie and Walt exhibited more than a 100% increase in their CR levels once the electric shock was removed similar to the response rate increase during extinction reported by Butter et al. (1963) for OF but not lateral frontal Ss. By the eighth extinction session, only Willie had zero CRs and had ceased rocking back to the onset of the scrambler noise. Thus, it appears that OF lesioned monkeys show abnormally high resistance to extinction not only of a positively reinforced instrumental response, but also of a conditioned avoidance response.

The impairment in conditioned aversion behavior shown postoperatively by the OF monkeys is consistent with the reversion and drive disinhibition hypotheses insofar as the recently acquired emotional reaction (RB as a CR) declined. It is not as clear, however, that the OF Ss had reverted to any particular behavior(s) which could be identified as preoperatively dominant, including the emotional reactions seen early in preoperative testing. In fact, generalized exploration and locomotion about the cage declined more uniformly postsurgically in the OF monkeys as a group than in the sham operated monkeys. Since the Ss also showed no obvious heightening of defensive-emotional reactions following OF surgery, this experiment provides no evidence that OF lesions release hypothalamically integrated, "primitive forms of

motor and motivational behavior patterns" (Brutkowski, 1965). The loss of inhibitory control over hypothalamic drive centers does not necessarily mean that the animal will show enhancement of a recognizable pattern of overt motor behavior. Rather, what may be enhanced as a result of the "release" of these centers is autonomic discharge, which may compete with CR performance. It might well be profitable, therefore, to monitor sympathetic indicators (e.g., heart rate or respiration rate increase, pupil dilation, piloerection, etc.) of hypothalamic activity in OF monkeys in threatening situations.

The strong resistance to extinction shown by the OF monkeys offers some support for the view that OF lesions impair the ability to suppress dominant responses (Mishkin, 1964) but not for the drive disinhibition hypothesis. However, it is not clear that the OF Ss are merely perseverating a response which was postoperatively reacquired. Neither Willie nor Ben recovered their preoperative CR frequency, and Walt lost the CR entirely. But as soon as extinction testing began, two OF Ss (Willie and Walt) showed marked increases in CR frequency to levels which exceeded their highest preoperative performance. It was as if their ability to perform the CR had not been lost during the postoperative testing but merely interfered with by electric shock or some event associated with reinforcement.

In the introduction the assumption was made that shock avoidance (compared to the other experimental situations) is highly aversive and stressful to the animals. In this context, one might further assume that removing the shock (as in extinction) greatly reduces the amount of threat or stress perceived by the monkey in the same situation. The relative degree of stress, then, might play an important role in

determining the kind and severity of impairment produced by OF lesions. The implications of this hypothesis will be discussed in Chapter VII.

## Chapter VI

## ALTERATIONS IN ORALITY, DIETARY, AND FOOD PREFERENCE BEHAVIOR

### Introduction

Many of the changes in activity and emotional responsivity following OF lesions have been reviewed in Chapter I. There is much in common between these alterations and the well known temporal lobe syndrome (Klüver, 1958; Klüver & Bucy, 1937, 1938, 1939; Pribram & Bagshaw, 1953). Specifically, both lesions produce changes in reactions to animate and inanimate objects which have been variously described as "increased fearlessness," "loss of fear," "increased tameness," and "loss of aggression," and both produce a loss of dominance rank in a social situation (Pribram & Bagshaw, 1953; Rosvold et al., 1954; Chapter III). These reports have indicated that damage to both OF cortex and the amygdaloid complex causes an increase in oral exploratory and manipulatory behaviors (Klüver & Bucy's "hypermetamorphosis"), although one has the impression that these alterations are more intense after ablation of the amygdala, as are the changes in dietary behavior (e.g., heightened quinine acceptance threshold and meat eating) even though a direct comparison has yet to be reported. There is also an indication from the predator film experiment (see Table 1, Chapter I), which will be presented elsewhere, that the OF animals showed indiscriminate approach to and oral exploration (licking) of color motion pictures of several natural enemies including the tiger, python, and cobra. This behavior, while not a pronounced feature of the OF monkey, bears a strong resemblance to Klüver and

Bucy's "visual agnosia" in that..."the ability to recognize and detect the meaning of animate and inanimate objects on the basis of visual criteria alone"... seems to be impaired (Klüver, 1958). The hypersexuality commonly reported after bilateral amygdalectomy was not seen following ablation of OF cortex in the present experiments.

The increased oral behaviors exhibited by the OF monkeys in their home cages and in social colonies have been reported as similar to those appearing in amygdalectomized monkeys (Butter, Snyder, & McDonald, 1970; Ursin, Rosvold, & Vest, 1969; Weiskrantz, 1956). In our experience, these abnormalities were manifested by the rapid acceptance and ingestion of any chewable object (i.e., in addition to normal chow and fruit slices, the OF monkeys eagerly ate quinine-adulterated fruit, orange rind, banana peel, etc.); rapid placement of nonfood objects (e.g., rubber stoppers and metal bolts) into their food pouches and storage for long periods; and bulimia in two of the four operated subjects. The bulimia was, in fact, so profound that while in the social colony these Ss kept the cage devoid of the fecal production of five monkeys including themselves. The following experiments were designed to systematically investigate these oral tendencies observed in the postoperative OF monkey.

## Experiment 1

## Alterations in Dietary Behavior

The first experiment attempted to determine the variety of edible objects orbital frontal monkeys would accept and whether these objects could be classified on the basis of nutritive value.

Procedure

On six occasions, from five to seven months after surgery, O offered the sham operated and OF monkeys a choice of eleven nutritive and non-nutritive edible items. Dietary testing was done at roughly two week intervals during afternoons when other testing was not in progress and other humans were not present. All of the test items were prepared in advance so that O was able to move about (excite) the Ss as little as possible while recording their acceptance or rejection. Each of the items was dropped one at a time into the food hopper on the front of the S's home cage. O then backed away from the cage turning so as not to stare directly into the S's eyes. If the monkey did not immediately approach and react to the item, O waited five min. before proceeding to the next cage. All of the waste pans were inspected to determine when and if inedible objects held by the OF monkeys in their food pouches were ejected and if two of the sham operated Ss, normally inhibited from eating by human presence, made any approach to the various test items when left alone.

Results and Discussion

Details of the reactions of each of the Ss to each of the 11 test items are presented in Appendix A.

Table 18 summarizes the reactions of Ss to nutritive and non-nutritive items. Choice of food items which were part of the S's regular diet (apple, orange, cabbage, and banana pellets) did not differentiate between the two groups. On the other hand, the OF monkeys accepted small portions of meat and fish on 50% of the presentations while the sham group showed uniform rejection of these items.

Table 18

Frequency, Relative Percentage (Parentheses), and Percentage Range (Below) of Oral Insertion and Rejection of Nutritive and Non-Nutritive Items

| | Sham Ss | | Orbital Frontal Ss | |
|---|---|---|---|---|
| Test Items | Oral Insertion | Rejection | Oral Insertion | Rejection |
| Nutritive | | | | |
| Hamburger | 0 | 12(100) | 6(50)<br>0-100 | 6(50)<br>0-100 |
| Tuna | 0 | 12(100) | 5(42)<br>0-100 | 7(58)<br>0-100 |
| Apple | 24(100) | 0 | 24(100) | 0 |
| Cabbage | 8(100) | 0 | 8(100) | 0 |
| Orange | 16(100) | 0 | 16(100) | 0 |
| D&G Whole Diet Pellet | 24(100) | 0 | 24(100) | 0 |
| Bread | 6(37)<br>25-100 | 10(63)<br>50-75 | 6(100) | 0 |
| Non-Nutritive | | | | |
| Paper | 9(37)<br>17-100 | 15(63)<br>0-83 | 17(71)<br>0-100 | 7(29)<br>0-100 |
| Cork | 16(100) | 0 | 12(75)<br>0-100 | 4(25)<br>0-100 |
| Gelfoam | 12(100) | 0 | 12(100) | 0 |
| Gelatin Capsule | 12(100) | 0 | 12(100) | 0 |

However, of the four OF Ss, only Walt showed indiscriminate, rapid acceptance of all items offered him (see Appendix A). An eager acceptance of large quantities of meat or fish similar to that which follows bilateral amygdalectomy (Klüver, 1958) was not observed, although the probability that an OF monkey would ingest small portions was increased to about .5. Nor was there the striking increase in ad lib food consumption (Purina Monkey Chow) found after amygdalectomy (Klüver, 1958; Pribram & Bagshaw, 1953). Of all the nutritive items offered, bread most clearly separated the lesion groups since the sham monkeys ate bread 37% of the times it was presented while the OF monkeys ate it 100% of the time.

Of all the non-nutritive test items, only acceptance of paper differentiated between the groups such that the OF monkeys ingested paper 34% more frequently than the sham monkeys (Table 18). However, it should be pointed out that the remaining non-nutritive, edible items were used in orality and reinforcement tests (see Experiments 2 and 3, below) and each of the monkeys had many prior chances to ingest these objects. It is possible that the familiarity with these test items affected the Ss' appetitive behavior so as to make cork, Gelfoam, and gelatin more desirable than paper. Finally, two of the non-nutritive objects, Gelfoam and gelatin drug capsules, were by their composition biased towards ingestion. Unlike all the other test items these two decompose rapidly in the mouth so that in the course of "normal" oral exploration they are likely to become irretrievable.

In summary, the OF monkeys as compared to the sham operated monkeys displayed an enhanced willingness to accept and ingest unpreferred foods and one nonfood item. Familiarity seemed to enhance the acceptance of nonfood items.

## Experiment 2

## Alterations in Preference Behavior

The second experiment was designed to test the extent to which the OF monkey's heightened oral tendencies affect preference behavior in a free-choice situation. This study was done in a Wisconsin General Test Apparatus (WGTA) which is, compared to the home cage, a better controlled situation offering the opportunity for more sensitive preference testing.

### Procedure

Preference behavior was tested in a Wisconsin General Test Apparatus (WGTA) which has been described elsewhere (Butter, 1969). At the beginning of each trial an opaque screen was raised and the monkey was presented a simultaneous choice of six items, three food: apple slice, banana slice, D&G whole-diet pellet; and three nonfood: cork, gelatin capsule, small metal bolt, each lying within a recessed well of a fixed, 21 in. long board. The relative position of each object was randomly varied on each of 15 daily trials. Ss were tested on three sessions. When an animal removed all the items from the wells or failed to respond for two minutes after the preceding selection the trial was terminated and a masonite screen lowered between the S's cage and the test board.

Records were kept of the sequence in which each of the test items was removed from its well on each of the trials (i.e., preference behavior) and of the number of trials on which different items were chosen (i.e., selection). Relative preference for food and nonfood items was determined by the preference rank for each of the items

averaged over the total number of trials on which it was chosen.

## Results[1] and Discussion

Comparison of the preference ranks listed in Table 19 shows that both the sham and OF monkeys tended to prefer food to nonfood items. There was, however, considerable intragroup variability in preference behavior. For example, Abba's preference for cork and gelatin capsules to whole-diet pellets and Jim's preference for cork to all other items. Intragroup variability also characterized the relative preference for each of the three food items but not the nonfood items for which OF monkeys showed a uniform preference for cork over capsule over bolt. Of the shams, Zeus preferred capsule to cork, Eban preferred bolt to capsule, and the preferences of the remaining two were like those of the OF monkeys. There were, then, no marked group differences in preferences for food and nonfood items. However, clear group differences did appear in the selection of nonfood items. As a group, the sham monkeys selected nonfood items on the average only 10 times in the 45 trials. In contrast, the OF monkeys selected the nonfood items 30 times in the 45 trials, and this group difference in the number of times nonfood items were selected is significant ($t = 4.92$; $df = 6$; $p < .01$).

These results further support the findings of the home cage dietary behavior tests (Experiment 1) as well as those of Ursin, Rosvold, and Vest (1969) which indicate that OF ablation produces

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[1] The preference behavior data from the WGTA experiment have been reported in an earlier publication (Butter, McDonald, & Snyder, 1969).

Table 19

Mean Order of Choice of Food and Nonfood Items and Frequency of Selection (Parentheses)

| | Sham Ss | | | | | Orbital Frontal Ss | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Abba | Eban | Ibid | Zeus | Sham Group Mean | Jim | Willie | Walt | Ben | OF Group Mean |
| **Food** | | | | | | | | | | |
| Apple | 2.1 (44) | 1.9 (42) | 2.1 (42) | 2.1 (45) | 2.0 (43.3) | 2.7 (45) | 2.0 (45) | 2.3 (45) | 2.2 (45) | 2.3 (45.0) |
| Banana | 1.9 (45) | 1.9 (34) | 1.8 (45) | 2.1 (45) | 1.9 (42.3) | 2.4 (43) | 2.0 (45) | 2.0 (45) | 1.9 (45) | 2.1 (44.5) |
| D&G Whole-Diet Pellet | 3.5 (17) | 2.1 (44) | 2.0 (42) | 1.8 (45) | 2.4 (37.0) | 4.1 (39) | 2.8 (35) | 2.8 (45) | 3.1 (45) | 3.2 (41.0) |
| **Nonfood** | | | | | | | | | | |
| Cork | 2.9 (18) | 3.2 (20) | 3.6 (7) | 4.0 (10) | 3.4 (13.8) | 2.3 (43) | 3.3 (33) | 3.6 (41) | 3.2 (28) | 3.1 (36.3) |
| Gelatin Capsule | 3.0 (30) | 3.8 (12) | 4.0 (3) | 3.8 (4) | 3.7 (12.3) | 3.7 (41) | 4.4 (22) | 4.6 (36) | 4.1 (41) | 4.2 (35.0) |
| Bolt | 4.5 (2) | 3.3 (10) | 4.7 (2) | 4.8 (3) | 4.3 (4.2) | 4.9 (28) | 4.8 (16) | 4.8 (26) | 5.4 (20) | 5.0 (22.5) |

altered dietary behavior and heightened oral tendencies much like those following amygdalectomy. Moreover, in the present experiment these changes were expressed as increased selection (number of times chosen) but not by increased preference (order of choice) for nonfood items. Thus, it is difficult to explain this heightened selection simply as a unitary failure to discriminate between food and nonfood, a concept which previously was suggested to account for the oral changes in amygdalectomized monkeys (Weiskrantz, 1956). Nevertheless, the strong tendency to examine objects orally, a well established component of the Klüver-Bucy Syndrome (bilateral amygdalectomy), is clearly present in the OF monkey also such that manipulative behaviors tend to be expressed as hyperphagic tendencies.

## Experiment 3

## Alterations in Reinforcement Values

The third experiment explored the effects of OF damage in an instrumental situation in which the incentive was switched from positively reinforcing to one of presumed neutral reward value in order to determine if enhanced selection of a non-nutritive item is accompanied by increased incentive value for that item.

### Procedure

At the conclusion of preference testing in the WGTA (Experiment 2), the sham and OF Ss were taught to displace a three in.$^2$ metal cover from a single, centered well in another 21 in. wide test board in order to retrieve a whole-diet pellet.

Following the shaping procedure, each S received 15 reinforced trials per day for five days. On each trial the opaque screen interposed

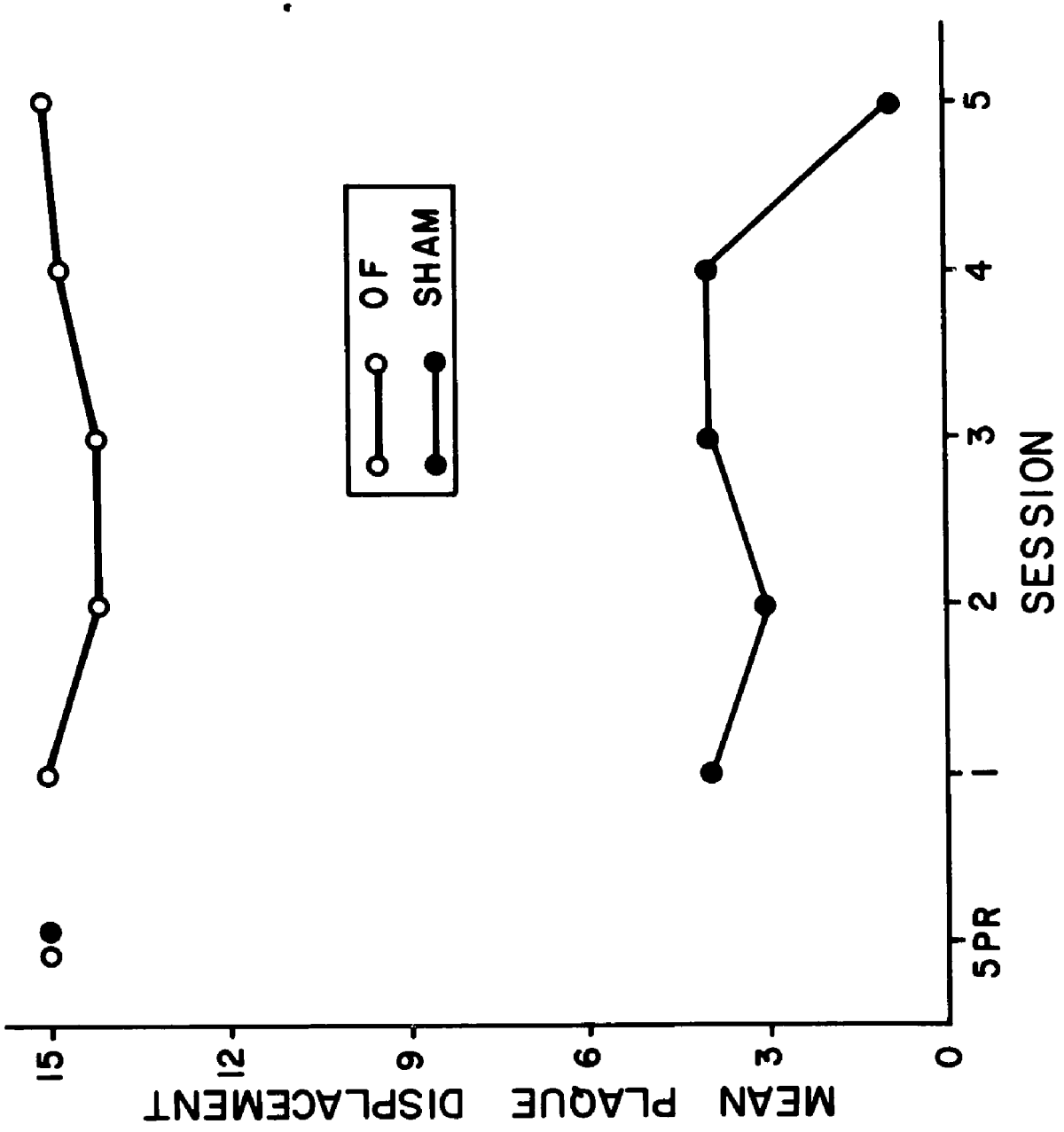
between the cage and test board was raised and kept open 1 min. Irrespective of the S's response latency, which was measured to the nearest second with a manual stopwatch. On the sixth session the food pellets were replaced by empty, gelatin drug capsules, the same as those used in preference testing (Experiments 1 and 2), which were used as the sole reward for the following five sessions. The procedures for the food-reinforcement and the capsule-reinforcement sessions were identical.

Results and Discussion

All Ss quickly learned to retrieve the pellet by pushing the metal plaque aside and performed consistently through the five pellet-reinforced sessions. As indicated in Figure 14, all Ss were consistently responding on all fifteen trials through the fifth pellet-reinforced session. On the first capsule-reinforced session, however, the sham operated Ss showed a reduction in frequency of plaque displacement which persisted through the following five sessions. In contrast, the OF monkeys maintained a high level of responding with no decrement in response latency during all tests with the capsule reinforcement. The difference between the two groups in frequency of plaque displacement was significant ($F = 17.42$, $df = 1/6$; $p < .01$).

It might be thought that the continued retrieval of capsules was due to either increased appetite (Klüver, 1958) or resistance to instrumental extinction seen following OF lesion (Butter, Mishkin, & Rosvold, 1963). However, the OF monkeys did not appear to work more quickly for the food pellets since their response latencies were not different from the sham Ss; nor does OF ablation increase rates of

Fig. 14 Mean number of plaque displacements of the OF and sham operated groups in the final, food pellet-reinforced session (5 PR) and in the subsequent five, gelatin capsule-reinforced sessions.


MEAN PLAQUE DISPLACEMENT
15
12
9
6
3
0
5PR
1
2
3
4
5
SESSION
OF
SHAM

instrumental responding for food (Butter, et al., 1963). Furthermore, a simple extinction deficit, although present, does not explain the OF monkeys' enhanced orality, as they ingested each of the capsules they retrieved. The present experiments (Butter, et al., 1969) and those of Ursin et al., (1969) demonstrate that OF monkeys, as well as amygdalectomized monkeys, select and eat normally rejected foods but still display discriminative, reliably ordered preferences throughout.

The continued instrumental responding for a non-nutritive, tasteless, but edible object might indicate that the OF monkeys, unlike the sham operated monkeys, found the ingestion of a nonfood item rewarding. Because preference behavior was dissociated from selection when several items were available (Experiment 2), the OF monkeys might no longer distinguish reinforcing from normally non-reinforcing stimuli. In other words, any object which can be orally explored and/or ingested might be reinforcing to an OF (or amygdalectomized) monkey (which does not preclude preference ordering when a choice is available.) This interpretation assumes that all mouthable objects take on positively reinforcing properties which can be relatively strong or weak depending on such factors as palatability, texture, etc.. Qualities such as palatability do seem to play some role in preference ordering since in the OF animals' selection of nonfood items (Experiment 2), cork was preferred to the capsule and the capsule to the bolt. This dissociation between preference behavior, on the one hand, and enhanced selection and, possibly, enhanced reinforcement value of a nonfood item on the other, implies that OF lesions affect appetitive motivational-reward mechanisms but not perceptual-preference behavior.

These results support the evidence that the hypothalamic appetitive mechanisms are normally under inhibitory control by the orbital frontal cortex (Brutkowski, 1964, 1965) and the amygdala (Pribram & Bagshaw, 1953), and that destruction of portions of this cortico-limbic system may cause a release of suppression of these diencephalic centers. It is not clear whether the perceptual-preference component would undergo similar changes with damage elsewhere in the cortico-limbic system or if these behaviors are centered elsewhere in the forebrain. It is clear, however, that the OF cortex is functionally and structurally associated with the amygdala (Nauta, 1962; Pribram & MacLean, 1953), both contributing importantly to limbic integration of behavior.

## Chapter VII

## DISCUSSION AND SPECULATIONS

The foregoing experiments have shown that OF ablations produce profound changes in the social and emotional behavior of rhesus monkeys. Following surgery, OF monkeys were observed to resume their role as the aggressive leaders in a social colony only to abruptly fall to the bottom of the hierarchy thereafter showing submission to the peers they had previously dominated (Chapter III). Total OF ablation abolished aggression directed toward humans (Chapter IV), and there was a correspondence between the onset of stereotyped, forced pacing in both home cage and social colony and the reduction of aggression. OF ablation disrupted retention of a conditioned avoidance response but retarded subsequent extinction of the same response (Chapter V). Compared to the sham operated controls, OF monkeys were more likely to accept and ingest typically rejected food and nonfood items. The OF Ss showed increased reinforcement value of a nonfood item, heightened orality, as well as increased resistance to extinction in an instrumental situation (Chapter VI). The concern of this chapter is to determine if there is any one hypothesis that accounts for these changes.

The behavioral alterations observed after OF ablations cannot be fully accounted for by the reversion hypothesis which states that OF lesions impair the suppression of previously dominant responses to which the Ss revert. The aversive and aggressive reactions to humans (Chapter IV) which changed after surgery were not those which

were initially dominant. The OF Ss also were not observed to revert to emotional behaviors which characterized them before they had acquired a conditioned avoidance response, although the well learned CR did decline postoperatively followed by increased resistance to extinction, as predicted by the reversion hypothesis (Chapter V). The relationship of the reversion hypothesis to the social behavior changes (Chapter III) and to the changes in orality, dietary, and food preference behavior (Chapter VI) cannot be adequately tested in these experiments.

The hypothesis that OF lesions cause loss of inhibitory control over hypothalamic drive centers so that the postoperative behaviors are the result of the "release" or "disinhibition" of these diencephalic centers (Brutkowski, 1965) can, like the reversion hypothesis, account for only some of these results. Consistent with the drive disinhibition view, the OF monkeys exhibited heightened orality and heightened reinforcement value of a nonfood item (Chapter VI), and they maintained their alpha positions in the colony for up to five months through overt aggression directed at their subordinates (Chapter III). With respect to aggression, however, the OF monkeys were observed to under—rather than overreact to humans (Chapter IV) and inescapable pain (Chapter V). Of course, there was evidence of hyperreactivity following OF ablation (see Chapters I and II) and, in the conditioned aversion experiment, it might be argued that the proper execution of the CR is, in fact, inconsistent with greatly heightened excitation even though no overt signs of such hyperemotionality were observed. Since neither the reversion nor the drive disinhibition hypotheses are consistent with all the results of these experiments, it might be

worthwhile to turn to other lines of evidence leading to an alternative explanation. The remainder of this chapter is an attempt to review these suggestions and to develop an hypothesis better able to incorporate these findings.

Recognizing the variable influence of the environmental milieu on reactivity following amygdaloid lesions, Rosvold, Mirsky, and Pribram (1954) concluded that, ..."unless the effect of an operation on behavior is studied in a variety of situations, the findings are at best of limited generalizability." More specifically, the differences in emotional reactions in social and instrumental tasks observed in OF monkeys by Butter, Mishkin, and Mirsky (1968) might be reconciled, they suggested, if ..."frontal damage...(alters) emotionality in opposite directions depending on the testing situation."

In agreement with Rosvold et al. (1954) and Butter et al. (1968, 1970) the present experiments indicate that the environment has a great deal to do with the kind and degree of change in emotional behavior after OF ablation, and that OF damage does not induce any overall losses in the S's capacity to behave emotionally. For example, OF monkeys were observed to engage in overt aggression with monkeys in adjacent cages (Chapter II) and postoperatively they were able to at least temporarily preserve their dominant status in the social colony (Chapter III), but they no longer displayed aggression toward humans (Chapter IV). In other words, aggression in OF Ss varied with the situation. We postulate that the greater the degree of threat and/or stress in the situation, the greater the deficit in aggression following OF removal. Thus, we find the greatest reduction in aggression when OF monkeys were confronted by humans (Chapter IV) possibly

because human approach had often led to handling, restraint, or other noxious events and since O continued to stare (threaten) no matter how the monkey reacted. In the inescapable shock situation (Chapter V) there was no object to aggress (except the submissive female and the S's own reflection) and the emotional reactions to shock quickly habituated preoperatively in both OF and sham monkeys. The least stressful of these situations was the social colony (Chapter III) because the test Ss were dominant over the other colony members preoperatively and, on postoperative introduction, continued to receive submission from their subordinates.

Since the OF monkeys initially assumed postoperative social dominance, the question remains why the delayed fall in status with a variable latency of 11 days to nearly 5 months? And what is the relationship between the level of threat or stress and the latency until the OF monkey's fall in dominance? As indicated in Tables 11-13 and Figure 2 (Chapter III), the OF monkeys did not receive equally intense challenges from Dax immediately after postoperative introduction into the colony. That is, the OF monkey (Walt) who fell first from social dominance to total submission was attacked more frequently and for a longer time by the displaced alpha male. Furthermore, Ben and Willie's loss of dominance at 4 and 6 months, respectively, was also coincidental with a rise in aggression directed at them from Dax. In summary, there does seem to be a relationship between level of environmental stress and the time at which the fall in social dominance occurs.

An examination of postoperative behavior in the colony suggests an interplay of events which, in animals unable to appropriately react to stress, might produce the loss of social status reported here.

We speculate that after the OF monkeys' postoperative introduction, they remain dominant as long as their peers continue to generally submit and not often challenge their leadership. As the peers, especially the displaced alpha, begin to mildly test the dominant status of the OF monkeys, behavior which is a regular part of macaque social life (see Introduction, Chapter III), they find the usual, aggressive reaffirmation of hierarchical position reduced in kind, frequency, or intensity of response. When the subordinate animals sense such a reduction in the alpha male's aggressive behavior, field-study data suggest that the tests of the OF Ss' dominance become more and more bold until they are directly challenged for leadership and lose. Other evidence (see Chapter III) suggests that the observed combination of decreased aggressiveness plus inappropriate or lack of properly signalled submission and, perhaps, an inability to perceive threat signals on the part of the OF monkeys led to repeated, severe attacks from the matrix animals which further reinforced the OF monkeys' position at the bottom of the hierarchy.

The inability of the OF monkeys to react appropriately to stress and/or threat leading to the delayed loss of social dominance and aggression (in some situations) is probably not due to delayed neurological changes. While many of the effects of OF ablation appear immediately after surgery (see Chapter II) and other emotional changes are greatly delayed, it is not likely that one or more neural systems are simultaneously undergoing fast and slow degenerative changes. Rather, the destruction of OF cortex seems to immediately and directly impair the monkey's ability to act aggressively, especially in highly threatening situations.

Many of the parallels between the behavior of OF monkeys and the behavior of monkeys suffering limbic (amygdaloid) damage have been reviewed in Chapters I and VI. After amygdalectomy, monkeys have been characterized as socially indifferent and unable to "foresee and avoid dangerous confrontations" (Dicks, Myers, & Kling, 1969). Such maladaptive social behavior causes the operated Ss to be ..."attacked and banished as would-be strangers from other groups, perhaps because of inappropriate behavior and responses to approach" (Dicks et al., 1969). It is clear that this description suits the OF monkey who has fallen to the bottom of the dominance hierarchy equally well; the major difference being that after amygdalectomy the changes are immediate while after OF ablation the change is delayed and seems to occur only after socially-induced stress becomes high. Plotnik (1968) has suggested a limbic (amygdaloid) threshold system which regulates the animal's sensitivity to social and environmental stimuli. We further suggest that this amygdaloid threshold mechanism (ATM) might act directly on the autonomic centers within the hypothalamus suppressing or desensitizing the central arousal network or, perhaps, peripherally within the sensory systems. The evidence for functional and structural associations between OF cortex and the amygdala (e.g., see Discussion, Chapter VI) suggests that OF cortex might also be involved in this threshold setting mechanism. We postulate that the ATM is modulated by inhibitory input from OF cortex and that the level of OF inhibition is regulated by the intensity of external and internal, cortically mediated, sensory stimulation. Thus, OF cortex indirectly elevates the threshold for the hypothalamic release of autonomic activation by desensitizing or suppressing the ATM (perhaps by way of the dorsomedial

nucleus of the thalamus).

While the selection and coordination of emotional response patterns more likely occurs within limbic and cortical structures, the coordination of lower-order, individual motor components (i.e., integration) and the addition of autonomic components (i.e., "coloring") of emotional behavior are accomplished within the hypothalamus. It is this latter aspect of emotionality which may be triggered by the ATM.

The negative feedback loop thus formed by ascending excitation into limbic structures and cortex giving rise to heightened descending inhibition from OF cortex to the ATM and into hypothalamus provides a functional network to avoid nonflexible, inappropriate, emotional overreaction in the presence of highly threatening stimuli. This interpolation of an ATM allows a re-evaluation of Brutkowski's (1965) "drive disinhibition" theory concordant with the results of these experiments.

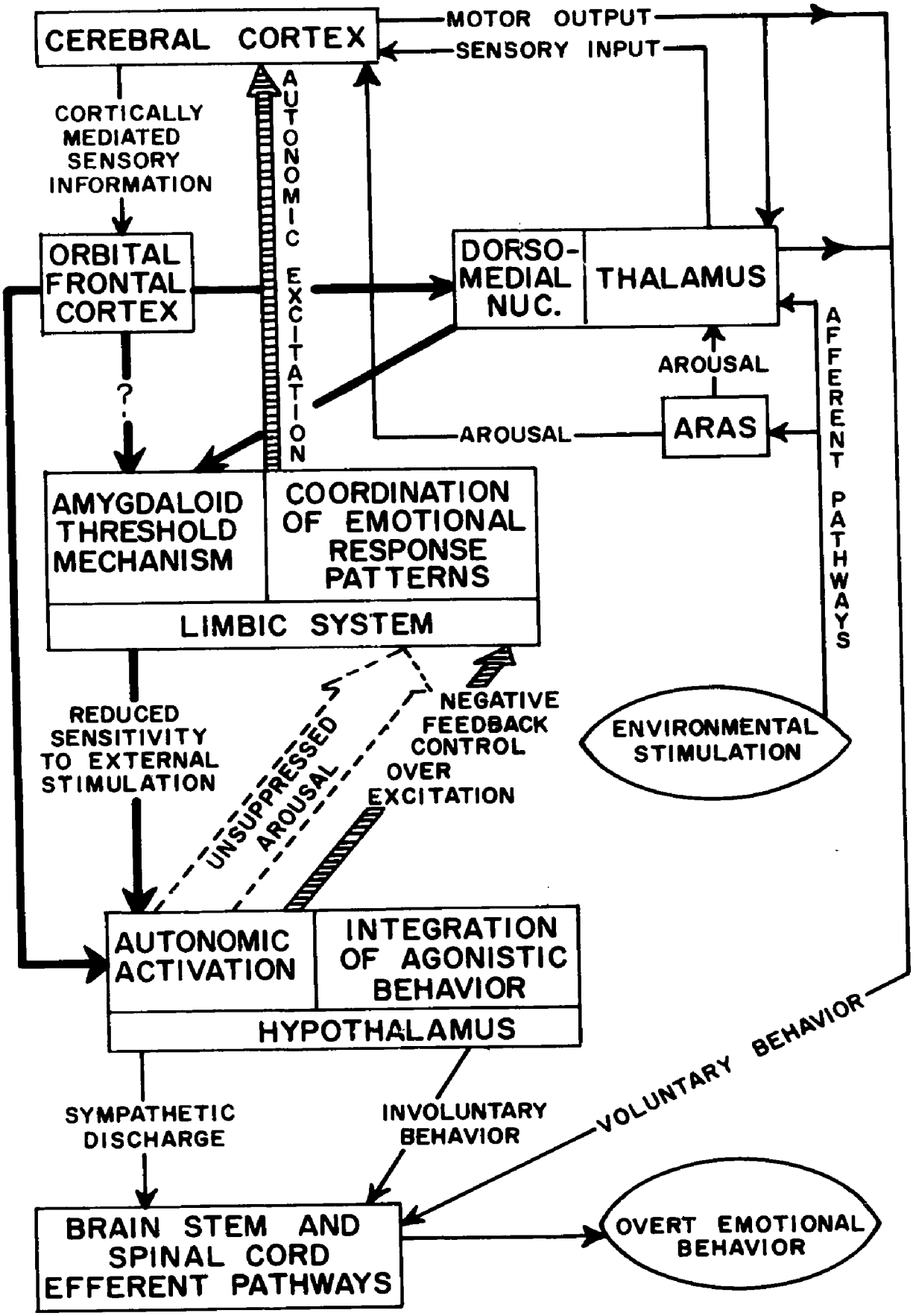
The ablation of OF cortex is assumed to remove the inhibitory influence over the ATM which allows the autonomic activity threshold to fall (become more sensitive to external stimulation) and no longer be adjusted. One would expect environmental stress to highly arouse an OF monkey as the limbic system receives unsuppressed autonomic input from hypothalamic centers. Above an adaptive level, such arousal might interfere with the cortico-limbic coordination of emotional behaviors (e.g., loss of aggression). With such a defect, the S might be so highly aroused that even simply pacing is interfered with so that he appears indifferent or unable to respond when attacked (see Chapter III). To restate it simply, the stress hypothesis assumes that (in OF Ss) the greater the degree of external threat,

the greater the uninhibited internal arousal, and the greater the disruption in emotional behavior. Figure 15 is a diagram of the stress hypothesis of cortico-limbic control of emotional behavior and is consistent with previously demonstrated anatomical connections.

In review, the assumption that OF cortex indirectly regulates ascending hypothalamic excitation by modulating the ATM suggests that destruction of OF cortex might desensitize the ATM and lower the threshold for autonomic arousal. Thus, an ascending influx of excitation, evoked by external threat, might block the neural integration of agonistic behavior rendering the S incapable of responding normally to stress.

Histological analyses of these and previous OF lesions (Butter et al., 1970) have suggested the posteromedial area as the locus for the emotional alterations described here. Of prime importance to the situationally-dependent, stress hypothesis is the evidence that posteromedial OF cortex, amygdala, medial subdivision of the dorsomedial thalamic nucleus and hypothalamus are anatomically interconnected (Nauta, 1962). Of the four OF Ss, Jim alone retained his alpha position in the colony through continued aggression (Chapter III), regained his aggression toward humans (Chapter IV) and showed no postoperative depression of the classically conditioned avoidance response (Chapter V). And Jim alone was spared damage to the medial half of posteromedial OF cortex, although he sustained the greatest overall OF lesion (Chapter II), indicating that the critical focus of the cortical mechanism controlling aggressive behavior may be some region within posteromedial OF cortex. Since apparently many structures are involved in the control of emotional behavior, the

Fig. 15 Stress hypothesis of cortico-limbic regulation of emotional behavior. Ablation of OF cortex removes the suppressive control over the amygdaloid threshold mechanism which chronically lowers the threshold for autonomic activation. Thereafter, in the presence of stressful stimuli, unchecked excitation interferes with limbic organization of emotional behavior. Descending inhibitory pathways: solid, heavy arrows; Ascending excitatory autonomic discharge: open, striped arrows; Stress-induced autonomic discharge after OF ablation: open, dashed arrow. All connections are consistent with available anatomical evidence.


CEREBRAL CORTEX
MOTOR OUTPUT
SENSORY INPUT
CORTICALLY MEDIATED SENSORY INFORMATION
AUTONOMIC EXCITATION
ORBITAL FRONTAL CORTEX
DORSO-MEDIAL NUC.
THALAMUS
AROUSAL
ARAS
AFFERENT PATHWAYS
?
AMYGDALOID THRESHOLD MECHANISM
COORDINATION OF EMOTIONAL RESPONSE PATTERNS
LIMBIC SYSTEM
REDUCED SENSITIVITY TO EXTERNAL STIMULATION
UNSUPPRESSED AROUSAL
NEGATIVE FEEDBACK CONTROL OVER EXCITATION
ENVIRONMENTAL STIMULATION
AUTONOMIC ACTIVATION
INTEGRATION OF AGONISTIC BEHAVIOR
HYPOTHALAMUS
SYMPATHETIC DISCHARGE
INVOLUNTARY BEHAVIOR
VOLUNTARY BEHAVIOR
BRAIN STEM AND SPINAL CORD EFFERENT PATHWAYS
OVERT EMOTIONAL BEHAVIOR

contribution of each might be better understood by directly comparing the effects of selective destruction of some of these structures, such as those of the orbitofronto-thalamo-amygdalo-hypothalamic system. It would certainly be extremely interesting to determine the functional relationship between posteromedial OF cortex and the basolateral nuclei of the amygdala which were previously implicated as being critical for changes in conspecific aggression following amygdalectomy (Rosvold, Mirsky, & Pribram, 1954).

Appendix A

Home Cage Dietary Behavior

| Test Items | Sham Ss | | | | Orbital Frontal Ss | | | |
|---|---|---|---|---|---|---|---|---|
| | Abba | Eban | Ibid | Zeus | Jim | Willie | Walt | Ben |
| Nutritive | | | | | | | | |
| Hamburger | IR-2/3<br>OER-1/3 | IR-3/3 | IR-3/3 | IR-3/3 | IR-2/3<br>OER-1/3 | OER-2/3<br>3OR-1/3 | II-3/3 | II-3/3 |
| Tuna | WNP-2/3<br>IR-1/3 | IR-3/3 | IR-3/3 | WNP-1/3<br>IR-2/3 | II-2/3<br>3OR-1/3 | IR-3/3 | II-3/3 | OER-1/3<br>3OR-2/3 |
| Apple | II-6/6 | II-6/6 | II-6/6 | II-6/6 | II-6/6 | II-6/6 | II-6/6 | II-6/6 |
| Cabbage | II-2/2 | II-2/2 | II-2/2 | II-2/2 | II-2/2 | II-2/2 | II-2/2 | II-2/2 |
| Orange | II-4/4 | OEI-4/4 | II-4/4 | II-4/4 | II-4/4 | II-4/4 | II-4/4 | II-4/4 |
| D&G Whole-Diet Pellet | II-6/6 | II-6/6 | II-6/6 | II-6/6 | OEI-2/6<br>II-4/6 | II-6/6 | II-6/6 | II-6/6 |
| Bread | 3OR-2/4<br>OER-2/4 | OEI-4/4 | OEI-1/4<br>OER-3/4 | OEI-1/4<br>OER-3/4 | II-4/4 | II-4/4 | II-4/4 | II-4/4 |
| Non-Nutritive | | | | | | | | |
| Paper | II-1/6<br>OER-4/6<br>IR-1/6 | II-1/6<br>OER-4/6<br>3OR-1/6 | II-1/6<br>OEI-5/6 | II-1/6<br>OER-5/6 | II-6/6 | II-3/6<br>3OR-1/6<br>OEI-2/6 | II-6/6 | OER-6/6 |
| Cork | II-1/4<br>OEI-3/4 | II-1/4<br>OEI-3/4 | II-2/4<br>OEI-2/4 | II-1/4<br>OEI-3/4 | II-3/4<br>OEI-1/4 | II-4/4 | II-4/4 | 3OR-2/4<br>IR-2/4 |
| Gelfoam | II-2/3<br>OEI-2/3 | OEI-3/3 | II-1/3<br>OEI-2/3 | II-2/3<br>OEI-1/3 | II-1/3<br>OEI-2/3 | II-3/3 | II-3/3 | II-3/3 |
| Gelatin Capsule | II-3/3 | II-3/3 | II-3/3 | OEI-3/3 | II-3/3 | II-3/3 | II-3/3 | II-3/3 |

Response Key

WNP = Would not pick up
IR = Immediate rejection
OER = Oral exploration followed by rejection
3OR = Hold in mouth > 30 seconds followed by rejection
OEI = Oral exploration followed by ingestion
II = Immediate ingestion

The fractions following each of the response codes indicate the number of times out of total presentations (maximum = 6) that each reaction occurred.

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