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ROLE OF PREFRONTAL AND ANTERIOR TEMPORAL CORTEX IN SOCIAL BEHAVIOR AND AFFECT IN MONKEYS

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Abstract. Prefrontal or anterior temporal but not cingulate cortex lesions lead to major deficits in all aspects of social behavior including maternal protectiveness, aggressiveness, group cohesiveness, defense of territory, maintenance of hierarchical status, and, even, sexual behavior. Lesions of visual association cortex, on the other hand, fail to produce such deficits. Rather, these deficits appear to be specifically emotional in nature and not related to impairments in perceptual or sensory functions. Prefrontal and anterior temporal cortical lesions also produce major losses in both facial expressions and in vocalizations suggesting these functions in the rhesus monkey participate primarily in emotional and social communications. In keeping with this interpretation, present studies show a major difficulty in bringing rhesus monkey vocalizations under instrumental or conditioned control. Thus, in this species, there exists a major difficulty of access between the volitional control mechanisms of the cortex and the vocalization apparatus. The present findings support the hypothesis of a dual control of the face and voice in man whereby there still exists prominently the emotional or affective element which mediates all involuntary or spontaneously emotive expressions of feeling. This more primitive and aged mechanism for face and voice control utilizes quite different neural control mechanisms than does the more recently derived system which provides for a volitional face and voice control. This more recent system has developed embedded within the posteriorly located analytic and mnemonic cortical tissues and provides for communications between individuals within the species at symbolic, verbal levels.

The present paper develops a hypothesis regarding the functions of prefrontal and anterior temporal cortex in the monkey. This hypothesis arose from comparison and contrast with the better-known functions of other regions of the primate brain.

Each of the several lobes of the cerebrum was separately removed in several different rhesus monkeys during studies of cortical connectionism (Myers 1967). To interpret the general significance of the resultant fiber degeneration patterns, a rough diagram was developed depicting the functional significances of the various cortical regions. The schema evolved to fit this need appears as the present Fig. 1. In establishing this crude map, each zone of the cortical surface was examined as to its probable function.

No difficulty was encountered in defining rough boundaries delineating the visual, the auditory or the somatic sensory-voluntary motor mechanisms. The broad, posterior expanses of special zones of cortex which receive the inputs of these several sense modalities were believed generally to be involved in analyzing the significance of these sensory inputs, in establishing memories, and in regulating motor responses in relation to them. The motor responses so generated were considered largely voluntary.

The frontal eye fields, located between the two rami of the arcuate sulcus, receive their main source of cortical stimulations from the visual cortical sector (*see*, for example, Myers 1967). Their electrical stimulation leads to controversive eye and head movements (Smith 1949, Wagman et al. 1961) while lesions in these zones temporarily disturb such movements (Holmes 1938). Thus, the frontal eye fields were considered a part of the motor outflow mechanism of the visual functional sector but separated off and located adjacent to the somatic sensory-voluntary motor apparatus. The frontal eye fields, thus considered, still belong to the posterior sensory analytic and volitional movement fields while the prefrontal cortex lies more anteriorly.

In attempting to roughly define the functional significances for all cortex zones, several regions remained whose contributions were unclear. These included the cingulate, the prefrontal, and the anterior temporal cortical regions. Examine available data as we might, evidence was lacking pointing to a receptive, a sensory analytic, a mnemonic, or a voluntary motor function for any of these regions. Thus, it was necessary to cast about for alternative functional categories that would adequately describe the significance of these cortical zones.

Development of hypothesis

A point of view regarding the possible functional importance of the prefrontal and anterior temporal cortex may be dealt with first. These two regions likely sustain rather similar functions because they are closely connected together through the uncinate fasciculus. The prefrontal cortex sends large numbers of fibres to the anterior superior portion of the superior temporal convolution while the temporal polar cortex sends many fiber bundles to end in the prefrontal cortex (Nauta 1964, *see also* Myers 1967). These two cortical regions also share relationships with the dorsomedial thalamic nucleus in common. The close tie between the orbitofrontal cortex and this thalamic nucleus has been known for some time (Walker 1938, Rose and Woolsey 1948) and has been reemphasized in the present conference. However, less well appreciated is that the anterior portion of the temporal neocortex also projects to the dorsomedial nucleus. However, the size of this projection is small and ends on only a few small nerve cell groupings located just off the thalamic midline (Whitlock and Nauta 1956, R. E. Myers, unpublished data). This commonality of interrelationship with the dorsomedial nucleus, then, also tends to reinforce the proposal of a commonality in the functioning of the prefrontal and the temporal polar regions.

What function may be proposed for these two zones? Consideration of available data at the time indicated a prominent relation between lesions of the prefrontal cortex and delayed response and delayed alternation deficits (Jacobsen 1935, Blum 1952, etc.). However, from an overall biological-ethological point of view, the demonstrated occurrence of delayed response deficits following prefrontal lesions failed to supply critical answers as to the role which these cortex zones may play in the everyday lives of animals.

On the other hand, human clinical data suggested that the human prefrontal cortex functions importantly in defining personality structure and in regulating interpersonal relations and emotion. Prefrontal lesions in the human lead to profound social behavior deficits. Patients with prefrontal lobotomy, for example, exhibit witzelsucht or "the making of poor jokes and puns and the telling of pointless stories, at which the patient is himself intensely amused." (cited from Dorland 1942). Patients with prefrontal lobotomies make irresponsible business decisions, are often promiscuous and overbearing in their sexual behavior, exhibit uncontrolled profanity and are often abusive (Harlow 1868, Kalodny 1929, Penfield and Evans 1935, Rylander 1939, Hécaen 1964).

Epileptic discharges originating within these zones (in relation to mesial temporal sclerosis, intrinsic tumors, sphenoidal ridge meningiomas, etc.) often lead to striking and bizarre changes in behavior. Seizure activity originating in these zones is often ushered in by auras consisting of stark feelings of anxiety or fear (Lennox 1951, Williams 1956, Efran 1957). During the epileptic attacks themselves or as a part of the confusional state afterwards, affected people may perpetrate acts of violence including deadly assault or murder (Pond 1961, Falconer and Serafetinides 1963). It often is dangerous to attempt to constrain such patients during the postictal confusional state. These general clinical findings suggest a relationship between these cortex zones and affective or social behavior.

The functional meaning of the cingulate cortex remains less clear. In general, the cingulate cortex is thought to be involved with autonomic regulations (Kaada 1960) and with motivation (McCleary 1961). These general suppositions along with important points of anatomical contact between the cingulate and the prefrontal cortex (Pandya et al. 1971) suggest the cingulate cortex also may function in the regulation of social behavior.

Scattered observations

Several apparently scattered findings are now described relating to earlier studies carried out in the Laboratory. Ultimately, these facts will fit into an interpretation of the neurology of social behavior.

Facial movements. The large unilateral lobar lesions earlier carried out in relation to the anatomical studies yielded an interesting and, at the same time, unexplained finding. Total one-sided removals of the entire frontal lobe led to only minor (10–30%) losses in facial movement on the opposite side (Myers 1968). Figure 2 depicts such an animal 14 days after total resection of his left frontal lobe. A nearly symmetrical use of the face quickly returned. By contrast, comparable lesions in the human would have led to major contralateral facial paralyses. As anticipated, the unilateral occipital and parietal lobe removals occasioned no deficits in contralateral facial movement while, paradoxically, the one-sided temporal lobe removal again produced a mild but definite contralateral facial weakness. The degree of the opposite sided facial movement deficit following the temporal cortical removals at times approached that observed following the total frontal lobe ablations. The finding of any facial weakness following temporal cortical removals was paradoxical because no relationship between the temporal neocortex and facial movements has heretofore been suspected. However, this deficit appeared repeatedly following our temporal cortex removals.

In further studies, the precentral gyrus alone was removed. A variable effect on contralateral facial movements was obtained, the lesions, in some instances, exerting no effect and sometimes producing the mild effect already described. On the other hand, cortical removals restricted to the prefrontal region caused opposite sided facial movement impairments equal to those which followed removals of the entire frontal lobe. The contralateral facial weakness associated with frontal lesions, though mild, still appeared more reliably following the prefrontal than the precentral lesions. These studies thus suggested a relationship be-

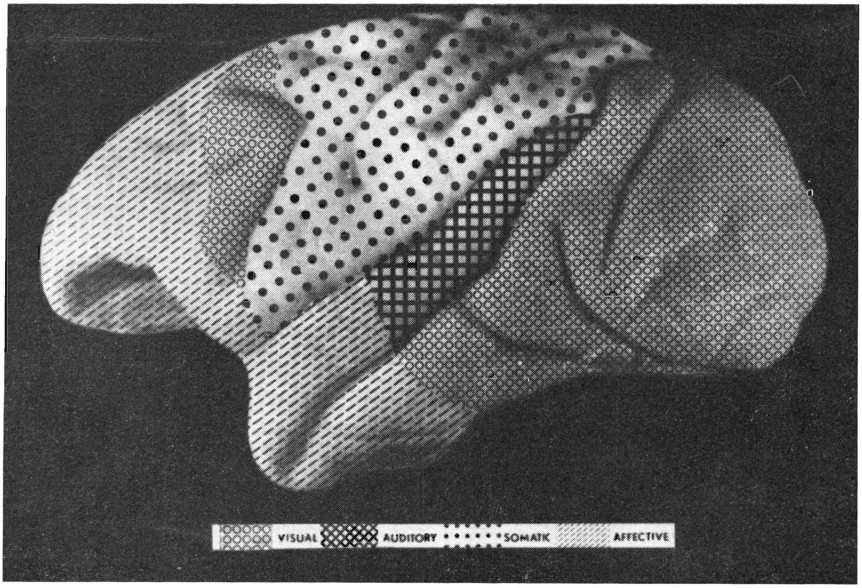

Fig. 1. Surface view of monkey brain grossly delineating the territories of the several functional sectors including the zones underlying vision, audition, and somatic sensation. These three functional sectors together constitute the cortical mechanisms regulating volitional movements. The cortex zones subsuming affect or emotion and regulating social and instinctual behavior patterns lie within the prefrontal and anterior temporal cortical regions.

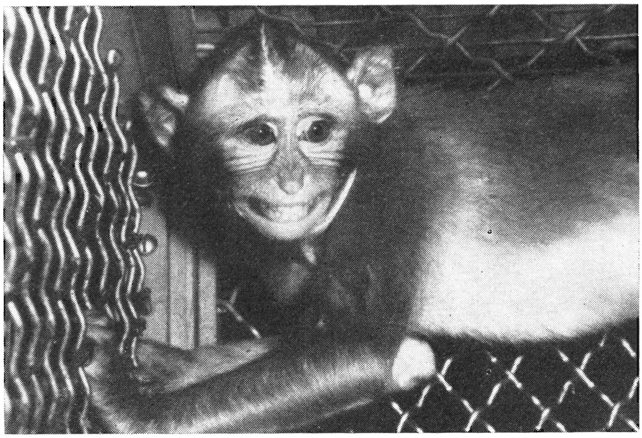

Fig. 2. A juvenile rhesus monkey following total resection of his left frontal lobe. Despite the inclusion of the entire precentral gyrus, this animal exhibited only a slight contralateral facial weakness. Note the general symmetry of his facial action in this defensive grimace.

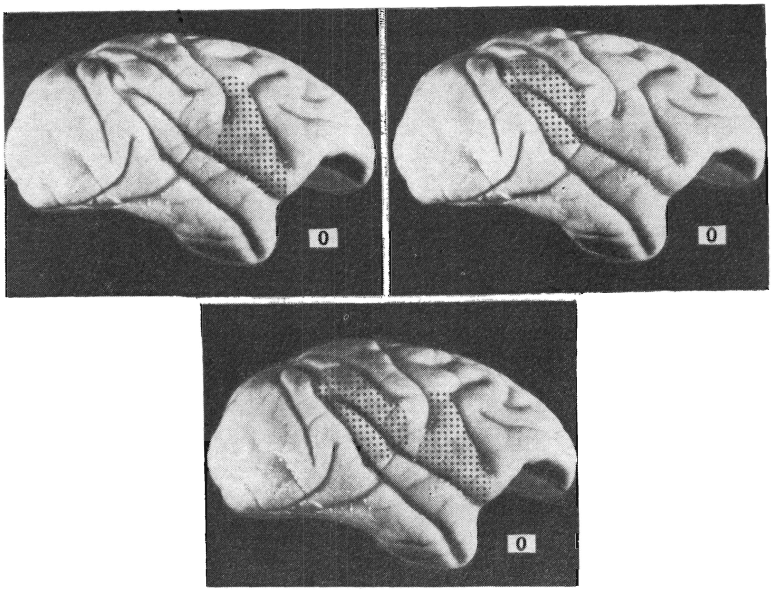

Fig. 4. Effects on monkey spontaneous vocalization of cerebral lesions in brain areas most closely homological to speech areas in man according to their general topography and location. None of these lesions or any combinations thereof led to long-lasting alterations in rhesus monkey spontaneous vocalizations. These results support the thesis that rhesus monkey vocal responses are supported by different neural mechanisms than is speech in the human (From S. Y. Yamaguchi and R. E. Myers, unpublished data).

Fig. 5. *Paradicticus potto.* This species exhibits only an impoverished face and voice use in expressing states of affect and in social communication. Such underdeveloped face and voice use characterizes prosimians in general (staff photograph, National Zoological Park, Smithsonian Institution).

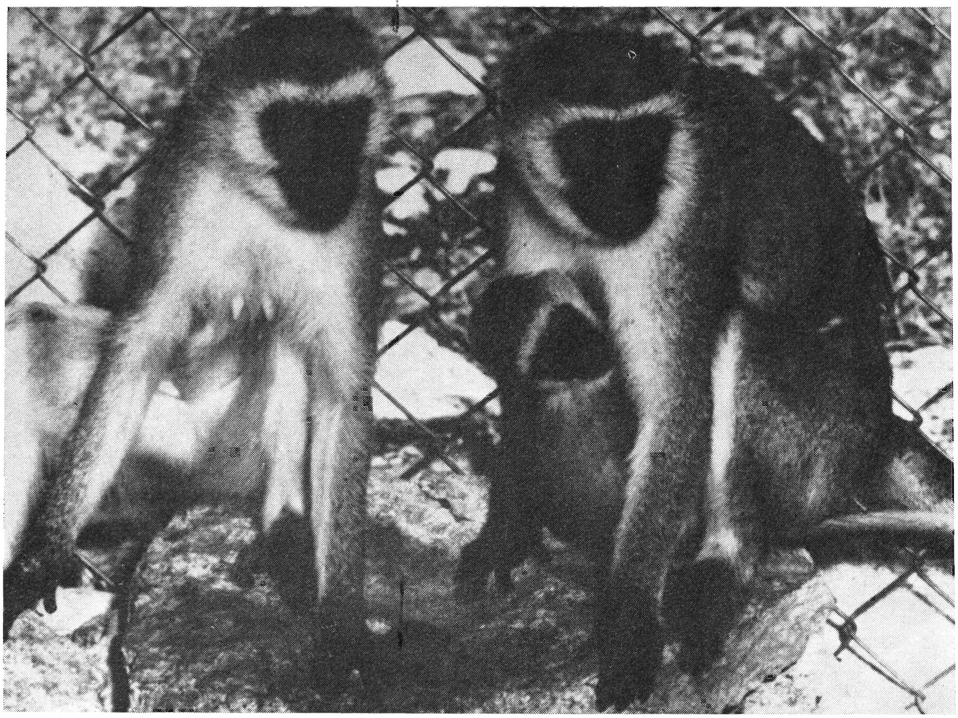

Fig. 6. Two African green monkey (*Cercopithecus aethiops*) females and offspring illustrating their relatively fixed faces. In contrast to the rhesus monkey, this macaque species still exhibits a somewhat impoverished face and voice use for affective and social communication.

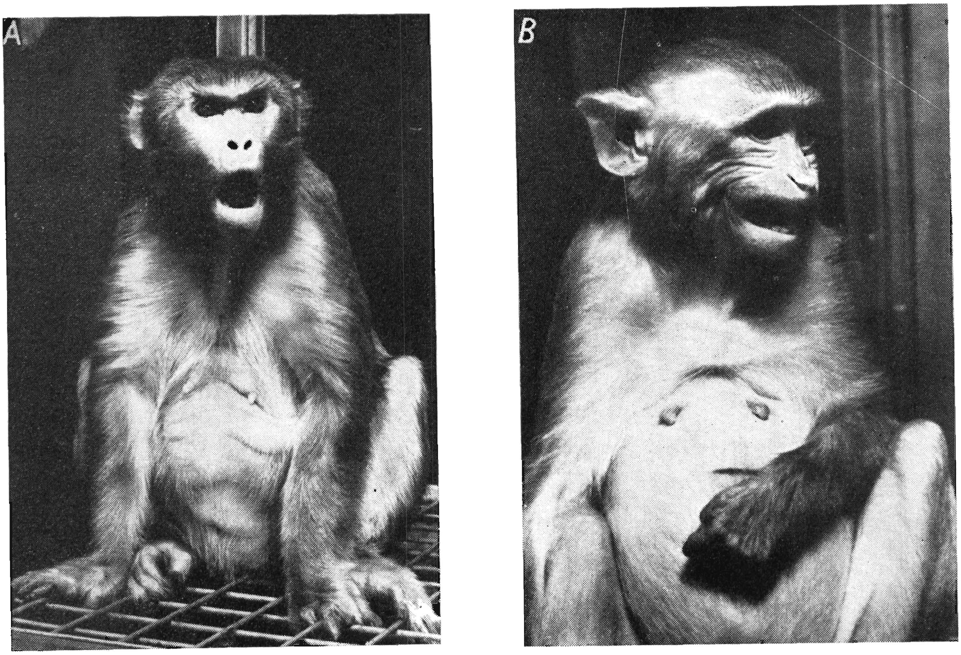

Fig. 7. An adult and a juvenile rhesus female manifesting two different affective states. The adult is exhibiting a mild threat expression. The juvenile, on the other hand, is expressing a state of submission. These behavior complexes or stereotypes involving both facial expressions and vocalizations and often, also, attitudes of the body, are utilized in the expression of affect in these animals and are also used for the maintenance of status within rhesus monkey social groups.

tween the prefrontal and the temporal cortex and contralateral facial movements. These curious findings remained unexplained at the time. We shall return again to these findings.

Failure of vocal conditioning. Studies on the neurology of vocalization in the rhesus monkey were initiated (Yamaguchi and Myers 1972). To study brain lesion effects on monkey vocalization, it seemed desirable to condition monkey vocalizations in such a way that a standard, controllable vocal emission rate could be generated. Thus, a concerted and extended effort was carried out to condition rhesus monkey vocalizations.

In the beginning, we believed that monkey vocalizations would be readily conditionable. However, to our surprise, these efforts at rhesus monkey vocal conditioning were without success. This failure extended also to attempts at establishing discriminative patterns of vocalization.

In these studies, the monkeys were brought into the conditioning room and transferred to a training box. Initially, attempts were made only to encourage them to vocalize by delivering single food pellets each time they spontaneously vocalized. Over a period of time, some animals did indeed increase their vocalization rates. However, this increase also may have been brought about by the animal's accommodation to the problem box and to their general expectation of food reward while in the test situation.

It appeared necessary, then, to attempt to differentiate the animals' patterns of vocal response according to whether a positive or a negative stimulus was presented. Efforts were made to teach the animals to inhibit their vocalizations in the presence of a red and to increase their vocalizations in the absence of a red light. Despite prolonged efforts at such conditioning, these animals failed to show signs of differential response rates in relation to the conditional stimuli. Later, these same animals quickly learned to control their rates of bar-pressing in accordance with the presence or absence of the same stimuli. Thus, the animals were capable of establishing differential patterns of responding to these stimuli, but rather experienced difficulties in bringing their vocal responses under such control that they could be regulated or modulated differentially. The curves of Fig. 3 illustrate these findings.

Thus, special difficulties existed in the conditioning of monkey vocalizations. This point of view was supported by earlier work with South American monkeys where a similar difficulty in conditioning monkey vocalization was found (S. A. Myers, 1965). However, in contrast to the present findings, Shirley Myers was able to demonstrate some signs of a conditionable vocalization control in a few South American monkeys. What remains common to the two studies, however, is the extreme difficulty which is encountered in attempting to develop differential vocal

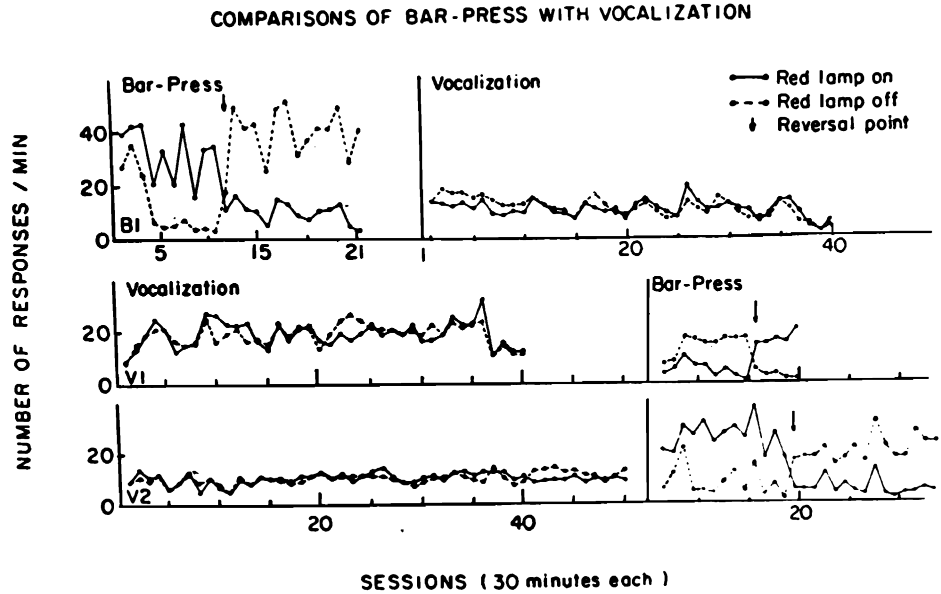

Fig. 3. Test results with 3 animals on differential bar-press and vocalization conditioning. A differential response pattern according to whether a red lamp is on or off easily emerged in relation to bar-press but not vocalization. These results reveal a major difficulty of access of the monkeys' vocal apparatus to the volitional control mechanisms of the brain. At the arrows, the reward-punishment values of the stimuli were reversed. (From Yamaguchi and Myers 1972.)

conditioned responses. These general results seem to imply a limited availability of the monkey vocal apparatus to voluntary motor mechanisms in the brain. We shall return to this point again.

Are there "speech" areas in the monkey brain? Even though efforts at monkey vocal conditioning failed, animals typically vocalized spontaneously in the test box at predictable and regular rates. Animals exhibiting high spontaneous vocalization rates were used to study the neurology of vocalization in the monkey. Cortical areas were chosen for removal which, by virtue of their locations, were considered potentially the most homologous to the human speech areas (*see* Fig. 4). Thus, in different animals, bilateral removals were carried out in the face region of the precentral convolution (similar in its location to Broca's speech area), on the mesial surface of the precentral convolution (similar in its location to Penfield's supplementary speech area), the inferior parietal convolution (comparable in its location to the supramarginal speech area), and the superior temporal convolution (similar in its location to Wernicke's speech area). Following any single one of these lesions in different animals, and even following their serial removal in the same animals, significant alterations in the patterns of spontaneous vocalization failed to appear. Thus, in the rhesus monkey, cortical areas located comparably to the human speech areas appeared not to significantly regulate or affect the emission of spontaneous vocal responses.

Phylogeny of facial expression. The phylogeny of facial expression within the primate order may now be considered (Myers 1968). Although the following discussion relates primarily to movements of the face, a similar generalization applies to vocalizations.

The prosimians are examined first. These forms, which include the lemurs, lorises, galagos and tarsiers, depend little upon their facial expressions for social signaling functions. The complexity of face use among these animals, in general, is of low order. Figure 5 presents the appearance of a potto, a typical prosimian, indicating its limited potential for facial expression.

The ceboidea and cercopithecoidea, the groups which include the new world and old world monkeys, yield rather a mixed picture. Some monkey species of each group continue to manifest a limited face use while others exhibit a more developed and varied face and voice use. When facial expressions do appear, they serve to express the affective states of the animals. An example of a species still exhibiting an impoverished use of the face is the African green monkey or *Cercopithecus aethiops.* Figure 6 depicts a small group of these animals where their fixed, mask-like faces are apparent. The faces of these animals reveal little about the emotional state of the animals. An example of another species displaying a more rich and complex use of the face is that of the rhesus monkey. Figure 7 portrays two rhesus monkeys each exhibiting a quite different emotional state through its facial expression.

Thus, the utilization of the face and, to some extent, of the voice for the communication of states of inner being between individuals within a social group seems to first develop prominently within the primate order at the "monkey" level. At the same time, facial expressions among these animals appears entirely involved in communicating specific states of emotion such as aggressiveness, defense, anxiety, threat, etc.

At the level of the *Pongidae* or higher apes, the first evidence appears for a more extensive use of the face for voluntary acts not bound up in the expression of emotion. The chimpanzee, for example, manifests such a rich and highly developed capacity for voluntary control of lip movements that this organ takes on the dimensions of a major exploratory organ. Chimpanzee lips are prominently used for tactual exploration and for manipulation of the environment in food inspection and food gathering. This type of face use, however, does not serve social communication functions, but, rather, allows for sensory exploration and information gathering. These latter functions, it may be proposed, represent the early stages in the development of facial musculature use for volitional acts.

At the human level, a definitive voluntary use of the face has developed. The faculty of speech represents such a volitional face and voice activity. The human ability to imitate or mimic states of affect as exemplified by "affected" or "false" smiles or laughter represents still other examples of volitional face use. However, the human still preserves a well developed propensity for spontaneous face and voice utilization in expressing genuinely felt emotions or inner states of being. Thus, unaffected or real smiles and laughter, or crying and screaming (as in fright or fear), exemplify a continued involuntary or emotional face use in the human. The richness and diversity of face use deriving from this dual control of the face and voice is largely absent in other primate forms including the higher apes.

These last paragraphs have developed the argument that lower primates manifest only in impoverished use of their face and voice for communication functions. At the "monkey" level, a richer face and voice use develops for social communication between animals within a species, but, at this early developmental stage, these manifestations appear largely, if not entirely, under the control of involuntary affect-expressing neural systems and reflect primarily inner states of feeling. With higher apes, and particularly, with man, there develops in addition to this more primitive system of involuntary affective control a volitional regulation which permits man, and, fractionally, the higher apes to use their faces and voices voluntarily for the expression of ideas and information largely gathered and cared for by the posterior sensory analytic and mnemonic cortex regions.

Studies on social behavior and affect

Island studies. We shall now return to the earlier hypothesis that the anterior temporal and the prefrontal cortical regions function in regulating social behavior and affect. The first definitive studies testing this hypothesis were carried out on Cayo Santiago, an island colony of free-ranging rhesus monkeys located offshore in Puerto Rico (Myers and Swett 1970, Myers et al., in press). One of seven social groups (Group E) inhabiting the island in 1967, consisting of 106 animals, was designated for experimental studies. Specific animals within this group were identified and extensively observed with respect to their patterns of interactions with other animals. One by one, these subject animals were removed for limited time periods for the surgical removal of either the prefrontal or the anterior temporal neocortical regions. Still other animals sustained bilateral ablations of the cingulate gyri. The animals, once operated upon, were returned as quickly as possible to their social groups on the island and observed for changes in their patterns of social interaction.

The effects were startling. The operated animals were released in proximity to or within their social group. With rare exception, the animals with prefrontal or anterior temporal resections, on release, passed through their social group and disappeared into the underbrush beyond. During the brief contact with their group, no evidence was found for any active rejection of or negative responding to the operates on the part of the group members. Rather, the operates, on their own, failed to approach and to reestablish their social group relations. This result is the more remarkable when it is remembered these animals have spent their entire lives until operation in association with their group. From infancy, these animals have developed a rich and complex system of relations with the other animals, and, particularly, with their family members. These contacts and interrelations have defined in a detailed manner the quality of the animals' existences prior to surgery. The failure to return to family and social group and the adoption of an isolated existence instead suggest a maximum in social behavioral deficit following either of the two lesions.

In contrast to the major effects of the prefrontal and temporal polar lesions, the animals with the bilateral cingulate resections not only rejoined their family and social groups, but otherwise appeared unaffected by the surgical procedures. Thus, the prefrontal and the temporal polar, but not the cingulate, cortical areas play significant roles in the regulation of social behavior and emotion in the rhesus monkey.

Gang cage studies. These latter experiments utilizing free-ranging animals were somewhat unsatisfactory because of the non-return of the prefrontal and temporal polar operates to their social group. This failure of return and the taking up of solitary lives precluded any detailed judgements as to the nature of the behavioral changes produced. Thus, further studies were carried out on six small social groups of rhesus monkeys held in large gang cages (E. A. Franzen and R. E. Myers, in preparation). These groups, each consisting of 6–12 animals, were derived from a single large social group removed from Cayo Santiago. Each enclosure group contained an adult male and several adult females along with their offspring.

The behavior of individual animals and the overall patterns of social interaction of these animals within the small social groups were studied in detail over many months. The methodology was that used for many years in field studies of the rhesus monkey and consisted of checklists describing a variety of behaviors exhibited by these animals within the social context. Behavioral categories observed included animal displacements, groomings, presentings, mountings, proximity scores, hierarchical changes, etc.

After determining the patterns of social interaction within these small social groups, individual animals were removed one by one and subjected to prefrontal, anterior temporal, or cingulate cortex removals. Four other animals were subjected to resections of major portions of the visual association areas bilaterally. One to two days following surgery, the animals were returned to their groups of origin and again observed in detail.

Once more, the animals subjected to cingulate gyrus removals failed to show any apparent changes in their patterns of interaction with other animals within their groups. However, the animals undergoing prefrontal or anterior temporal cortex removals exhibited global alterations in all categories of social behavior. Major losses were sustained in their grooming frequencies, maternal behavior, sexual behavior, overall participation in group activities, contiguity to other animals, etc. Clear-cut decreases in the use of facial expressions and vocalizations also appeared. These two lesions individually robbed the animals of much of the richness and complexity of their social behavior. Following surgery, their patterns of response to social signals emitted by other animals appeared subdued and largely devoid of affect. The deficits were more severe following the prefrontal than the anterior temporal lesions but the syndromes produced by both lesions were closely similar. However, the animals with the prefrontal removals exhibited prominent aimless pacing activities not apparent in the temporal operates.

These gang cage studies showed that, in addition to the loss of social group affinity which follows prefrontal or temporal polar lesions, far-reaching deficits in all aspects of social behavior also appear when these animals are artificially retained within their social groups by wire mesh walls.

The social behavioral deficits exhibited by the prefrontal operates might be thought to be due to some type of visual agnosia since animals with such lesions have been described as suffering from deficits in visual perception (Kennard 1939). Similarly, the deficits following the temporal polar lesions also might be attributed to perceptual distortions produced by lesion encroachment onto adjoining cortical areas known to be visual in importance (areas 20 and 21). To investigate these possibilities, four animals from the small social groups were subjected to extensive bilateral ablations of visual association cortex. These animals, on restoration to their groups, exhibited no definable behavioral deficits. This unexpected negativity of findings following the extensive visual associational lesions served to underscore the specificity of the social behavioral deficit following the anteriorly located cortical lesions. Thus, it seemed unlikely the deficits could be accounted for as some type or other of visual agnosia or imperception.

Social signaling. At the same time as the gang cage social studies were carried out in the field, other investigations were pursued in relation to patterns of test box vocalizations in the central laboratory (R. E. Myers and S. Y. Yamaguchi, unpublished data). Animals with known rates of spontaneous vocalizations were subjected to prefrontal or anterior temporal cortex removals. Significantly, these ablations led to major losses in vocalization frequencies. Again, the effects of prefrontal lesions were the more severe. However, with both lesions, significant permanent deficits in vocal responses were seen. When lesions of both of the two zones were combined, spontaneous vocalizations largely disappeared. Bilateral cingulate resections affected vocalization rates to a much less extent.

Synthesis

We may now try to put together these separate lines of evidence into a single coherent interpretation. We have seen that the posterior expanses of cortex function primarily in the analysis of sensory input, in memory function, and in the origination of volitional responses in direct or indirect relation to these inputs. In contrast, the anterior zones of cortex including the prefrontal and the anterior temporal cortex appear to play a role primarily in regulating social behavior, in social signalling, and in the underlying states of affect. These zones of cortex play a role in emotion and affect not only as to their expression in the form of behavior, but also in relation to the actual existence of these vital affective states. The basis for this last assumption is the non-return of the animals to their familial and social groups and their losses of all aspects of involvement in social activities.

The prefrontal and anterior temporal polar regions in the rhesus monkey have been shown to initiate or regulate facial expressions and vocalizations. At the same time, posteriorly located analytic and mnemonic systems that largely organize voluntary movements seem to play little role in the direct control of these activities. The general lack of effect on vocalization of lesions in the "speech areas" and the general difficulty of conditioning of vocal responses in the rhesus monkey seem to reflect this fact.

The utilization of the face and voice in the monkey, then, is believed largely under affective control and to be almost entirely involuntary.

Monkey facial expressions and vocalizations seem predominantly given over to the expression of inner states of being and to play primarily social signalling roles. It has been suggested that such a more complex use of the face and voice in social communication develops for the first time at the monkey level of primate evolution. At the time of its early evolution, complex face and voice use is restricted largely to expressions of affect. However, with further primate evolution through higher apes and man, a second separate and distinct control over the facial and vocal apparatus evolves yielding finally in man the added capability of voluntary control over the face and voice for the more detailed expression of the content of our consciousness and of the meaning of our past and present experience.

The work reported in the present paper was carried out in the Laboratory of Perinatal Physiology of the National Institutes of Health and included the contributions of a number of scientists working on a variety of aspects of the problem of the neurology of social behavior. Cited in the text and constituting the major portion of the work are the efforts of Drs. Shun-ichi Yamaguchi, Chester Swett, Michael Miller and Karlynn Bucher and of Miss Elizabeth Franzen. Their important contributions to the present report are gratefully acknowledged.

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