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ALTERATIONS IN AVERSIVE AND AGGRESSIVE BEHAVIORS FOLLOWING ORBITAL FRONTAL LESIONS IN RHESUS MONKEYS

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Abstract. We utilized the methods of comparative psychology and of ethology to assess the effects of frontal lesions on species-specific aversive and aggressive behaviors in rhesus monkeys. Removal of orbital frontal (OF) cortex enhanced aversive reactions and reduced aggressive reactions in several threatening situations, including a social colony. The deficit in aggresion was not due to enhanced aversion or to locomotor hyperactivity. Nor did the OF monkeys lose the capacity to execute aggressive reactions. Rather, their degree of deficit seemed to vary with the degree of threat in the test situation. Moreover, these emotional alterations are produced by lesions restricted to the posteromedial portion of OF cortex, which is closely associated with limbic structures, as well as by lesions of the dorsomedial nucleus, with which this portion of OF cortex is interconnected. While lesioning either of these structures reduced aggression and enhanced aversion, amygdalectomy reduced both aggression and aversion. The view that monkeys with OF lesions are overaroused by threatening situations was not supported by analysis of autonomic responses following OF lesions. The emotional alterations produced by OF lesions may be due to the disturbance of stress mechanisms which prepare the organism for reacting appropriately to highly threatening situations.

INTRODUCTION

The experiments reported in this paper originated in observations of monkeys undergoing conditioning and extinction of instrumental responses (Butter et al. 1963). In that experiment we noted that following lesions of orbital frontal (OF) cortex, rhesus monkeys appeared to show alterations in their emotional behavior, although on the basis of our casual and unsystematic observations, we were uncertain and in disagreement about the nature of these changes. To some observers it appeared that the OF monkeys were hyporeactive emotionally; others had the opposite impression, i.e., the OF monkeys appeared emotionally hyperreactive to environmental stimulation. Apparently, this disagreement is not uncommon, for a perusal of the literature disclosed that other investigators have likewise disagreed in their evaluations of emotional alterations following frontal lobe lesions in animals; instances of increased and of decreased emotional reactivity, usually accompanied by changes in general activity, have been reported (*see* Kennard et al. 1941, Brutkowski 1965). Because of these inconsistencies and the scarcity of systematic observations, we undertook a series of experiments to determine the extent and the nature of the emotional alterations which follow frontal lobe lesions in monkeys.

Conceptual and methodological considerations

Before describing our experimental findings, it is appropriate to consider some conceptual and methodological issues which arise in the experimental analysis of emotion and describe our position with regard to these issues.

What is emotion and how can one best evaluate and measure it in animals? Various answers have been proposed to these questions; indeed, it almost appears that each writer who has considered these problems has his own set of answers. In general, however, two contrasting approaches to emotion are currently used by investigators of animal behavior. According to the first approach, emotion is viewed as having primarily a negative influence on adaptive behavior; that is, emotional reactions, involving skeletal and autonomic components, are thought of as disorganizing or disrupting ongoing activities (Estes and Skinner 1941, Brady 1967). In contrast, the second approach considers emotion primarily as a positive factor in adaptive behavior. According to this latter view, emotion is thought of as patterns of overt and internal reactions by means of which the organism copes with and adapts to its environment, and especially those situations involving threats by predators and by conspecifics, as well as situations in which sexual and maternal drives operate. Although neurophysiologists and experimental psychologists frequently pay lip-service to this latter view of emotions, it is primarily ethologists, anthropologists and comparative psychologists who have consistently put these views into practice by using techniques of detailed behavioral analysis in the field.

Each of these conceptual approaches to the problem of emotion has a corresponding methodological approach. Not surprisingly, those who view emotion primarily as a disruptor of behavior use aversive (and artificial) stimuli, typically electric shock, almost exclusively. The disrupting effect of aversive stimuli on behavior is usually evaluated by the extent to which these stimuli suppress instrumental responding, or, less frequently, consummatory reactions. On the other hand, those who view emotions as particular patterns of adaptive reactions to environmental demands tend to use a much greater variety of stimuli and situations to elicit emotional behavior; these are frequently similar or identical to those encountered by the organism in the feral environment and typically have some functional significance for the animal. A greater variety of response measures is also used in these latter studies in contrast to those which follow the first approach; these include species-specific patterns of behavior termed agonistic (aversive and aggressive reactions) as well as maternal, sexual, play and other social behaviors. These responses, in contrast to those employed in the context of the first approach, provide direct measures of emotional behavior. Thus, while the first approach provides highly quantified data generated within tightly controlled situations, the second approach provides a much richer variety of behaviors which are part of the animal's adaptive repertoire and which thus have "ethological validity". Because of these advantages, we have chosen to analyze emotional behavior in monkeys within the conceptual framework and by the methods of the "functionally adaptive" view of emotions. It is assumed that this approach will eventually lead to a more valid interpretation of the adaptive significance of frontal cortex with regard to emotional behavior than would be possible using other methods.

In the studies reported here we have limited analysis of emotions to aversive and aggressive behaviors. While this restriction inevitably limits the generality of our conclusions, there is no doubt that these behavior patterns are part of the rhesus monkey's natural repertoire of behaviors, for they have been observed in field studies as well as in the laboratory, and various investigators agree that these behaviors play important roles in territorial defense, sexual behavior and especially in defining social hierarchies (Carpenter 1942, Chance 1956, Altmann 1962, Varley and Symmes 1966, Sade 1967). Furthermore, these reactions can be consistently elicited from rhesus monkeys by various events in the laboratory.

Aversive and aggressive behaviors, then, would seem to provide valid and reliable measures of emotionality in rhesus monkeys. Finally, we must consider the particular reactions that we observed and recorded and their validity as measures of aggression and aversion. The reactions we observed are relatively stereotyped patterns that have been described in numerous prior studies (Altmann 1962, Bernstein 1964, Kaufmann 1967) and are listed in Table I. Some of them have clear face validity: for example, retreating from an object or averting the head and eyes from an object are responses which all observers unhesitatingly classify as aversion; likewise lunging at or biting an object are consistently judged as aggressive reactions. In addition, there are a number of other behaviors, which we, along with other investigators, have classified as aggressive or aversive because they are highly correlated with those having face validity and are likewise seen in social interactions and territorial defense. For example, grimacing (in which the lips are drawn tightly across the teeth) very often accompanies bodily aversion and submission in social situations but is not seen with aggressive reactions, and so it is classified as an aversive reaction. Conversely, a response such as mouth opening (in which the lower jaw drops) very often accompanies patently threatening or aggressive responses in social situations, and so it is classified as an aggressive reaction. Stereotyped responses as grimacing and mouth opening are apparently gestures which have signal value and are used as "displays" in social situations (Hinde and Rowell 1962, Andrew 1964).

TABLE I

Aversive, aggressive and other reactions toward human observers, doll and model snake[a]

Aversion	Aggression
Head and eye aversion (*1*)	Ears flattened (*1*)
Arm defense (*1*)	Frown (*1*)
Leg defense (*1*)	Mouth open (*1*)
Grimace (*1*)	Head lunge (*1*)
Lick lips (*1*)	Arm thrust (*1*)
Chew (*1*)	Bark (*1*)
Flinch (2)	Shake cage (*2*)
Cower (*2*)	Aggress (reflected image) (*2*)
Body turn (*2*)	
Climb (*3*)	Attack (*3*)
Jump (*3*)	Bite (*3*)
Move away (*3*)	
Present rear (*3*)	

a Numbers in parenthesis refer to weights assigned to each kind of reaction in determining overall aversion and aggression scores.

b Observed only toward doll and model snake.

Accompanying each of the reactions listed in Table I is a number, which refers to the weight assigned to each kind of response for purposes of data analysis. According to this weighting system, a weight of *1* is assigned to facial gestures or movements involving primarily one portion of the body; a weight of *2* is assigned to movements involving the whole body without locomotion, and a weight of *3* to movements which involve displacement of the body in space. While the choice of these particular numbers is completely arbitrary, differentially weighting responses takes account of the fact that short duration, rapidly executed movements, such as mouth opening, are likely to be more frequently executed than is a response such as attacking. Secondly, it seems intuitively reasonable that a response such as attacking or biting is a more intense display of aggression than is a facial threat gesture. Thus, while the particular choice of numbers is arbitrary, we feel that the use of a weighting system of this kind provides a more valid indicator of total aggressive or aversive behavior than would be provided by unweighted frequencies.

Emotional reactions to humans in monkeys with orbital or dorsolateral frontal lesions

In the first experiment, we investigated aggressive and aversive reactions of rhesus monkeys with frontal or control lesions to human observes (Butter et al. 1968). We chose humans as the emotion-provoking object in this initial study for it is well known a human readily elicits emotional reactions from a rhesus monkey, especially when he stares at the monkey's eyes. The test we used was a simple and direct one, originally described by Mason, Green and Posepanko (1960). The observer (*O*) approaches the monkey in its living cage and standing just out of arm's reach, stares impassively at the monkey's eyes when they are turned toward him for 20 sec. The *O* then records the frequency and order of occurrence of behaviors observed. We compared the emotional reactions of monkeys with orbital frontal (OF), dorsolateral frontal (DLF) and inferotemporal (IT) lesions with those of unoperated controls. Figure 1 shows examples of typical OF and DLF lesions produced in the NIH laboratory where this study was conducted. Note that there is little overlap between the OF and DLF lesions and that the OF lesion involves ablation of all cortex on the orbital surface, extending under, but not invading the temporal lobes.

Figure 2 shows mean weighted frequencies of aggressive and aversive reactions (listed in Table I) to each of three *Os* each of whom observed the monkeys' reactions on three separate occasions. The *Os*

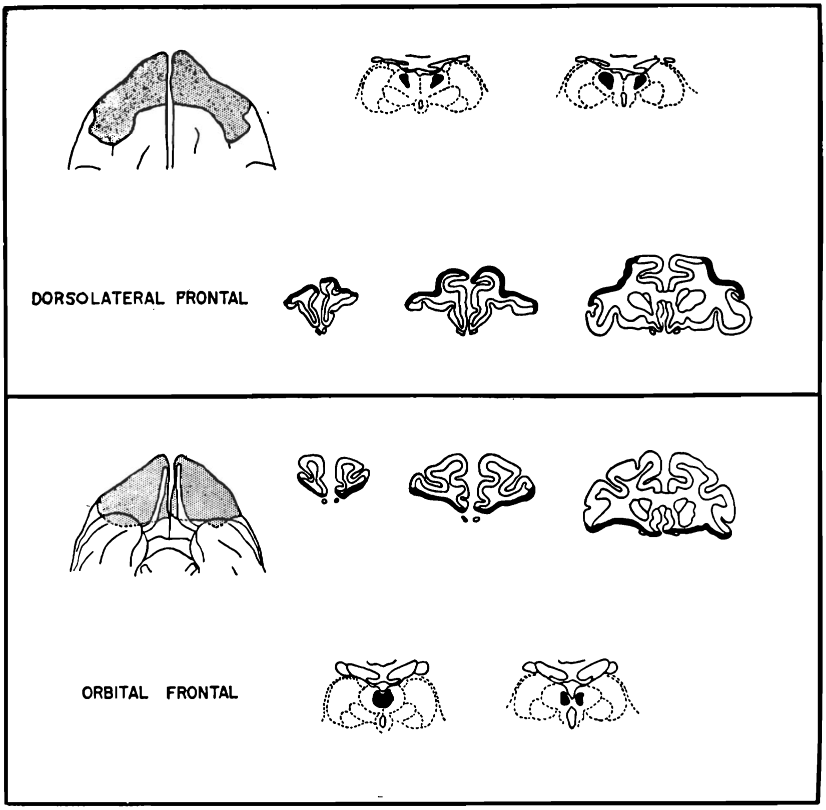


Fig. 1. Reconstructions of a dorsolateral frontal lesion (top) from a dorsal view and an orbital frontal lesion (bottom) from a ventral view. Cross sections through the lesions and through areas of the thalamus showing retrograde degeneration are also shown.

differed in their judgements of aggression; M.M.'s judgements of aggression were consistently higher than those of A.M., irrespective of group differences. In addition, each of the Os judged the OF monkeys to be the least frequently aggressive of all the groups, but statistical analyses failed to disclose any significant group differences. Furthermore, in the judgement of each of the three Os, the OF monkeys showed the most frequent aversive reactions of all groups, and this group difference was statistically significant for each of the three Os' judgements. This result did not depend on the weighting system used, for the same group differences were found when unweighted scores were used. Moreover, the OF monkeys consistently received the highest ratings of the four groups on all response measures of aversion with the exception of "running from side to side in back of the cage".

The outcome of this brief experiment was somewhat surprising, in

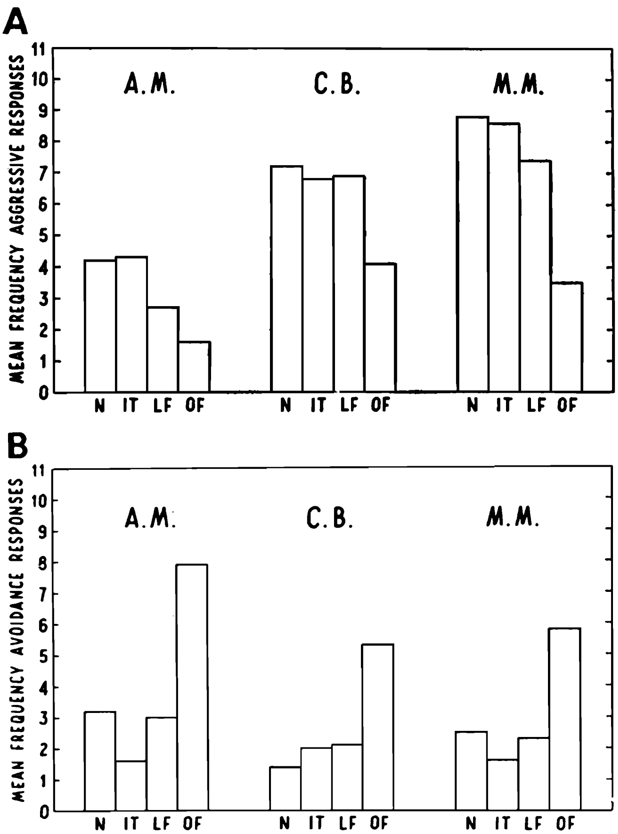


Fig. 2. Mean weighted frequencies of aggressive (*A*) and aversive (*B*) reactions to three observers (A.M., C.B., M.M.) of unoperated (N), inferotemporal (IT), dorsolateral frontal (LF) and orbital frontal (OF) monkeys.

that we did not anticipate heightened aversive reactions in the OF monkeys, especially since studies of conditioned avoidance suggested reduced fear following frontal lesions (Pribram and Weiskrantz 1957, Waterhouse 1957). For this reason, and since the observations made in this experiment were very limited, we decided it would be worthwhile to make more extensive observations, both of emotional reactions to humans over a longer period of time and of reactions to other stimuli before and after frontal or control lesions in monkeys.

Emotional reactions to humans and animal-like objects in monkeys with orbital frontal lesions

In this experiment (Butter et al. 1970) we judged reactions to human *O*s as in the previous study, except that each monkey was observed on at least 20 occasions before and after surgery, and again on five occasions 10 months following surgery. In addition, we observed and recorded the monkeys' emotional reactions to two objects — a large-eyed, animal-like doll and a model snake — both before and after surgery. In each test session these objects were moved every other minute for 10 sec, a procedure we found to be effective in eliciting emotional reactions. In these tests, *O*s sat behind a one-way screen and independently time-sampled the subject's reactions in 5 sec periods and recorded them in coded form. Following pre-operative testing, the monkeys were divided into two groups, which we attempted to match for emotional reactivity. One group received bilateral OF lesions, and the other received bilateral control lesions of inferotemporal or superior temporal cortex. During the post-operative recovery period and at regular intervals during the ensuing survival period we observed the general behavior of all the animals and evaluated their reactions to various stimuli.

For 5–10 days following surgery, the OF monkeys were depressed, lethargic, often appearing drowsy or somnolent, and were hyporeactive to environmental stimuli such as loud noises or being touched with a stick or handler's gloves. During this period, 3 of the 5 OF monkeys were also anorexic. These initial symptoms were not due to unspecific surgical trauma, for they were not seen in the control animals during the same period of time. Following this period of behavioral depression, the OF monkeys developed opposite abnormalities: they became hyperreactive to environmental stimulation and showed stereotyped pacing like that reported in prior studies of OF lesions (Ruch and Shenkin 1943, Livingston et al. 1948) when an observer approached or other novel stimulation occurred. Coincidental with the development of pacing, the OF monkeys began to show heightened orality including coprophagia; they would eagerly accept and mouth inedible objects. Most of the OF monkeys continued to show these hyperreactive and oral tendencies throughout the post-operative survival period of approximately 10 months. In contrast, the control animals did not show any of these tendencies post-operatively.

Turning to the analysis of emotional reactions to humans, the scores of one of the two *O*s are presented in Table II. Since there were no differences between the scores of monkeys with superior temporal and those with inferotemporal lesions, their scores are combined into a single control group (group T) in Table II. As seen in this Table, there was no effect of either OF or temporal neocortical surgery on aversive reactions, nor were particular kinds of aversive reactions altered by surgery. However, the OF monkeys, unlike the T monkeys, showed consistent and marked decrements in aggression, even 10 months following surgery. While the second *O*'s judgements of absolute frequencies of reactions differed from those of the first O, both of them agreed on the direction and magnitude of this decrement in aggression and the absence of other effects. In addition, both Os observed pacing to varying degrees in the OF monkeys throughout post-operative observations. However, there was no relationship between incidence of pacing and of aggressive reactions. In fact, the monkey that showed the greatest loss of aggression post-operatively showed the lowest incidence of pacing.

TABLE II

Mean weighted aversive and aggressive reactions of T (temporal) and OF (orbital frontal) monkeys to human observers on successive blocks of five observations

		Pre-operative				Post-operative					
		1	2	3	4	1	2	3	4	5	10 months post-op
Aversion	T	23.5	21.3	21.5	20.3	25.0	14.5	20.4	25.3	23.8	20.5
	OF	17.0	16.6	15.0	19.6	16.8	16.6	17.8	18.0	15.0	12.0
Aggression	T	36.3	36.0	35.3	38.5	41.0	38.5	35.5	34.0	47.5	51.8
	OF	28.2	33.8	50.0	47.2	1.2	3.0	2.2	6.2	3.6	3.4

Figure 3 shows averaged aversive and aggressive reactions of the monkeys to the doll. Since the two Os' judgements of frequencies of different reactions were highly correlated (correlation coefficients ranged from +0.87 to +0.96), their scores were averaged in this Figure. And since the monkeys with inferotemporal and superior temporal lesions were not different in these tests, as in other tests in this experiment, their scores are combined into a single T group. With regard to aversive reactions, both groups showed decrements over successive pre-operative sessions. Following surgery, the scores of the T group remained at the same level as in the third pre-operative session. The OF group, on the other hand, showed a marked rise on the first post-operative session, but not in subsequent sessions. This rise in aversion scores was not due to enhanced frequencies of all aversive reactions, but only three: head and eye aversion, body turning, and moving away from the doll, i.e., only those reactions which directly measure physical averting or withdrawal behaviors. The doll also evoked a variety of aggressive reactions, the scores for which are also shown in Fig. 3. Pre-operatively, both groups showed decrements in aggressive response frequencies from the first to the second session. Post-operatively, the T group maintained the same level of responding it had shown at the end of pre-operative training while the OF group's scores declined further and remained lower than those of the T group for the duration of post-operative testing, even at 10 months following surgery. This decrement in aggression, like the decrement in aggression toward humans, was due to lowered frequencies of all aggressive reactions, and not any particular ones. As in other test situations, the OF monkeys showed locomotor pacing in these tests. However, time spent pacing was not correlated with aggression scores. In one series of tests with the model snake, the OF monkeys likewise showed decrements in aggression compared with the T monkeys, but no alteration in aversive reactions.

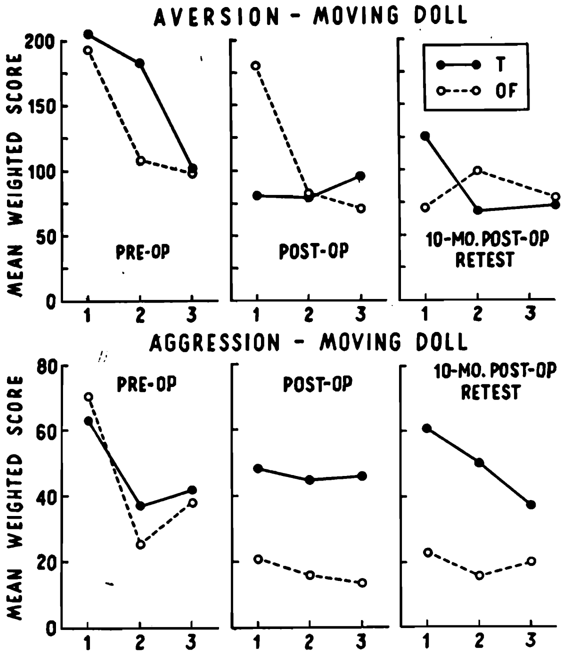


Fig. 3. Mean weighted frequencies of aversive and aggressive reactions to a doll by monkeys with temporal (T) and orbital frontal (OF) lesions.

Thus, the most consistent finding that emerged from this series of tests is a deficit in aggression seen in all three test situations. This deficit in aggression does not seem to be an indirect consequence of some other behavioral alteration; it could not have been due to enhanced aversion, since this effect appeared in only one test session. Nor was the decrement in aggression consistently related to locomotor activity. Moreover, a general lethargic or hyporeactive condition did not accompany these changes. In fact, at the time that testing occurred most of the OF monkeys were hyperreactive to environmental stimulation. While these findings suggest a direct and genuine effect of OF surgery on aggression, the deficit is apparently not due to a loss of the capacity for executing aggressive reactions. Rather, the degree of deficit in aggression varied with the test situation, appearing more severe in tests with humans as stimuli than in the other two tests. Thus, the effect of OF surgery on aggression is situationally dependent rather than capacitative.

With regard to the effects of OF lesions on aversion, these results are inconsistent with the findings described previously; enhanced aversion to humans was not seen in this study and appeared only in the initial post-operative tests with the doll. In the present experiment, unlike the prior one, the monkeys were observed over extended periods of time, both before and after surgery. It is possible, then that familiarity of the *O* is a crucial factor determining whether aversion is enhanced following OF surgery.

In order to test this interpretation, monkeys were tested for emotional reactions to a human, as well as to a doll, for only a short period of time prior to surgery and again following OF or sham surgery, which involved the same procedures used in OF surgery except for the removal of tissues (A. Harrison-Abeles and C. M. Butter, unpublished experiment). These animals were also tested in separate sessions for autonomic responses to the presence of a human and a doll, the results of which will be reported later in this paper. Since we wanted the conditions of testing for autonomic and overt reactions to be comparable, the monkeys were tested for reactions to a human in a situation like that employed with the doll and snake in the prior study, rather than in their living cage. The monkeys were tested in an illuminated test chamber in two 30 min sessions before and again after surgery. During each session a compartment adjoining the animal's test cage was illuminated for 10 sec every 2 min. A person, clearly visible to the monkey through a large glass window, was seated in the compartment, and during these 10 sec periods the person rocked back and forth every 2 sec. Two *O*s seated behind a one-way window to one side of the test chamber time-sampled the monkey's emotional reactions to the person in the adjoining compartment. The results of this experiment are shown in the left side of Fig. 4. In this situation, the monkeys with OF lesions, unlike the sham-operated monkeys, all showed increased frequencies of aversive reactions as well as decreased frequencies of aggressive reactions to a human. These changes in emotional reactions were also found in tests with a doll as the stimulus object, conducted in a manner similar to tests with a human serving as the stimulus (*see* right side of Fig. 4). These findings, then, support the conclusion that aversive reactions are enhanced following OF lesions providing that the animals are not exposed for long periods of time pre-operatively to the stimulus object used to provoke emotional reactions.

As mentioned previously, we did not initially anticipate enhancement of aversive reactions as a consequence of OF ablation, since prior studies of conditioned avoidance would seem to indicate that frontal lesions reduce fear. Of course, conditioned avoidance situations employing electric shock differ markedly, both with respect to the UCS and to

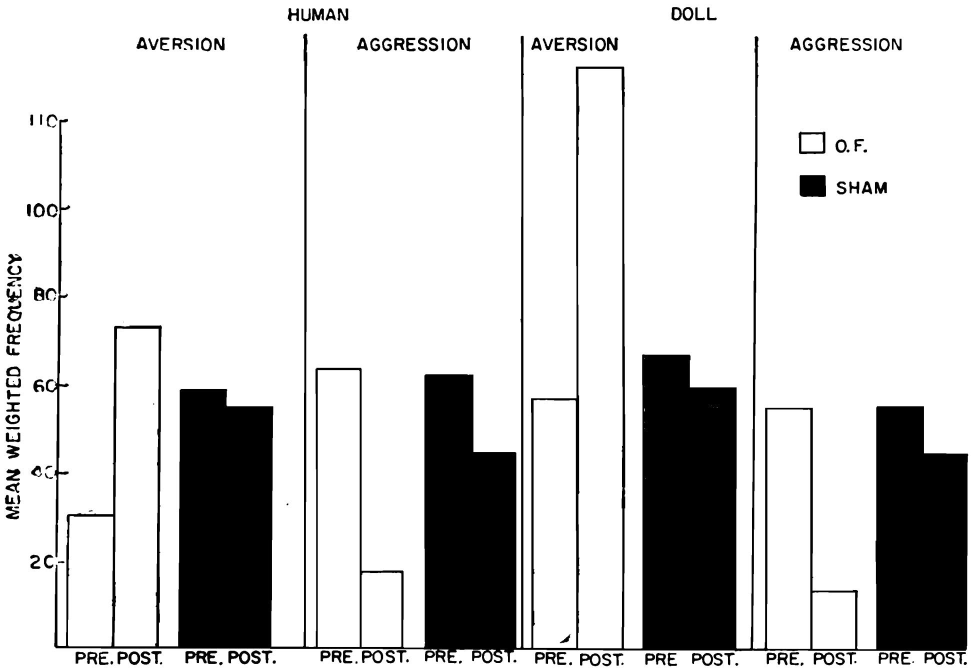


Fig. 4. Mean weighted frequencies of aversive and aggressive reactions to a human and to a doll of orbital frontal (OF) and sham-operated monkeys.

the response measures, from the test situations we have used to study emotional reactions. In addition, prior studies of conditioned avoidance employed lesions different from those in the present series of experiments. In one, posterior OF lesions were combined with medial temporal lesions (Pribram and Weiskrantz 1957), while in the other, prefrontal lobotomies were performed (Waterhouse 1957). It is possible, therefore, that the different outcomes of these studies, compared to ours, are attributable to lesion differences. In order to clarify this problem, we turn now to two studies of the effects of OF lesions, like those made in our studies of emotional behavior, on conditioned avoidance performance.

Conditioned avoidance performance in monkeys with orbital frontal lesions

In the first of these studies (C. M. Butter, M. Mishkin and E. H. Rosvold, unpublished experiment), monkeys with OF lesions and unoperated control monkeys were first trained to press a lever in a chamber in order to terminate electric shock. They were then trained according to the Sidman avoidance procedure (Sidman 1953) to lever press in order to delay the onset of shock. Each lever press delayed the onset of shock for 15 sec. If the animal failed to press the lever within this period of time, it received shocks of 0.2 sec duration every 2.5 sec. All the animals learned to lever press in order to avoid shock. However, compared with the control animals, the monkeys with OF lesions showed consistently lower rates of lever pressing over 19 sessions (*see* Fig. 5).

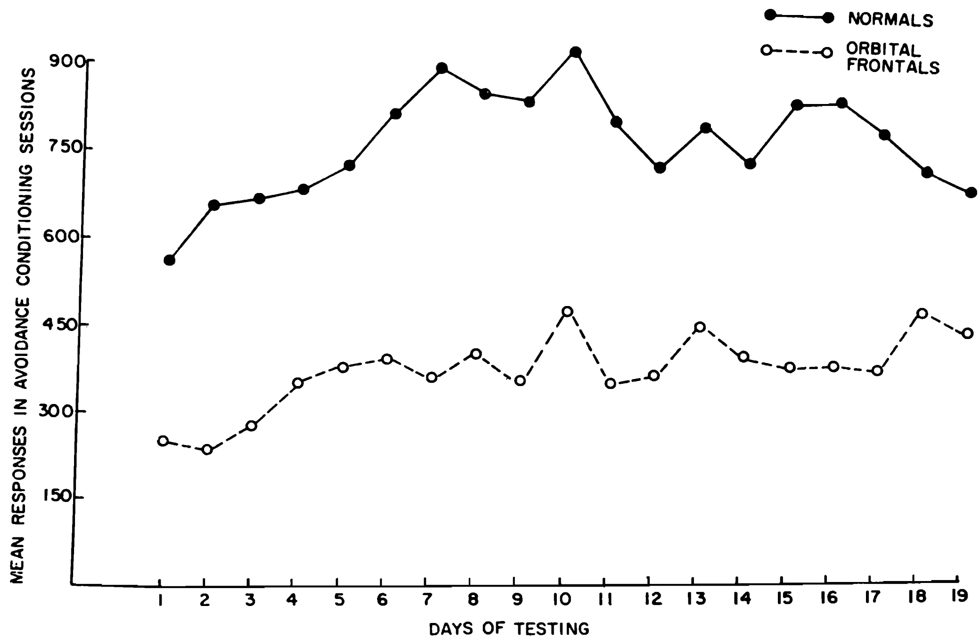
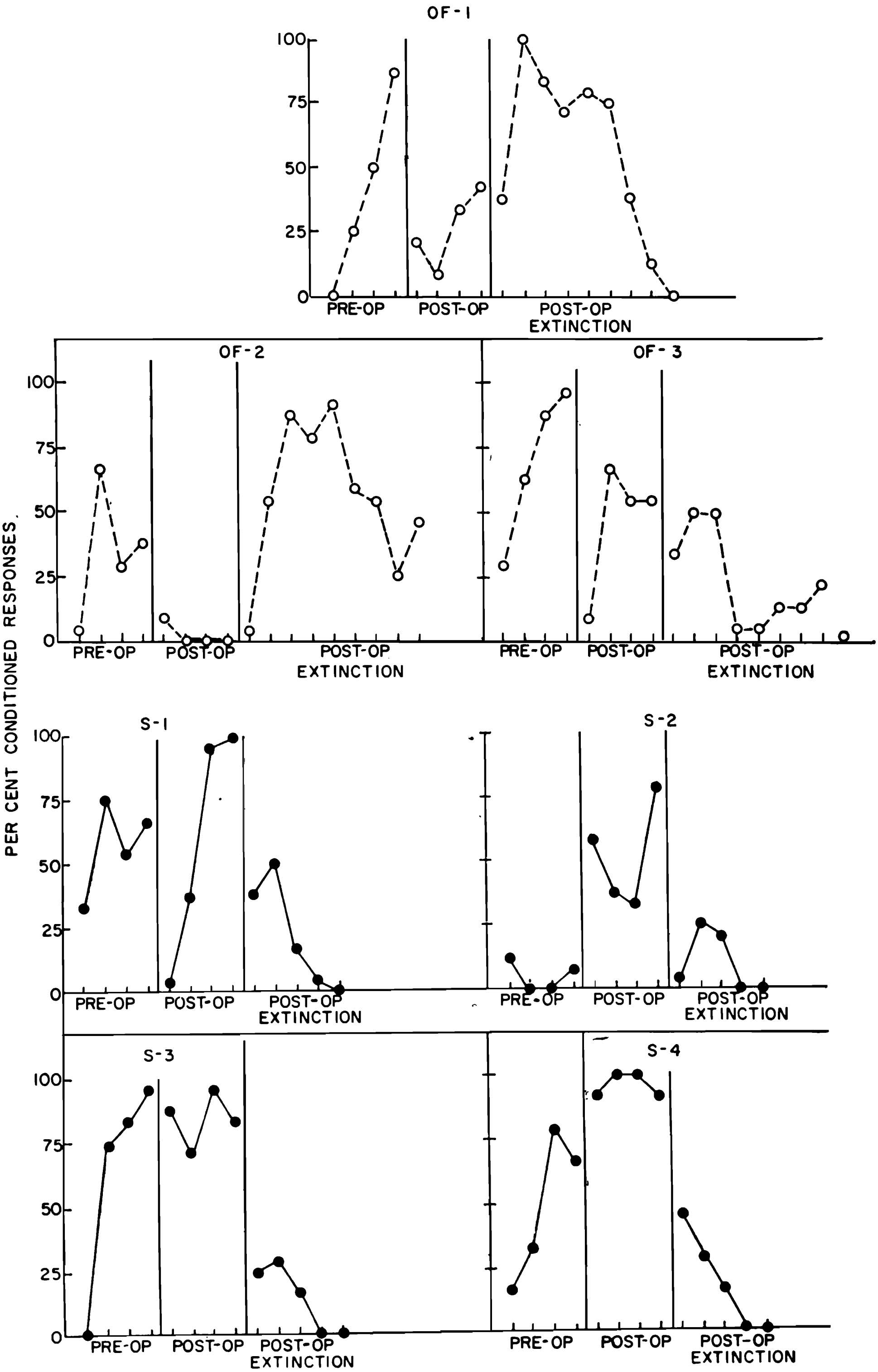


Fig. 5. Mean responses of orbital frontal and normal monkeys in successive conditioned avoidance sessions.

The second experiment (Snyder 1970*a*) in which we have found decrements in conditioned avoidance following OF lesions differs in three major respects from the first: the animals were tested before as well as after surgery, a conditioned stimulus was employed and the conditioned response was a (conditioned) escape reaction directly elicited by electric shock. This last feature of the experiment was unintentional: the


OF-1
OF-2
OF-3
S-1
S-2
S-3
S-4
PER CENT CONDITIONED RESPONSES.
100
75
50
25
0
PRE-OP
POST-OP
POST-OP
EXTINCTION

original purpose of the experiment was to study classical defensive conditioning, using as response measures the aversive reactions listed in Table I, as observed and recorded by hidden *O*s. However, as it turned out, the animals, who were shocked through the bars forming the floor, walls and ceiling of the apparatus, learned to escape or at least minimize shock by sitting back on their ischial callosities. Consequently, the monkeys also learned to avoid (or partially avoid) shock by performing this response to the CS. The CS was a loud doorbell which on each trial rang for 10 sec and in the last 5 sec was accompanied by electric shock. Each session consisted of 12 trials and inter-trial intervals randomly varied between 1 and 3 min in order to avoid temporal conditioning. Figure 6 presents per cent "sitting-back" CRs for each animal in four pre-operative acquisition sessions, and in four post-operative retention sessions, followed by extinction tests. Pre-operatively, all the monkeys, with the exception of Eban, learned to perform the "sitting-back" CR to the CS, and CRs on the last two pre-operative sessions ranged from 33 to 92% for the six animals. Unlike the other animals, Eban locomoted continuously in all pre-operative sessions. This high level of activity apparently interferred with performance of the CR, for in retention sessions following sham surgery, Eban's level of motor activity decreased and like the other sham-operated controls, he showed high levels of CR performance. The monkeys that received OF lesions, on the other hand, all showed decrements in CR performance. Compared to the control monkeys, their average level of CR performance in the four post-operative retention tests was consistently lower than is was in the last two pre-operative sessions. While the OF monkeys showed consistent decrements in CR performance, their UCRs were unaffected post-operatively. Thus, their deficit cannot be attributed to altered sensitivity or reactivity to shock. Nor was there any relationship between level of locomotor pacing (as measured by frequency of 5 sec periods in which pacing occurred) and CR performance.

As seen in Fig. 6, the sham-operated monkeys all showed large decrements in CR performance on the first extinction session and subsequently extinguished the CR to a criterion of no more than one CR in two consecutive extinction sessions. The OF monkeys failed to show this initial decline in CR frequency. In fact, two of them, Willie and Walt, showed enhanced levels of CR performance in most extinction sessions compared to their level of CR performance in retention tests.

Fig. 6. Per cent conditioned avoidance responses of orbital frontal (OF) and sham-operated (S) monkeys before surgery (pre-op), following surgery (post-op) and in extinction sessions following surgery (post-op extinction).

This enhanced CR performance in extinction was especially dramatic in Walt, who failed to show any CRs in the last three retention sessions. This finding strongly implies that shock may suppress or disrupt conditioned avoidance performance following OF lesions. In addition, it may be noted that the OF monkeys showed abnormal perseveration of the CR in extinction, a phenomenon which has been previously reported in extinction of a food-rewarded instrumental response (Butter et al. 1963) following OF lesions in monkeys.

Thus, in these two studies of conditioned avoidance, which employed different procedures and different response measures, OF lesions depressed performance. Consequently, the opposite effects of frontal surgery on aversive emotional reactions and conditioned avoidance performance cannot be attributed to lesion differences; OF removal produces both effects. It is more likely, therefore, that situational differences account for these different outcomes of OF removal. Furthermore, electric shock may be the crucial factor determining the direction of change in aversive situations following OF removal, for in the conditioned avoidance study cited above, two of the OF monkeys showed enhanced performance when shock was removed in extinction. As suggested above, this result may be less paradoxical than it appears if one assumes that shock interferes with performance following OF lesions. This interpretation is consistent with Brutkowski's (1965) suggestion that conditioned avoidance performance could be disrupted by heightened fear as well as by a loss of fear. In fact, it is reasonable to apply this interpretation to our findings, since we have shown that OF lesions do, in fact, enhance aversive emotional reactions, which may be used as an index of fear.

Alterations in social behavior following orbital frontal lesions in monkeys

To sum up our findings as we have presented them so far: OF removal in monkeys produces a marked and long-lasting deficit in aggression to threatening objects and increases the frequency of aversive emotional reactions to threatening, relatively novel objects. The emotion-provoking stimuli used in these experiments, with the possible exception of the model snake, do not closely resemble the kinds of objects and events that would be encountered by rhesus monkeys in their natural environment. Therefore, we extended our analysis of emotional alterations following frontal lesions to social behavior. This choice seemed to us especially appropriate, since the most frequent and unambiguous expressions of primate emotion occur in a social context and social behavior seems to form a pervasive and perhaps fundamental aspect of total primate behavioral organization.

The social behavior of rhesus monkeys is highly organized into stable patterns of aggression and submission which form the dominance hierarchy, and thus we decided to study the effects of frontal lesions on behavior in this context. To investigate the effects of OF lesions on social dominance, we wanted a situation which could be often repeated and within which intense and frequent social interactions would occur. Past experiments suggest that these requirements are met by the introduction of a new monkey into a group (Kawai 1960, Bernstein 1964, Bernstein and Draper 1964, Hansen et al. 1966, Southwick 1967).

In this experiment, then, male rhesus monkeys were successively introduced into a permanent colony of four unoperated male rhesus monkeys before surgery, 2–3 weeks following either sham surgery or OF surgery, and again at bimonthly intervals up to 8 months following surgery (Snyder 1970*b*). The colony was housed in an 8 ft × 3 ft × 6.5 ft observation cage. Two *O*s observed the colony from behind a one-way screen, and they recorded agonistic interactions by a method similar to those described by Altmann (1962) and Bernstein (1964). The permanent (matrix celony was observed regularly over the initial 2-month period during which it was allowed to stabilize prior to the introduction of any test animal. The observational records indicated that over this period, a stable, linear hierarchy formed. This hierarchy, with one exception, was maintained in the intervals between removing one test animal from the colony and introducing the next one. Pre-operatively, all of the test animals achieved the dominant position in the group, an unintentional result of the test monkeys being somewhat larger and older than the members of the permanent colony. Figure 7 shows the dominance hierarchies formed when each of the four sham-operated monkeys was introduced into the permanent colony before and after surgery. The numbers in this Figure refer to the agonistic index, which is a measure of the dominance behavior of one animal over another relative to the total interactions between the two. For example, in the upper left hand corner of Fig. 7 the number "0.99" between Abba and Dax in the "pre-operative" column means that 99% of all the recorded agonistic interactions between these two animals were those in which Abba was dominant over Dax, Dax was submissive toward Abba, or both kinds of reactions occurred. As seen in this Figure, the sham-operated monkeys retained their dominant position in the hierarchy following surgery and continued to do so when retested at bimonthly intervals. Like the sham-operated animals, the OF monkeys were dominant over all the others in the colony prior to surgery (*see* Fig. 8.). And when they

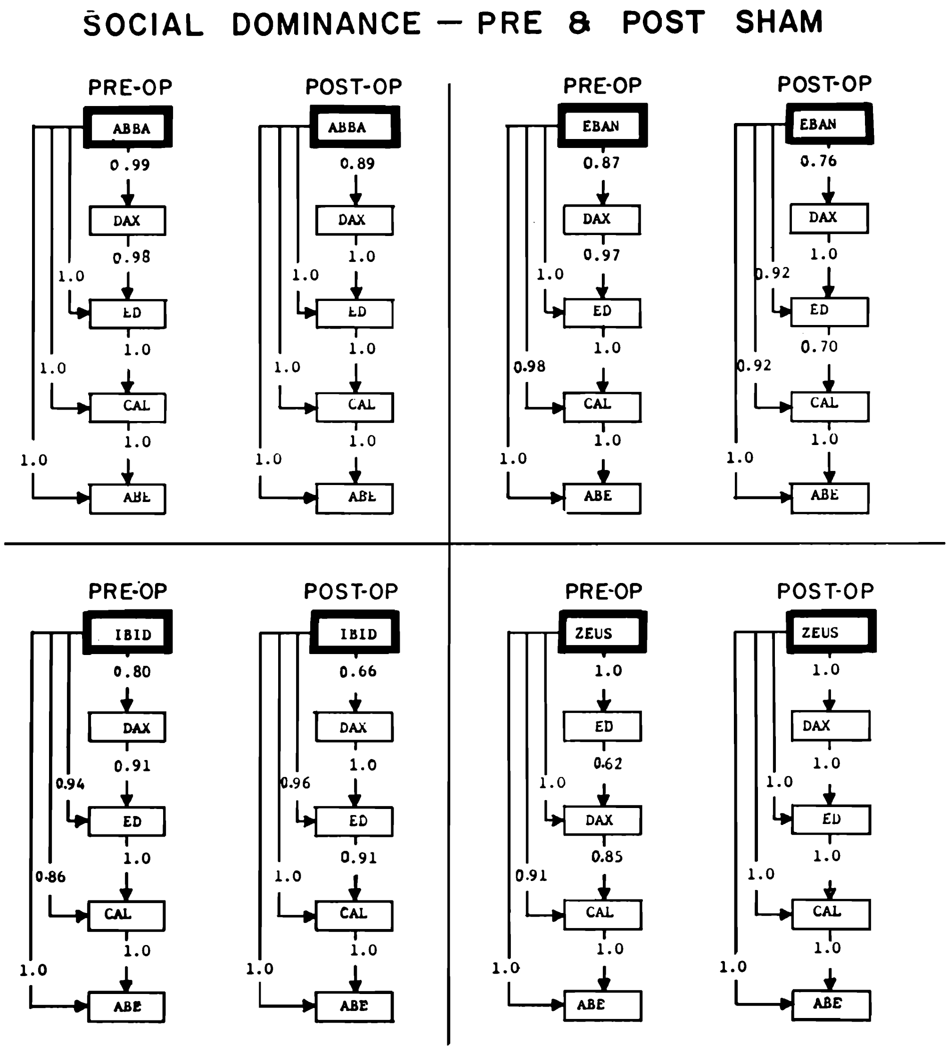


Fig. 7. Dominance hierarchies before and after sham surgery performed on monkeys whose names are shown in heavy black boxes. *See* text for explanation of numbers in figure.

were reintroduced into the colony for the first time following surgery, the OF monkeys all exhibited high frequencies of aggression toward the other members of the colony and retained their dominant positions. However, each of the OF monkeys eventually fell in the dominance hierarchy, but at different times. During the first 5 days in which he was reintroduced into the colony after surgery, Walt behaved just as he did prior to surgery. Following a week-end in which no observations were made, Walt was observed to be submissive to all other monkeys in the colony and showed only infrequent aggression toward Abe, the scapegoat of the colony. Walt remained at the bottom of the hierarchy for the remainder of his stay in the colony (5 days), and the post-operative scores plotted in Fig. 8 are for this period of time during which he was submissive to all others. Moreover, observations made at bi-monthly intervals indicated that Walt retained his submissive position in the hierarchy. With regard to Ben and Willie, like Walt they too retained their dominant positions in the hierarchy when first reintroduced into the colony following surgery, but they retained this position throughout the first post-operative test period. It was only during subsequent retesting, 4 months following surgery for Ben and 6 months following surgery for Willie, that they fell to the bottom of the dominance hierarchy. The post-operative observations of these two animals, shown in Fig. 8, were made in these subsequent tests. Like Walt, Ben and Willie continued to be entirely submissive toward the other members of the colony when they were retested following their fall in the hierarchy. The control monkeys, on the other hand, retained their dominance when retested post-operatively.

OF removal, then, produces a loss of social dominance in a group, although this loss is not seen immediately upon reintroduction into the colony following surgery. In other words, in a social situation, as in the other situations described previously, OF removal leads to a loss of aggression and heightened aversion. These findings are in striking contrast to the effects of prefrontal lobotomy on social behavior in a situation similar to ours (Brody and Rosvold 1952). In that experiment, the lobotomized monkeys ceased submitting to the more dominant monkeys in the colony and became aggressive toward them. As a result, the stability of the entire hierarchy was upset. It is possible that our frontal monkeys might also have shown this inappropriate aggression had other members of the colony been dominant over them initially.

The effects of OF lesions on social behavior more closely resemble those of amygdalectomy than those of prefrontal lobotomy. Like OF removal, amygdala lesions result in a sharp decline in aggressiveness toward other monkeys and consequently a fall in social rank, at least in monkeys frequently challenged pre-operatively by a subordinate (Mirsky 1960, Rosvold et al. 1964). Similar findings have been reported in squirrel monkeys (Plotnik 1968). The major difference between the results of these experiments and our results is the time at which these alterations are seen: while the fall in social rank is seen immediately after amygdalectomy, it is delayed for variable periods of time following OF lesions.

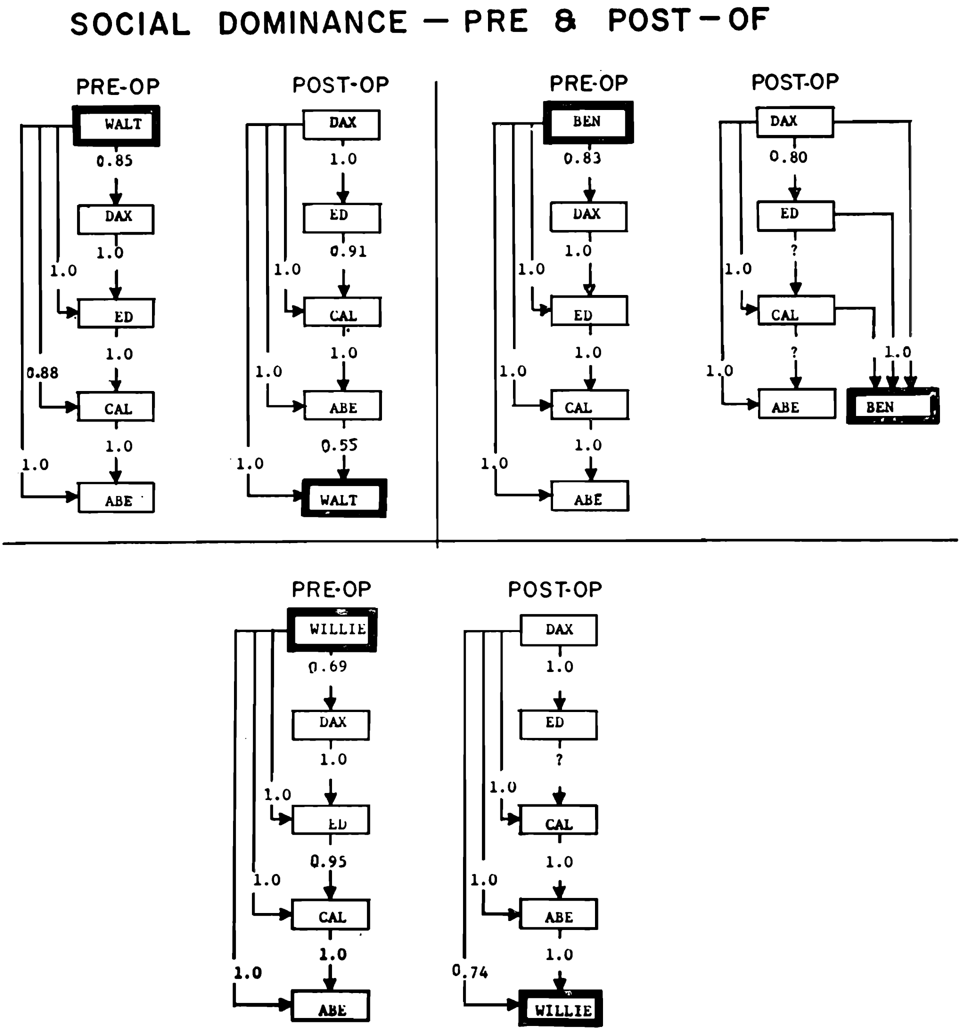


Fig. 8. Dominance hierarchies before and after orbital frontal surgery, performed on monkeys whose names are shown in heavy black boxes. *See* text for explanation of numbers in figure.

What might account for this delayed effect of OF removal on social behavior? For one thing, it is clear that the delay was specific to the social situation; the OF monkeys showed a decrement in aggression toward humans and inanimate objects prior to their fall in the social hierarchy. This dissociation between aggression in the social and nonsocial situations implies that there is some factor or factors which operate, but only at some times, in the social situation to produce the loss of aggression. The most obvious variable factor in the social situation is the behavior of the other monkeys, especially their threatening and aggressive behavior, toward the OF monkeys. Analyses of aggressive reactions of other members of the colony toward the OF monkeys seems to support this view. The monkey occupying the second position in the colony (Dax) was a very scrappy animal who frequently initiated aggressive actions toward each of the test animals, even though their reprisals usually forced him to withdraw. These aggressive challenges occurred most frequently immediately after a test animal was introduced or reintroduced into the colony. In those sessions in which the three OF monkeys first showed a loss of social dominance they received direct attacks more frequently than they did in the final pre-operative sessions. In fact, the first OF monkey to fall from social dominance received nearly three times as many threats and attacks from the second ranking male during the first two post-operative observation periods than the other two OF monkeys received when they were reintroduced into the colony. It is possible, then, that following surgery the OF monkeys were not able to cope successfully with continual threats from the second ranking monkey and so lost their dominant positions. Of course, it is also possible that the second monkey recognized some behavioral alteration in the OF monkey, which gave him confidence to continue his attacks. This alternative interpretation cannot be rejected since it is difficult to specify the causal relations when dealing with social interactions.

Comparison of the effects of partial orbital frontal, dorsomedial nucleus and amygdala lesions on emotional behavior in monkeys

So far we have presented evidence that OF lesions in monkeys reduce aggressive reactions and heighten aversive reactions in threatening situations, both social and non-social. As we noted previously, the alterations in socioemotional behavior following OF lesions closely resemble those described following amygdalectomy, except for the variable delay. The effects of OF lesions resemble those of amygdalectomy in several other respects as well. The shift from an initial depressed and hyporeactive state to a long-lasting hyperreactive state as described in a previous section of this paper, has also been described following amygdala lesions (Pribram and Bagshaw 1953, Weiskrantz 1956). Moreover, the oral tendencies of OF monkeys, which have been documented in detail elsewhere (Butter et al. 1969) are one of the most striking effects of amygdalectomy (Pribram and Bagshaw 1953, Weiskrantz 1956). Learning tasks, too, reveal similar deficits following amygdala and OF surgery: OF removal produces perseveration in extinction (Butter et al.

1963) and in discrimination reversal performance (Mishkin 1964, Iversen and Mishkin 1970), as do amygdala lesions (Weiskrantz 1956, Mahut and Cordeau 1963, Dorff 1964).

This evidence for a close functional relationship between OF cortex and the amygdala is consistent with evidence for close anatomical ties between these two structures. The posteromedial sector of OF cortex, together with its thalamic projection nucleus, *n. medialis dorsalis*, and the amygdala, form an interconnected circuit and send fibers to common hypothalamic sites (Nauta 1962). Electrophysiological findings, too, suggest an affinity between posteromedial OF cortex and the amygdala: electrical stimulation of this frontal region readily elicits autonomic changes and arousal reactions like those elicited from the amygdala and other anterior limbic structures (Kaada 1960). Further, in our behavioral experiments, histological analysis of OF lesions suggested that the posteromedial sector of OF cortex may be a critical focus for emotionality changes (Butter et al. 1970, Snyder 1970*a*).

In order to test this hypothesis, we observed emotional reactions to human observers and to a doll before and after selective posteromedial orbital frontal (PMOF) lesions or lesions of the remaining anterolateral orbital frontal (ALOF) cortex. In addition, because of the close anatomical relationships between PMOF cortex, the amygdala and dorsomedial nucleus, we also compared the effects of lesioning these latter two structures on emotional behavior in monkeys.

Emotional reactions to humans were evaluated while the animals were in their living cages, by the same methods used in the initial experiment. Two *O*s judged emotional reactions 10 times before surgery and again following surgery. Emotional reactions to a doll were observed and recorded by the same methods referred to previously (Butter et al. 1970).

The OF lesions, like those described previously (Butter, et al. 1970), were made by subpial aspiration. Bilateral dorsomedial nucleus (pars magnocellularis) lesions were performed stereotaxically with 1 mm diameter platinum wire insulated with Epoxylite except for 1 mm at the tip. Radio-frequency current of 1 v was passed for 20 sec at each of the three following sets of Horsley-Clark coordinates: Ant. 9.0, Lat. ±1.5, Dors. 9.0; Ant. 7.0, Lat. ±1.5, Dors. 8.5; Ant. 5.0, Lat. ±2.0, Dors. 7.0. Bilateral amygdala lesions were also made stereotaxically by the same procedures used for dorsomedial nucleus lesions except that the electrode tip was bared for 2 mm. Current was passed at the following coordinates: Ant. 18.5, Lat. ±9.0, Vent. −5.0, −4.5; Ant. 18.5, Lat. ±11.0, Vent. −5.0, −4.5; Ant. 17.5, Lat. ±9.0, Vent. −5.0, −4.5; Ant. 17.5, Lat. ±11.0, Vent. −5.0, −4.5; Ant. 15.0, Lat. ±12.0, Vent. −5.0, −4.5.

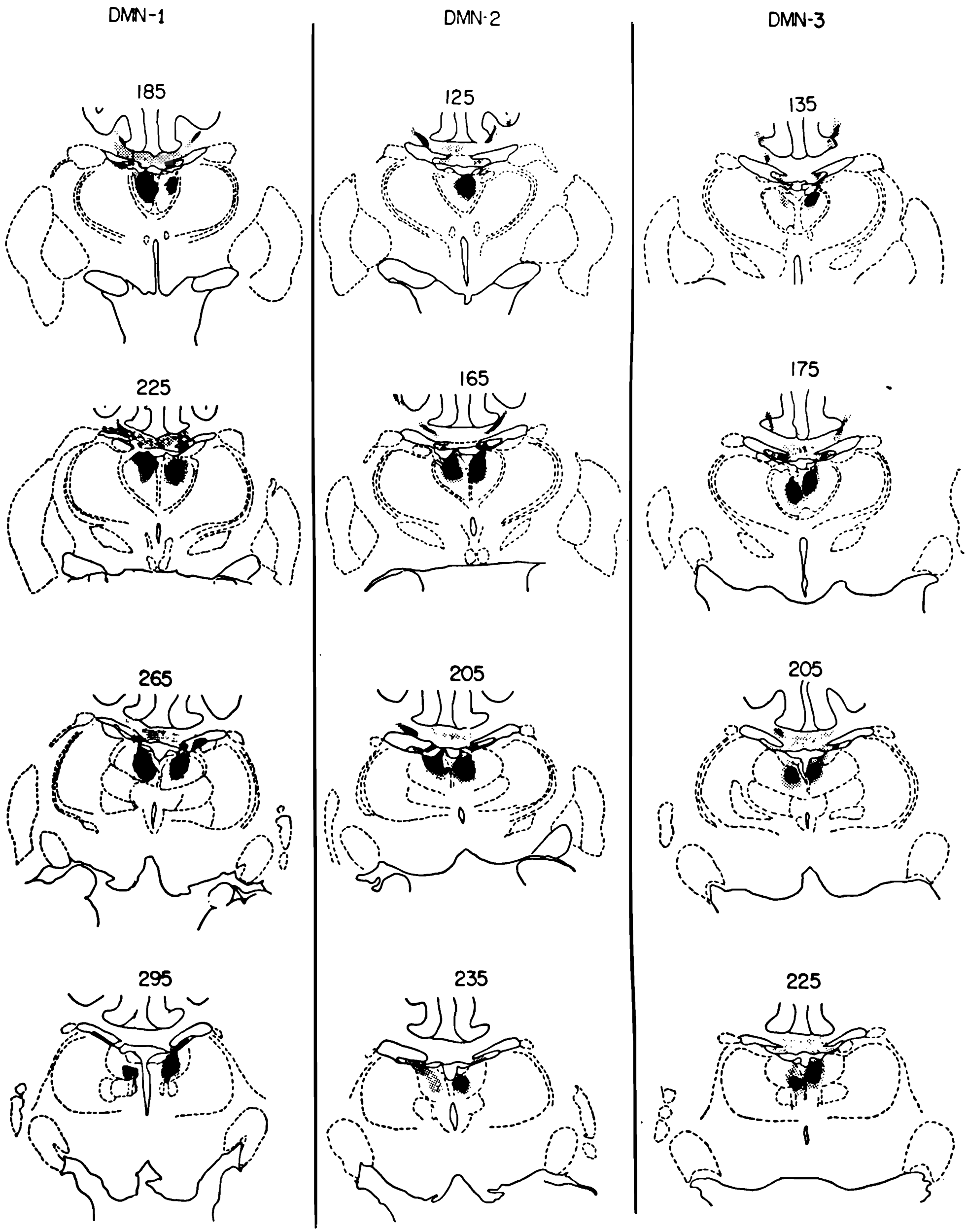


Fig. 9. Cross-sections through the thalamus of monkeys with lesions of the dorsomedial nucleus (DMN). Areas of destruction are shown in black, while areas containing degeneration and gliosis are stippled.

Amygdala lesions were also made in one animal by aspiration after retracting the temporal pole by the procedure described by Pribram and Bagshaw (1953).

Following the completion of post-operative testing, the monkeys were sacrificed and their brains were prepared for histological examination by procedures described previously (Butter et al. 1970). Of the eight monkeys intended to receive lesions of n. medialis dorsalis, pars magnocellularis, three incurred major bilateral damage of this structure with the least destruction of nearby structures (*see* Fig. 9). Of these structures, moderate to severe damage was found in the fornix, stria medullaris, n. anterior dorsalis, n. centralis superior lateralis and n. parataenialis. In addition, slight to moderate damage was located in cingulate cortex, n. medialis dorsalis, pars parvocellularis, the medial and lateral habenular nuclei, several midline nuclei (n. centralis superior, n. centralis densocellularis, n. centralis intermedialis, n. paraventricularis) and in two intralaminar nuclei (n. paracentralis and n. parafascicularis).

Figure 10 shows cross-sections through two amygdala lesions — one which was stereotaxically made, (AMY-1), the other by aspiration (AMY-2). The brain of AMY-1 involved extensive damage to n. lateralis. n. basalis and n. anterior of the amygdala. N. medialis was moderately damaged, while n. corticalis and the periamygdaloid nucleus were only slightly damaged. In addition, slight to moderate damage was found in pyriform cortex, substantia innominata, the anterior commissure, ansa lenticularis, globus pallidus, anterior hippocampus and the caudate nucleus. The aspirative lesion in AMY-2 involved all the amygdala except for some sparing of n. centralis and n. anterior. The pyriform cortex, temporal polar cortex, uncus and hippocampal gyrus were also severely damaged.

Figures 11 and 12 show reconstructions of the PMOF and ALOF lesions together with cross-sections through the lesions and through the thalamus. The PMOF lesions, as intended, removed virtually all the cortex between the posterior halves of the medial and lateral orbital sulci without involving major damage to surrounding cortex or to adjacent subcortical structures. In addition, the PMOF lesions produced severe degeneration and dense gliosis confined to the magnocellular division of n. medialis dorsalis. The ALOF lesions spared PMOF cortex although they did encroach upon the ventral part of the dorsolateral convexity (*see* Fig. 12). These ALOF lesions resulted in only slight and scattered degeneration in the medial portion of the parvocellular division of n. medialis dorsalis.

Several animals in which DMN lesions were not placed as intended served as operated control animals. These animals had lesions in struc-

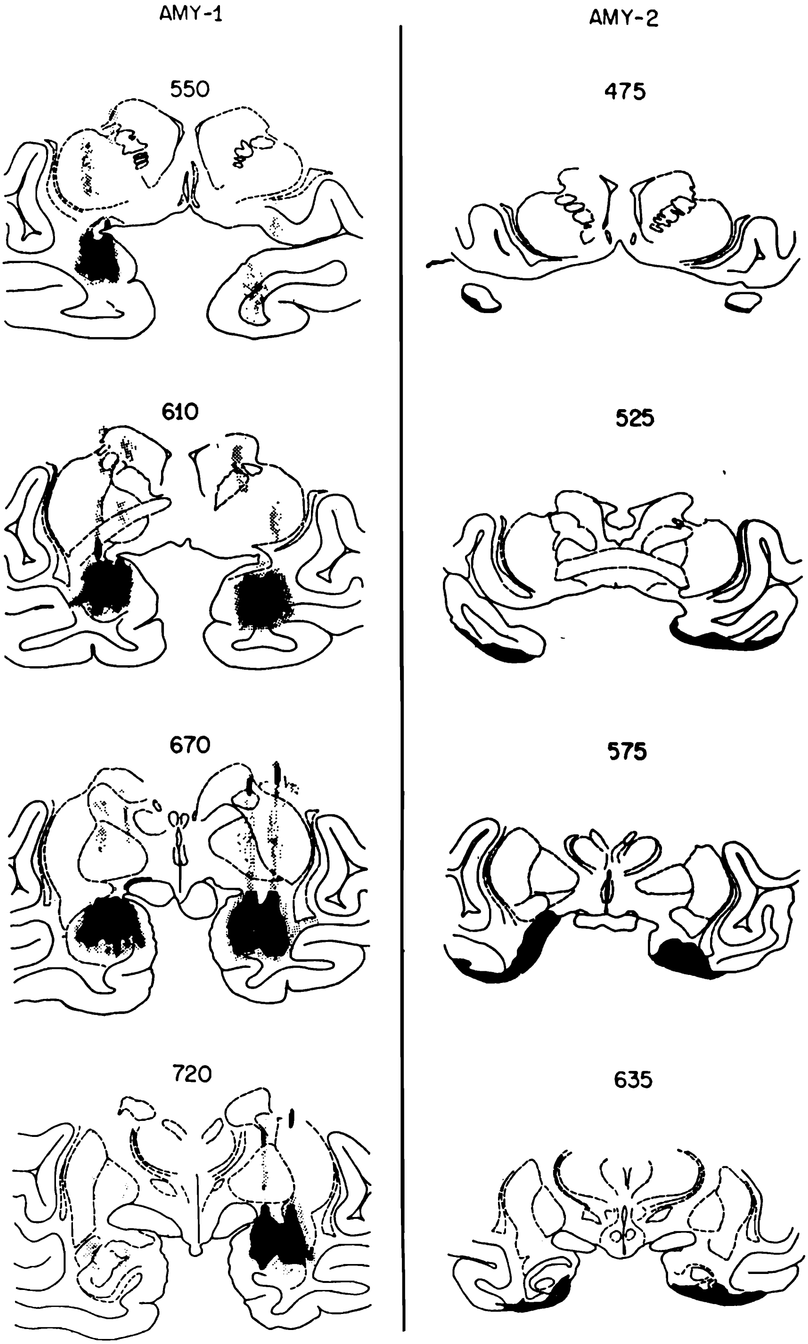


Fig. 10. Cross-sections through the brains of monkeys with amygdala lesions. Areas of destruction are shown in black, while areas containing degeneration and gliosis are stippled.

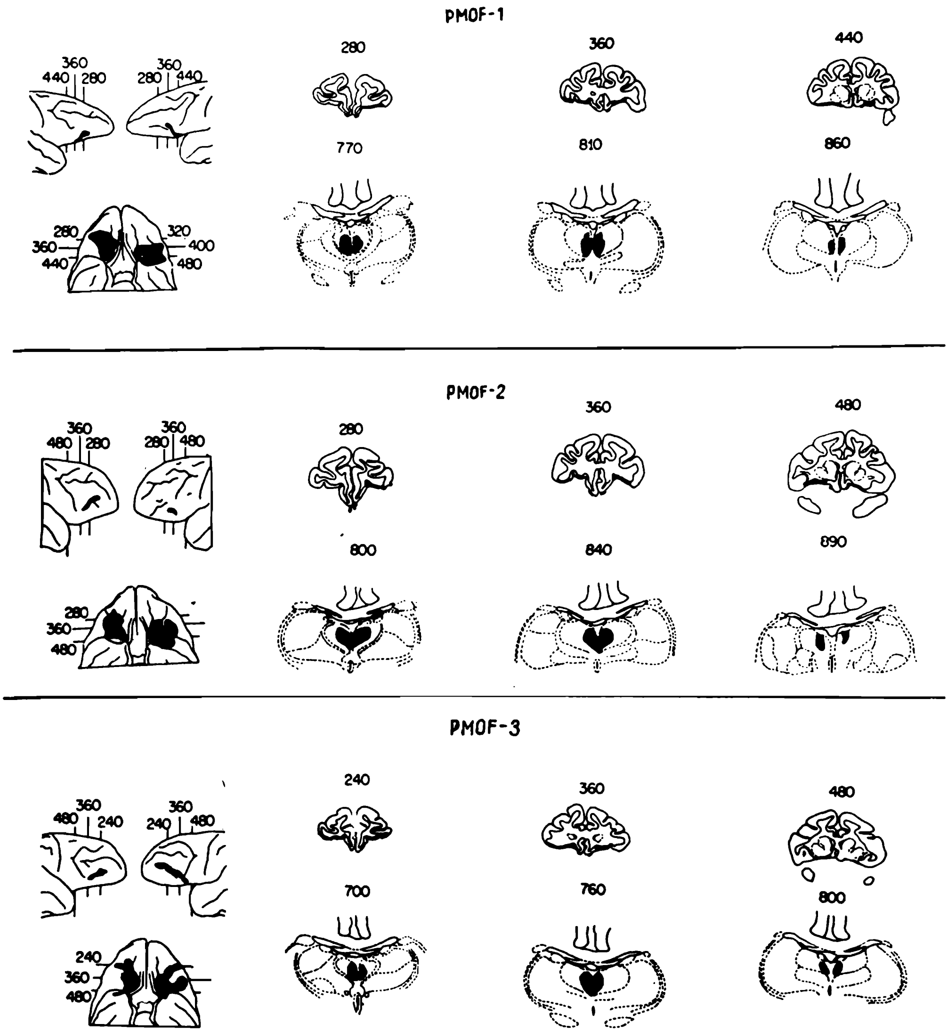


Fig. 11. Reconstructions of posteromedial orbital frontal (PMOF) lesions, together with representative cross-sections through the lesions and through the thalamus showing retrograde degeneration.

tures dorsal to the dorsomedial nucleus. Since these structures were also damaged in the three DMN monkeys, they served as appropriate controls.

Following surgery, the monkeys with PMOF lesions showed changes in general behavior similar to those displayed by monkeys with complete OF lesions, including anorexia and lethargy. However, these symptoms were less prolonged and less intense than those observed in monkeys with complete OF removal in prior experiments. The monkeys with

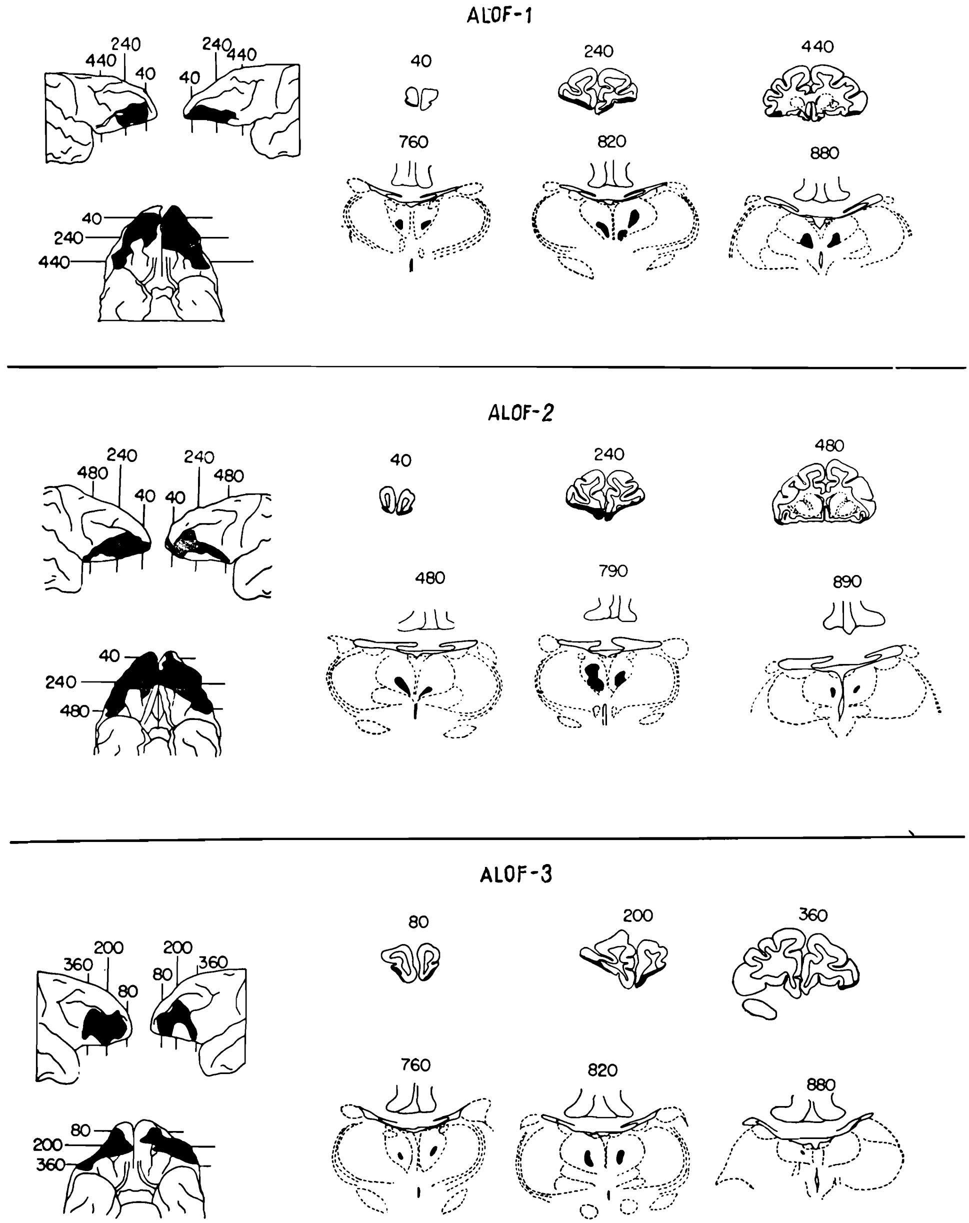


Fig. 12. Reconstructions of anterolateral orbital frontal (ALOF) lesions together with representative cross-sections through the lesions and through the thalamus showing retrograde degeneration.

PMOF lesions also showed locomotor hyperactivity after the initial depressed phase had ended. While PMOF lesions produced alterations in general behavior similar to although less pronounced than those seen after entire OF lesions, ALOF lesions failed to produce these effects, except for locomotor hyperactivity. On the other hand, amygdala lesions produced even more striking and long-lasting behavioral depression than we have seen following complete OF lesions. For a period of 12 days to 3 weeks following surgery, these animals were lethargic, drowsy and quite unreactive to most forms of stimulation; they also showed marked anorexia, although following this initial depressive stage they showed pronounced oral tendencies. All these symptoms have been previously reported following amygdalectomy (Pribram and Bagshaw 1953, Weiskrantz 1956). In contrast to these effects of PMOF and amygdala lesions on behavioral reactivity, dorsomedial lesions did not produce detectable alterations in general behavior.

Turning to the effects of surgery on emotional reactions to human Os, Fig. 13 and 14 show weighted frequencies of aversive and aggressive

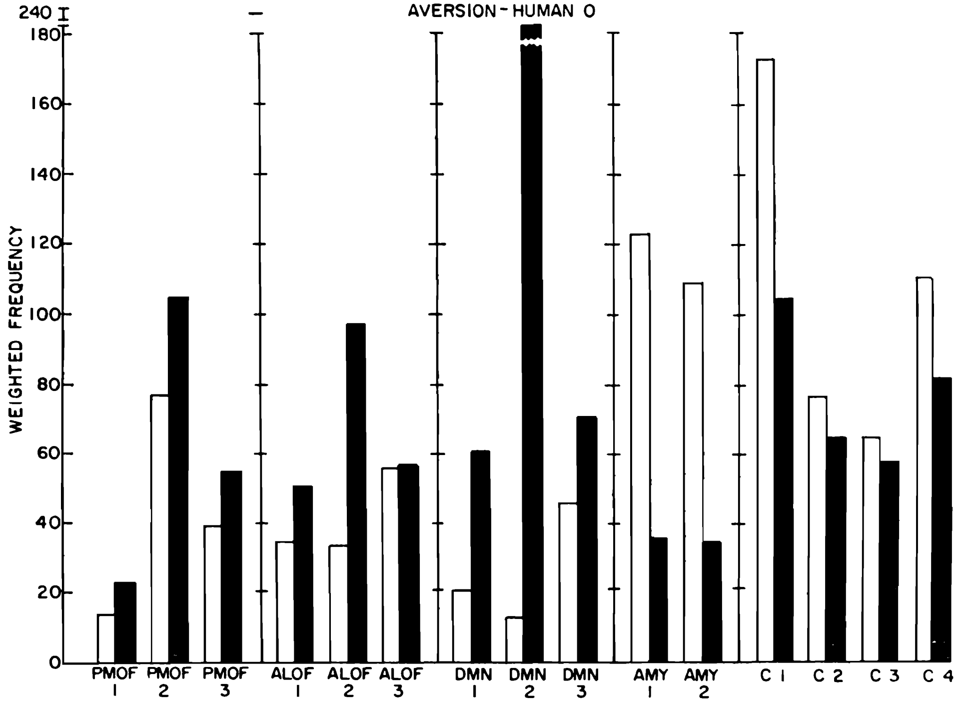


Fig. 13. Weighted frequencies of aversive reactions to an observer by monkeys with posteromedial orbital frontal (PMOF), anterolateral orbital frontal (ALOF), dorsomedial nucleus (DMN), amygdala (AMY) and control (C) lesions. White bars, scores before surgery; black bars, scores after surgery.

reactions toward two Os by each of the subjects in a series of 10 observations before and again after surgery. While the operated control monkeys all showed small to moderate decreases in frequencies of aversive reactions post-operatively, all the PMOF and ALOF monkeys showed increases in this measure. As seen in Fig. 13 the monkeys with dorsomedial nucleus lesions also showed enhancement of aversion; in fact, one of them, DMN-2, exhibited a spectacular rise in frequency of aversive reactions, far greater than that shown by subjects with OF lesions. On the other hand, the amygdalectomized monkeys, as anticipated from prior results, showed marked decrements in aversive behaviors. While the control animals showed small changes in frequencies of aggressive reactions following surgery, both the PMOF and ALOF animals showed considerable decreases in this measure post-operatively, with the exception of ALOF-3 (*see* Fig. 14). Likewise, the monkeys with dorsomedial nucleus lesions and those with amygdala lesions showed large decrements in frequencies of aggressive reactions.

Whereas PMOF and ALOF removals did not differentially affect

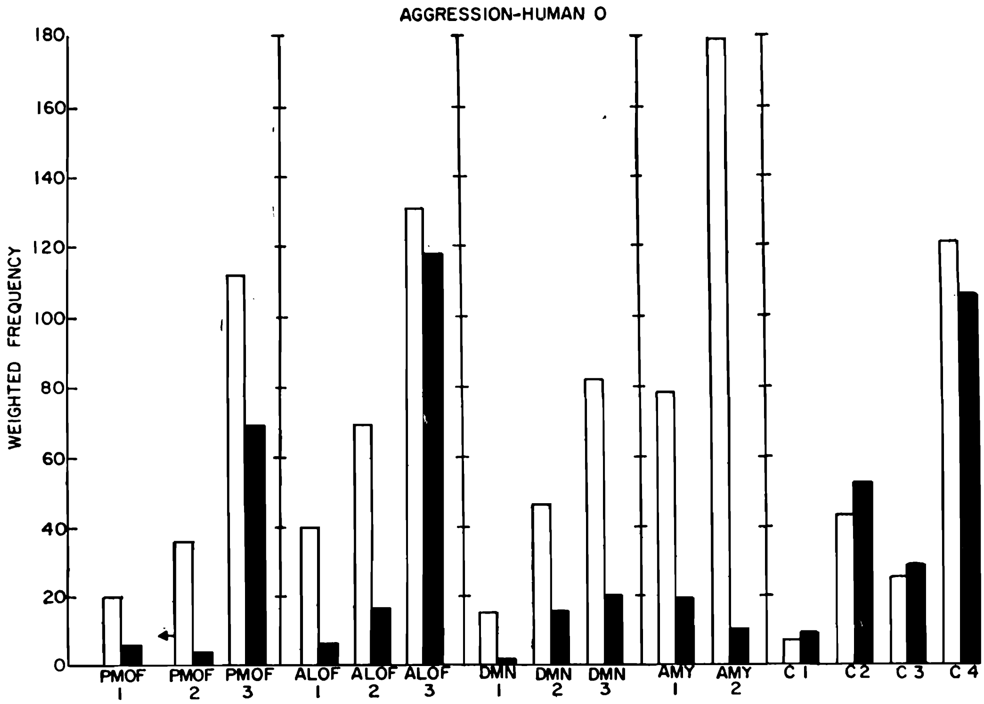


Fig. 14. Weighted frequencies of aggressive reactions to an observer by monkeys with posteromedial orbital frontal (PMOF), anterolateral orbital frontal (ALOF), dorsomedial nucleus (DMN), amygdala (AMY) and control (C) lesions. White bars, scores before surgery; black bars, scores after surgery.

emotional reactions to human Os, PMOF lesions did have a selective effect on emotional reactions to the doll. As seen in Fig. 15, which shows frequencies of aversive reactions to the doll averaged for two Os, PMOF lesions resulted in increased frequencies of aversive reactions, while ALOF lesions, like control lesions, resulted in moderate decreases in aversion scores. DMN lesions produced decrements in frequencies of aversive reactions, but these were smaller than those of the control monkeys. As anticipated, both animals with amygdala lesions showed

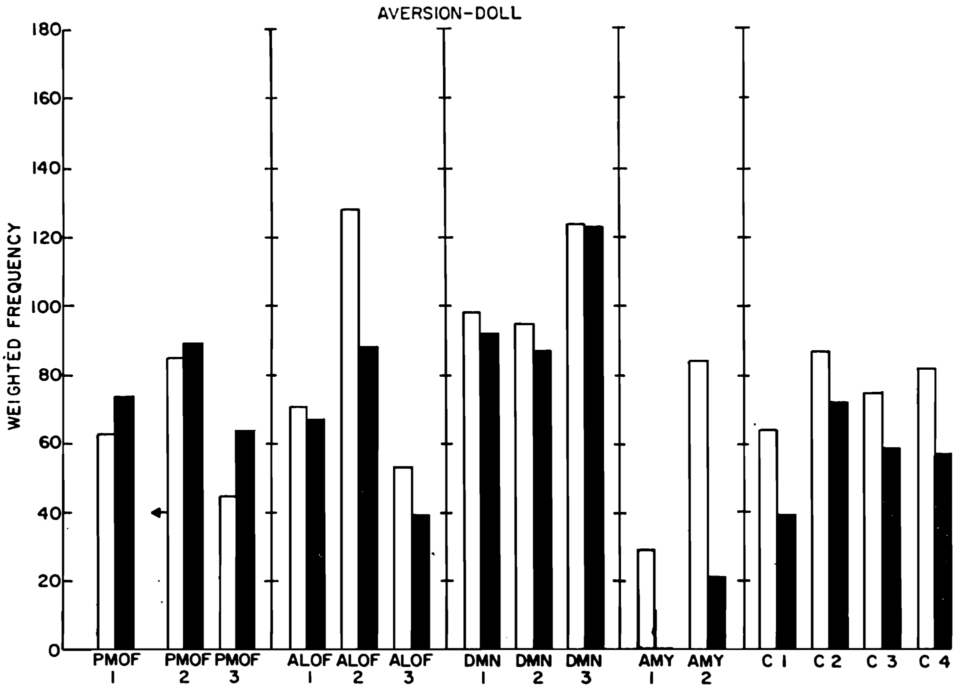


Fig. 15. Weighted frequencies of aversive reaction to a doll by monkeys with posteromedial orbital frontal (PMOF), anterolateral orbital frontal (ALOF), dorsomedial nucleus (DMN), amygdala (AMY) and control (C) lesions. White bars: scores before surgery; black bars: scores after surgery.

large decreases in aversion following surgery. The PMOF lesions also had a selective effect upon aggression in this situation: as seen in Fig. 16, the PMOF monkeys, unlike the ALOF monkeys, showed sizable decrements in frequencies of aggressive reactions to the doll. In addition, the monkeys with dorsomedial nucleus lesions and amygdala lesions all showed large decrements in this measure of aggression.

To summarize the results of this study, we obtained only partial confirmation of the hypothesis that PMOF cortex is the focus of the changes in emotional behavior seen following complete OF lesions. While

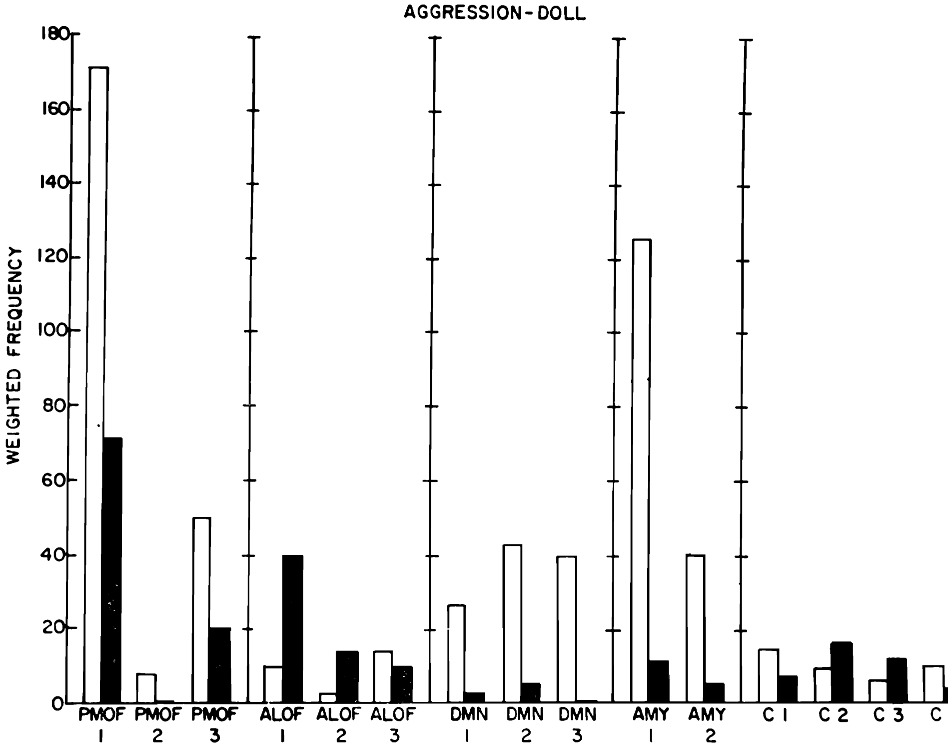


Fig. 16. Weighted frequencies of aggressive reactions to a doll by monkeys with posteromedial orbital frontal (PMOF), anterolateral orbital frontal (ALOF), dorsomedial nucleus (DMN), amygdala (AMY) and control (C) lesions. White bars, scores before surgery; black bars, scores after surgery.

the monkeys with PMOF lesions showed the anticipated changes in aversion and aggression in both experiments, the monkeys with ALOF lesions also showed similar changes but only in one experiment. What might account for the discrepant results of the two experiments with regard to the ALOF animals? The observations of reactions to humans and to the doll were made during the same period of time following surgery; thus, the ALOF monkeys' lack of impairment in tests with the doll cannot be attributed to a transient effect of the operation. On the other hand, it is possible that the two situations differred in the degree of threat to the animals such that the presence of a human is more likely to reveal a slight impairment than the presence of the doll. A comparison of frequencies of aversive reactions to the human *O* and to the doll supports this interpretation. With appropriate adjustments for time differences in the two test situations, prior to surgery all 15 monkeys showed greater frequencies of aversive reactions to either human O than they did to the doll. Aggressive behaviors, too, were elicited more frequently by humans than by the doll in 14 of the 15 monkeys prior to surgery. This finding, then, supports the view that the presence of a human was more threatening than was the doll under these conditions of testing. According to this interpretation, the ALOF monkeys' alteration was limited to the more threatening of the two situations; conversely, it would appear that PMOF lesions, compared with ALOF lesions, are more sensitive to a less threatening situation. Although our findings indicate only a partial dissociation between the effects of PMOF and ALOF lesions on emotional behavior, they clearly implicate PMOF cortex in the control of aversion and aggression.

The findings of this experiment also point clearly to an involvement of the dorsomedial nucleus in emotional behavior. It is possible, however, that the emotional alterations of the DMN monkeys were due to damage to structures surrounding the DMN nucleus, especially to dorsally situated midline nuclei, stria medullaris and the fornix, which were consistently damaged. However, several of the control animals, which sustained at least as much damage to these structures as did the DMN animals, failed to show alterations in emotional behavior. Thus, it is unlikely that the behavioral effects observed can be attributed to damage to these structures. Furthermore, the DMN lesions produced only variable damage to more ventrally placed midline and intralaminar structures. In addition, the behavioral effects that we have observed following DMN lesions are quite different from those reported in a study in which DMN lesions involved extensive damage to midline thalamic structures in monkeys (Brierly and Beck 1958). Their lesions, unlike ours, produced "loss of fear", "vacant facial expression", hyperactivity and distractability. Thus, while damage to structures surrounding the magnocellular division of the dorsomedial nucleus cannot be ruled out as a contributing factor to these behavioral alterations, histological analysis and the contrasting findings of Brierly and Beck render this interpretation doubtful.

Irrespective of the localizability of our DMN lesions, they clearly produced effects like those of OF lesions in our test situations. Apparently, then, this region of the thalamus controls emotionality in a manner similar to OF cortex, and more specifically, PMOF cortex, with which the magnocellular division of the dorsomedial nucleus has direct and reciprocal interconnections. Our results are not the first to suggest a role of the dorsomedial nucleus in emotional behavior. Besides the findings of Brierly and Beck referred to previously, Roberts (1963) had reported that dorsomedial nucleus lesions in cats enhanced escape reactions to electric shock, while Spiegel, Wycis, Freed and Orchinik (1951) found that lesions of this structure reduced aggression in human patients. Thus, other investigators have not only implicated the dorsomedial nucleus in emotion, they have also obtained results which are qualitatively similar to ours.

With regard to the effects of amygdalectomy, reduced aggressive and aversive reactions have been reported previously. Although the disturbance underlying these emotional alterations remains to be clarified, the contrast between the effects of amygdalectomy and those of OF and DMN lesions suggests that the amygdala plays a different role in the control of emotion, at least with regard to aversion.

GENERAL DISCUSSION

In this final section we will deal with the problem of interpreting the observations reported here in order to shed light on the disturbance underlying the effects of OF lesions on emotional behavior. Although we are very far from any clear resolution to this problem, the following analysis may help to clarify the nature of the problem and point to directions that future research should take.

But before analysing the lesion effects, it should be pointed out that our findings may aid in resolving inconsistencies and contradictions in past research (*see* Brutkowski 1965). Two aspects of our findings are relevant in this regard. First, it is clear that the behavioral abnormalities seen soon after OF removal are very different from, in fact opposite to, the abnormalities which ensue and persist for at least many months following surgery. Thus, reactivity to environmental stimulation and appetite are abnormally low or high, depending on the amount of time that has elapsed since OF surgery. In addition, aversive emotional reactions are rarely seen during the initial acute phase, whereas they are enhanced, under certain conditions, in the second, chronic phase. Secondly, it is equally clear that OF removal produces opposite effects on aversive and aggressive behaviors in the chronic phase. By focussing on one of these classes of behavior, an observer might conclude that frontal lesions produce "tameness" or, conversely, heightened emotional behavior. However one may evaluate other investigators' observations, the present findings clearly indicate that one cannot describe frontal lesion effects on "emotionality" as a single category of behaviors any more than one can describe these effects without specifying time since surgery.

Turning to the problem of interpreting the alterations in emotional behavior we have described here, we deal first with those interpretations which do not adequately account for the findings. As mentioned before. analysis of our findings suggests that these alterations are not simply due to increased locomotor activity or to lethargy. Nor can these changes in emotional behavior be accounted for by an impairment in suppressing strong response tendencies, a term that has been used to characterize deficits shown by frontal monkeys in learning situations (Mishkin 1964). For, those emotional respones which are enhanced following OF removal (i.e., aversive reactions) were not necessarily the dominant responses pre-operatively, nor were aggressive reactions, as a class, the least frequent pre-operatively. Moreover, the most consistent effect of OF lesions — the decrement in aggression — obviously cannot be due to disinhibition of responses (Rosvold and Mishkin 1961) or of drive (Brutkowski 1965), terms which have been used to describe the effects of frontal lesions on classical and instrumental conditioning.

While interpretations of other effects of frontal lobe lesions do not readily apply to our results, it is possible that further analyses of these results may be helpful in understanding them. As we have pointed out previously, the emotional alterations following OF removal vary according to the circumstances of testing. The increase in frequency of aversive responses to humans following OF ablation is not seen when the observer has become familiar by extensive pre-operative testing. Also, the degree to which aggressive reactions are decreased in frequency depends upon the test situation for this deficit was more severe when the emotion-provoking stimulus was a human observer than when it was a doll. Further, at a particular time following surgery the OF monkey may exhibit no apparent alteration in aggression toward other monkeys, while showing little or none of the aggression toward humans that it displayed pre-operatively.

Further analysis of these findings suggests that one factor determining the severity of the OF monkey's deficit in aggression is the degree of threat provided by the test situation. For, the presence of a human observer, toward which the OF monkeys showed a severe impairment in aggression, evoked more emotional responses from normal monkeys than did the presence of a doll, toward which the OF monkeys showed a less severe impairment in aggression. Moreover, the OF monkeys showed a loss of aggression in the social situation when the monkey occupying the second position in the colony threatened and attacked them frequently. Thus, one might infer from these facts that following OF lesions, monkeys are particularly impaired in reacting to highly threatening situations in an effective manner characteristic of the species — that is, by aggressive gestures and attack. What kind of disturbance might underlie an inability to react aggressively to highly threatening situations? One possibility is a disturbance of arousal; there is evidence that hyperarousal is produced by frontal lesions (Kennard et al. 1941, Malmo 1942, Issac and Devito 1958, Lynch et al. 1969). According to this view, the influx of excitation generated in subcortical arousal mechanisms by stressful situations is not properly modulated following frontal lesions. Assuming that the degree of perceived threat is determined by the level of activity in the arousal system, what is perceived as moderately threatening by the normal monkey would be perceived as intensely threatening by the frontal monkey. Consequently, the frontal monkey shows a decrement in aggression, and an increase in aversion, as a normal monkey might in an intensely threatening situation.

Although this hypothesis is highly speculative, it is amenable to experimental test. According to this view, monkeys with OF lesions would be expected to show autonomic sings of increased arousal to the same stimuli toward which they show deficits in aggression and increased aversion. In order to test this hypothesis, the following experiment was performed (A. Harrison-Ables and C. M. Butter, unpublished data). Seven monkeys were tested first for emotional reactions to a human and to a doll and then for autonomic reactions to the same stimuli. Emotional responses to the doll were observed according to the same procedures used in prior experiments; emotional reactions to a human were observed and recorded in a similar manner, according to procedures described above. Following the behavioral observations, the monkeys were placed in restraining chairs and EKG and respiration were recorded while the animal was in the test situation. EKGs were recorded from silver-silver chloride electrodes taped to the chest. EKG signals were fed into a tachometer, amplified and recorded on a polygraph. Respiration was recorded by a strain gauge strapped to the chest; amplified signals from the strain gauge were also recorded on polygraph paper, as were signals denoting the onset and offset of the light which illuminated the human or doll. Prior to testing with the doll or human, all subjects were habituated to the onset and offset of light in the compartment adjoining the test chamber. The procedures involved in these tests were the same as those used in prior behavioral tests, except that the period between stimulus presentations varied between 2 and 4 min, the precise time depending upon when the animal was quiet and showing regular respiration and heart rate. In addition, the first two trials in each session were habituation trials in which the adjoining compartment was illuminated, but no stimulus object was present. Following the completion of testing, four of the monkeys received bilateral lesions of OF cortex, while the remaining three were sham controls which underwent surgical procedures as in OF surgery except for the removal of OF cortex. Following a 2-week recovery period, all the animals were retested in the same manner as they were tested prior to surgery.

The results of behavioral testing, which have been described previously, are shown in Fig. 4. To summarize these findings, following OF surgery, the monkeys showed both a greater increase in frequency of aversive reactions to both human and doll and a greater decrease in frequency of aggressive reactions to these stimuli than did the sham controls. Table III shows average EKG reactions of the two groups to

TABLE III

Average EKG reactivity to doll and human before and after OF (orbital frontal) or sham surgery[a]

	Doll		Human	
	Pre-op	Post-op	Pre-op	Post-op
OF-1	107.3[b]	102.5[b]	101.3	103.1
OF-2	104.0[b]	106.9[b]	102.0[b]	103.0[b]
OF-3	102.8	103.5	99.9	100.6
OF-4	105.8	104.4	104.0	103.8
$\bar{X}$	104.9	104.3	101.8	102.6
S-1	101.1	100.7	100.1	100.5
S-2	100.8	100.8	101.2	102.4
S-3	103.7	100.6	101.5	102.5
$\bar{X}$	101.9	100.7	100.9	101.8

a Reactivity defined as:

$$\frac{\bar{X}_{\text{EKG Stim.}} - \bar{X}_{\text{EKG Prestim.}}}{\bar{X}_{\text{EKG Stim.}} + \bar{X}_{\text{EKG Prestim.}}} \times 100 + 100,$$

where:

$\bar{X}_{\text{EKG Stim.}}$, average heart rate in stimulus periods,

$\bar{X}_{\text{EKG Prestim.}}$, average heart rate in prestimulus periods.

b Including sessions in which animal showed movement.

the human and to the doll. The scores shown in this Table are average percentages of heart rates in 10 sec periods preceding each trial. A value of 100 indicates that there was no change in average heart rate in the stimulus period compared to the prestimulus period; values greater than 100 indicate an increase in average heart rate, while values less than 100 indicate a decrease in average heart rate compared to the prestimulus heart rate. As seen in Table III, all the animals, with the exception of OF-3 in tests with the human, showed EKG reactions to the stimulus objects. However, the OF monkeys, like the sham controls, failed to show consistent increases in EKG reactivity to either the human or doll following surgery. Actually, peak heart rate reactions to these stimulus objects were greater than the average values shown here, since heart rates tended to increase in the first few seconds of each stimulus presentation and then decline to the prestimulus rate in the remainder of the period. However, analysis of peak EKG reactivity failed to disclose any consistent group differences. There was a positive, high correlation between heart rates and aversion scores toward the same objects ($r = +0.76$) for the OF monkeys, but not for the sham controls ($r = +0.29$). However, there was no significant correlation between heart rate and aggression scores for either group. Finally, respiratory irregularity, which frequently accompanied EKG increases in stimulus periods, was not affected by OF surgery (Table IV).

TABLE IV

Average per cent respiratory irregularity to doll and human before and after OF (orbital frontal) or sham surgery

	Doll		Human	
	Pre-op	Post-op	Pre-op	Post-op
OF-1	52.0	55.0	54.0	56.5
OF-2	59.0	43.5	44.0	29.5
OF-3	46.5	31.5	45.5	33.0
OF-4	43.5	36.5	39.5	29.7
$\bar{X}$	50.2	41.6	45.7	37.2
S-1	44.5	51.5	51.5	52.0
S-2	33.5	34.5	34.5	38.5
S-3	34.5	34.5	35.0	23.5
$\bar{X}$	37.5	40.2	40.3	38.0

Thus, the results of this experiment failed to provide any evidence that OF lesions produce hyperarousal, at least in threatening situations in which the OF monkeys showed alterations in emotional behavior. Consequently, the hypothesis that OF monkeys showed decreased aggression and heightened aversion because of abnormally high arousal is in serious doubt. Of course, it is entirely possible that frontal lesions dissociate behavioral from autonomic arousal, as the results of recent experiments suggest (Kimble et al. 1965), so that EKG and respiration indices do not parallel behavioral arousal. Nevertheless, until evidence to the contrary is provided, we are forced to conclude that the postulated relationship between autonomic states and emotional states in OF monkeys does not exist.

On the other hand, this conclusion does not entail rejection of the hypothesis that frontal lesions produce some autonomic dysfunction. For the finding that the loss of aggression in OF monkeys is most severe in highly threatening situations suggests that OF ablation may disturb neurohumoral mechanisms which prepare the organism for responding appropriately to conditions of stress. In fact, the possibility of an OF lesion induced breakdown in stress mechanisms is not entirely speculative, for it has been shown that monkeys with selective lesions of posteromedial OF cortex collapse much sooner than do unoperated monkeys when barometric pressure is rapidly reduced by means of a decompression chamber (Fulton 1951).

It would be rash to speculate further concerning the basis of the OF monkey's emotional alterations. However, one final point should be made: our results suggest a close relationship between OF cortex and the limbic system with regard to the control of emotion. For the findings reported here indicate that PMOF cortex, which is closely tied to limbic structures functionally and anatomically, is critically involved in emotional expression. Moreover, our findings also imply that the anatomical interconnections between PMOF cortex, the DMN nucleus and the amygdala as described by Nauta (1962) may provide the structural basis for a mechanism controlling emotions. Furthermore, the similarities and differences between the behavioral effects of lesioning these structures suggests that PMOF cortex and the DMN nucleus share some common role which is different from that of the amygdala. Certainly one conclusion to which our findings clearly point is that when considering limbic control of emotions, the OF cortex must also be considered. Another conclusion, and one the implications of which are more difficult to comprehend, is that the frontal lobes partake in many different functions, including those involved in emotional behavior, as well as those involved in conditioning and problem — solving behavior.

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