CHAPTER IV
DISCUSSION

Hughlings Jackson, by putting his concept of levels of central nervous activity, has been of great help for the understanding of the nervous functions. The basic functional organisation of nervous system for somatic activities lies in reflex arcs. A certain degree of co-ordinated behaviour in the caudal animal segments following transection of neuraxis is not an uncommon observation. With the growing needs of the organism as the phylogeny advanced, spinal behavioral activity was marked by its lessened range. Supra-segmental mechanisms developed in the brainstem and cerebral hemispheres to keep pace with the "progressive encephalisation of function".

The somatic sensory inputs coming from mostly the peripheral structures in the body travel centrally in
the spinal cord and form an important relay in brainstem areas. Here are present the lower centres which regulate the postural activity and other special type of activities produced in relation to external environment. These sensations are then projected to sensory areas of the brain where sensations reach consciousness. The information received by these sensory cortical areas, where the impulses are scrutinised, analysed and integrated before motor cortex is directed to execute the orders. Thus there lies quite an important part of the brain in between the sensory and the motor cortex which helps in integrating the sensory inputs into sensory areas with the motor execution from the motor side.

The central organisation of autonomic function is but little different from the somatic in this respect. Central autonomic mechanisms exhibit a crescendo of complexities. Many of the autonomic mechanisms capable of autonomous activity at spinal level, resemble somatic reflex arcs in many ways. The sensations coming from the various internal organs pass up the spinal cord in the form of diffuse fibre collections as compared to the well defined tracts on the somatic side. Besides setting up visceral reflex arcs at various levels of cord such pathways also extend to the brain where suprasegmental control mechanisms may be brought into play with feed back to the reflex centres. As a result of anatomical and electrophysiological studies most of these fibres are shown to project into the hypothalamus (Aidár et al. 1952),
some ascend at least as high as the thalamus whereas a few reach the cerebral cortex (Amassian 1951). Keeping in line with the presence of important postural and other regulation centres on somatic side in these brainstem regions, there also are located some of the spectacular autonomic mechanisms in addition to the flood of ascending and descending impulses passing through the reticular formation and modifying the activities of higher regions. In the diencephalon, autonomic functions are centred largely in the hypothalamus which is intimately related to the reticular formation of the brainstem. This small but a very important area of hypothalamus is distinguished by the richness of its fibre connections. Through the direct and indirect nervous connections with many other parts of the brain, lower brainstem, spinal cord and pituitary, it serves as a cross road for complicated circuits subserving patterns of behaviour, exteriorization of emotions, regulation of autonomic activity, appetite and thirst, regulation of secretion of pituitary and body temperature etc.

The hypothalamus receiving visceral afferents and also executing autonomic activities seems to be analogous to what the sensory and motor cortices represent on the somatic side. Recently it has been realised that in addition to the neocortical mechanisms there are very large and important areas in the brain, named as limbic system mostly present as a sort of cap on the top of the upper brainstem and which play an important part in the regula-
tion of visceral and endocrinal activities. This region has many significant connections with the hypothalamus and also possibly directly with the lower centres. The limbic system occupies the same position as the neocortical association areas and brings about integration of various autonomic activities.

Limbic system occupies an important place in regulation of not only visceral and endocrinal activities but also of affective behaviour. There is the developing concept that the constancy of "milieu interieur" is maintained mainly as a result of proper regulation of activities of internal organs which are in turn influenced by autonomic outflows and endocrinal secretions. Limbic system plays the dominant role in regulating the autonomic activities of the body. Not only the different parts of limbic system are well connected but it has rich connections with hypothalamus - 'the head ganglion of the autonomic' and possibly other centres in reticular formation of brainstem. Limbic system also regulates the endocrinal functions through its regulation of the secretory activity of the trophic hormones of anterior pituitary which ultimately lead to the regulation of secretion of the other endocrines. And finally this is the region from where the affective behaviour of the individual is regulated, integrated and controlled. Thus limbic system seems to have the unique distinction of maintaining and regulating the constancy of internal milieu.

Experimental studies on the somatic side (neocortex) reveal that specific response can always be predicted from
a particular sensory or motor area on stimulation or after ablation. No such specificity can, however, be obtained from the neo-cortical association areas. Much the same way one finds that specific visceral responses in terms of food intake, cardiovascular, respiratory and endocrinal activities and affective behaviour etc. can be obtained on stimulation or after ablation of a particular hypothalamic region (analogous to motor areas of neocortex). Responses from the limbic system, on the other hand, are not specific. One may well predict that there will be some change in visceral activity but there will always be an amount of unspecificity about it.

In view of this unspecificity observed from the limbic system the task becomes comparatively easier to explain the conflicting results that may be obtained on stimulation or ablation of limbic system. Unspecific changes in autonomic and endocrinal activities as well as affective behaviour may be observed on stimulation or ablation of different limbic structures. The effects produced will also depend upon extent of area involved. Destruction of small region may not produce any significant change. Thus while limbic system aims at amalgamating, adjusting and integrating the various visceral and endocrinal activities so that the body is maintained in the best possible condition to respond to the necessities imposed by the often changing environment, it does not have a specificity of its own. It, however, leads one to conclude that limbic system
regulates the internal activities in a similar manner as neocortex regulates the external activities. And also limbic system behaves as a well integrated functional entity rather than congregation of discrete areas performing isolated and specific functions.

Present study has also shown that sometimes even opposite results in terms of various visceral activities could be elicited from same anatomical zones of limbic system. Changing of parameters, aneusthesias and techniques had a profound influence on the results obtained. Individual variations and species differences were always there. Both facilitatory and inhibitory responses could be obtained from same regions in different animals or in same animal at different occasions.

If now an attempt is made to discuss the results obtained during the course of present study in light of what has been put forward above it shall possibly lead to a better understanding of the integrated picture as a whole and might explain the conflicting results obtained at times. The various autonomic activities are being briefly discussed in the following pages under separate headings before a general discussion is brought out on salient points towards the end of this chapter. The sequence of headings of different systems have been kept the same as in the other chapters of review of literature, materials and methods and of results.
The present study suggests that the cardiovascular medullospinal mechanisms can be influenced from different regions of limbic system. Rise of blood pressure was recorded in majority of the anaesthetised and the unanaesthetised animals on stimulation of posterior orbital gyrus and anterior cingulate. This confirms the previous observations by Spencer (1894); Bailey and Sweet (1940); Delgado and Livingston (1948); Saths and Brendler (1948); Smith (1945); and others in animals and by Livingston et al. (1947); Chapman et al. (1949) and Pool and Harskohff (1949) in man. In few of the animals a fall in blood pressure was also observed on stimulation of these regions. Crouch and Thompson (1939) proposed that each autonomic nervous centre, exerted both a sympathetic and para-sympathetic influence, with the predominance of one of these components in different areas and in different species. In addition different stages and types of anaesthetics used (Bailey and Sweet, 1940) could selectively influence one system thereby freeing the other component to exert its own effect. These factors might thus explain the opposite effects recorded from same regions in different animals. The occasional reversal of response obtained on increasing the intensity of stimulation may perhaps be due to spread of current to adjoining areas and involving a point producing opposite effects. Pressor and depressor points have been shown to be located hardly a few mm. apart in various regions.

Stimulation of temporal lobe structures, generally caused a fall in blood pressure in unanaesthetised and
anaesthetised animals and is in conformity with the work of Kaada (1951) and Wood et al. (1958). Interestingly enough, the cats showed a rise in blood pressure on stimulation of temporal polar region while the monkeys registered a fall. The differential response obtained may be perhaps due to species difference.

Pathways for corticofugal excitatory and inhibitory cardiovascular effects are largely unknown. It has been suggested that majority of corticospinal cardiovascular neurons are relayed in or pass through the hypothalamus (Spiegel and Hunsicker, 1936). From hypothalamus many of the descending pathways synapse in vasomotor centres of medulla while some pass outside the medullary vasomotor region and reach spinal cord. These pathways may thus help to understand the cardiovascular responses obtained from limbic regions. Wall and Davis (1951) proposed that arterial pressure effects evoked by stimulation of temporal pole are possibly mediated via bundle of fibres which travels with temporopontine tract to tegmentum and pons. The possibility of the brainstem reticular formation structures participating in vasopressor and vasodepressor activities have also been suggested. It would thus be clear that various cardiovascular responses obtained from different limbic regions might be mediated through hypothalamus or through connections with the reticular formation finally influencing the medullary vasomotor mechanisms, while some might be directly influencing the various spinal vasomotor loci.
Since no definite correlation between heart rate and blood pressure was observed on stimulation of different limbic regions in the unanaesthetised series of animals (Table 3) it was visualised that the changes in blood pressure are probably brought about by change of vasomotor tone. Studies were, therefore, attempted to see simultaneously the changes in peripheral vasomotor tone along with heart rate and blood pressure. As is evident from the results (Table 4) no consistent relationship could be observed between these as well. The rise in blood pressure was accompanied in some animals by an acceleration of the heart rate and peripheral vasoconstriction. In others rise of blood pressure could be seen with vasodilation and with no change or even a decrease in heart rate. The rise in blood pressure with acceleration of heart rate and vasoconstriction, or fall in blood pressure with bradycardia and vasodilation are not difficult to understand. But in those cases where rise or fall of blood pressure cannot be explained on the basis of changes in heart rate or in hand volume the possibility of changes in blood flow in other parts of the body should always be kept in mind. It has been shown that changes in splanchnic and cutaneous vasomotor tone in opposite directions might be produced on stimulation of certain hypothalamic areas while there may be no change produced in blood pressure. Thus the peripheral vasodilation or vasoconstriction alone may not be sufficient to explain the changes in blood pressure. Hoff and Green (1936) showed that peripheral vasomotor reactions were independent
of changes in arterial pressure and peripheral redistribution of blood may be initiated from cerebral cortex. It may, therefore, be surmised that inconsistent relationship between these three aspects of cardiovascular system may be influenced separately or the various factors might be working in different directions. This would produce a variety of combinations and therefore different pictures at such occasions.

In conformity with the other available reports localised electrolytic lesions involving various frontal and temporal regions did not produce any definite change in the cardiovascular activity. Extensive surgical lesions of the frontal lobe on the other hand led to slight fall in blood pressure and increase in heart rate with associated fall in rectal temperature. The fall in blood pressure associated with fall of rectal temperature supports the changes in hand volume being responsible for changes in blood pressure. The possibility of such a relationship has been discussed in more detail under the heading of body temperature.

**RESPIRATORY SYSTEM**

Changes in rate and amplitude of respiration were observed on stimulation of different areas of limbic system. The increase in rate and depth noticed on stimulation of posterior orbital gyrus in unanaesthetised animals and inhibition in anaesthetised animals is in uniformity with the work of many workers (Hess et al., 1952; Spencer, 1894; Bailey and Sweet, 1940; Delgado, 1947; Livingston et al., 1947; Sachs and
Brendler, 1948; Kaada et al., 1949 and Turner, 1954). The exact mechanism to explain the difference in response obtained in the anaesthetised and unanaesthetised animals from same zones is not well understood. It is likely that anaesthesia may be held responsible for such a disparity.

Stimulation of anterior cingulate led to increase in rate or depth of respiration or both in majority of the anaesthetised and unanaesthetised animals and is in agreement with the observations of Kaada (1951), Kremer (1947) and Speakman and Babkin (1949). Inhibition of respiration reported by Smith (1941 and 1945), Wood (1948) and Pool (1954) cannot be said to be in conflict with the results of the present study. Actually they had stimulated the part of anterior cingulate in front of the area studied during the present work. The acceleratory and inhibitory areas lying so close is quite possible and hence can well account for these opposite responses obtained.

In majority of the animals of both the anaesthetised and unanaesthetised series, slowing of respiration or complete arrest was observed on stimulation of amygdala, pyriform cortex, hippocampal formation and temporal tip. Similar observations were made by Kaada et al., (1949); Kaada (1951); Wall and Davis (1951); Glusman et al. (1953); Wood et al. (1958) and Ursin and Kaada (1960). In view of the wide extent of the cortical and subcortical fields yielding inhibitory responses one may think of the possibility of such a response through spread of current to other structures rather than the effect of stimulation of a particular region. Kaada (1951) attempted to rule out these factors by suppressing one or other connections by
local anaesthetics and reported that the responses obtained from the weaker inhibitory zones are not to any significant degree caused by physical spread of current to the more reactive adjacent cortical fields.

Hess (1938 and 1948) suggested that when metabolism, circulation and muscle tone are altered, respiration is also influenced in a corresponding manner. Simultaneous changes in respiration and blood pressure were observed in quite a good number of animals. It would be evident from these results that both these activities could be influenced on stimulation from a particular zone. On many occasions changes in respiration could be observed which did not seem to have any relation with the changes in blood pressure. This is highly suggestive of certain areas having independent control of respiration.

It was interesting to observe that the changes in respiratory activity and certain somatic motor effects could both be obtained from same regions of the limbic system. The participation of somatic structures and their importance in the normal respiratory activity is well recognised. These results, therefore, would be of added interest to show, that possibly same structures are influencing the somatic as well as the autonomic component of respiration and thereby tend to bring about a co-ordinated response. The pathways for such an integrated response are not well defined. It has been suggested that cortico-subcortical routes mediating inhibitory and facilitatory effects are probably through hypothalamus (Dell, 1953; Poirier and Shulman, 1954 and Segundo et al., 1955) and
this also serves for the somatic effects. The weaker inhibitory effects on respiration and other spontaneous somatic effects from more extensive medial and orbito-insulotemporal zones are suggested to be mediated through thalamus and brain-stem reticular formation. Thus it seems that influence of these superimposed structures and mediation through these descending pathways, is fairly important to coordinate and regulate the ponto-medullary respiratory mechanisms.

In these days when psychosomatic study of human brain and behaviour is gaining an upper hand, one cannot ignore the psychic influences on respiration which seem to be of manifold nature. It has long been known that in the course of intellectual work the respiratory frequency increases and the amplitude tends rather to be reduced. The respiratory responses seem to be an integral part of emotional expression such as laughing, crying, weeping etc. Often the emotional changes are first detected by the observer through the changes in the type or frequency of respiration (Brasson, 1920; Zonaff and Neumann, 1903). These changes in respiration can, at times be so pronounced that they may be interpreted as indication of certain psychic disorders (Finesinger and Mazick, 1940). It is not at all surprising, therefore, that limbic system which exercises a great influence on the integration of emotional behaviour should also influence respiration considerably. The results of the present study do support such a concept.

The fall in respiration rate was observed after most of the frontal and temporal lobe lesions. It is difficult to explain such a fall in rate.
BODY TEMPERATURE

To study the role of limbic system in regulation of body temperature, the changes in rectal temperature after electrolytic and extensive surgical ablations were taken into consideration. Though the rectal temperature alone may be an insufficient measure of central body temperature (Mead and Homarito, 1949) and its limitations are recognised, yet it was the only accessible method which could be adopted in animals of the present study because of certain technical difficulties. The chronic studies give information about temperature regulation in the unanaesthetised animal which is indispensable and cannot be gained from acute studies. Majority of the animals of this ablation series registered fall in rectal temperature both after frontal and temporal lobe lesions. Rise in temperature was also observed but in few only, whereas the remaining animals did not show any change.

Majority of these animals showing fall in temperature had fall in respiration also and hence the fall in rectal temperature cannot be attributed to respiration which serves as one of the thermoregulatory effector systems. In the present series it was observed that 5 of the animals which showed fall in rectal temperature also registered fall in blood pressure but rise in heart rate. This fall of pressure in the presence of increased heart rate might be attributed to vasodilation. Since changes in cutaneous blood flow are associated with temperature changes, vasodilation causing a fall in temperature, it is suggested that possibly the fall
of temperature observed in the present series might be because of vasodilation produced. No such measurements of changes in blood flow could however be done in these animals but was undertaken in another group of animals of stimulation series. It would be apparent from the results (Table 4) that changes in blood flow through the hand when recorded on stimulation of different frontal and temporal limbic regions did show both vaso-dilation and vaso-constriction. Changes in cutaneous blood flow may, therefore, be responsible for changes in body temperature.

The changes in rectal temperature did not last for long in majority of these animals and tended to come to normal at the end of 1½ - 2 months. This is in contrast to the marked specific and persistent changes observed in body temperature after hypothalamic lesions. The role of hypothalamus in the regulation of body temperature is a well established fact. From these observations and experimental evidences one might conclude that limbic system as such might not be responsible for regulation of body temperature but may be modifying the hypothalamic control through the vast connections it has with this part. It is also suggestive that the changes produced in body temperature from the limbic regions might be secondary to the changes of vascular system produced from these regions.

GASTROINTESTINAL SYSTEM

The present study lends support to the intimate relation-
ship of limbic system to gastrointestinal activity. Stimulation of amygdala and posterior orbital surface have in majority of the animals produced a significant increase in volume, free and total acidity and pepsin contents of the gastric juice. The effect produced is similar to one obtained on stimulation of vagi. Dell and Olson (1951) have shown vagal projections into the posterior orbital surface. Amygdala has also been shown to be intimately connected with hypothalamus. It has been suggested that some of the fibres from amygdala are routed through antero-medial hypothalamus, stimulation of which produces similar changes in gastric secretion. In view of these connections, it is not difficult to understand the effects produced on gastric secretion by stimulation of these regions. Temporal tip stimulation produced an increase in gastric secretion but no appreciable change could be obtained on stimulation of anterior cingulate and hippocampus. This confirms the work of Sen and Anand (1957).

Results of the aspiration series have been quite variable and same anatomical zones have produced an increase and decrease in gastric secretory response in different animals. In this series handling and struggling of the animals, passing of the stomach tube orally, keeping the animals tightly held during collection of juices have all been extraneous factors and seem to have obviated the results to quite a good extent. The apparently opposite results produced may perhaps be better understood in view of these factors coming into play and modifying the secretory responses. It will be reasonable not to attach much significance to these results.
The results observed on gastrointestinal motility are not so clear cut. Stimulation of posterior orbital surface has in majority produced increased gastric motility. Stimulation of amygdala has shown an increase in some and inhibition in others. The other limbic structures of temporal lobe have in general produced an inhibition of gastrointestinal motility. Stomach and duodenum receive efferent autonomic fibres from the vagal and splanchnic nerves. It has been shown that inhibitory as well as augmentory gastric motor responses can be elicited on peripheral stimulation of either of these nerves (Carlson et al., 1922; McSwiney, 1931; and Kuntz, 1945). Bilateral cervical vagotomy eliminates the gastric effects evoked from the anterior cingulate and orbito-insulotemporal polar fields while section of the splanchnic or trigeminal nerves leaves the responses intact (Kaada, 1951). These observations support the supposition of a dual vagal representation on the medial and basal aspects of cerebral hemispheres. Each of the two areas may exert its influence on the gastric motility in the absence of the other (Kaada, 1951).

The available data give no definite answer to the question whether the responsive cortical fields act directly on the dorsal motor nucleus of the vagus in the medulla oblongata or whether the impulses are transmitted through some intermediate stations. Pathways mediating the augmentory effects from olfactory bulb, tract and pyriform cortex through the amygdaloid nuclear complex; from orbital surface through internal capsule to area below the anterior commissure (Eliasson, 1954); and from anterior cingulate cortex to the vicinity of anterior commissure
(Eliasson 1952) have been demonstrated. It appears that these paths from the orbital and anterior cingulate areas coincide with those mediating the cardiovascular and somatomotor inhibitory effects from the same areas through the hypothalamus. These connections suggest of the possible descending pathways which may be concerned in the gastric secretory and motor responses. Temporal lobe effects are suggested to get channeled through the amygdala which again might be influencing a dual effect through its well known connections with the hypothalamus.

Hyperaemle and ulcerative changes observed in gastrointestinal mucosa after these lesions were similar to those observed by Heath (1954) after lesions in the septal regions and by Hosvold and Delgado (1956) after caudate and putamen lesions. It is well known that psychodynamic conflicts and emotional stress play a significant role in causation of peptic ulceration. Presence of ulcerative and other gastrointestinal disturbances have been often associated with psychic disorders and behavioral changes. The role of limbic system in influencing such behavioral disturbances is also well recognised. It is, therefore, not difficult to understand that stimulation of different limbic structures may produce changes in gastrointestinal pathology. The mucosal changes observed were similar to the ones produced by stimulation of the anteromedial hypothalamus and some of the frontal and temporal regions (3en, 1957). The submucosal dilatation of vessels and superficial haemorrhagic areas seen may be due to involvement of blood supply. The limbic areas are known to influence vasomotor tone and hence might be responsible for such changes. Marked ballooning of the gut after lesion of hippocampus, amygdaloid region and frontal tips also suggests the influence of these regions over the
mechanics of the gastrointestinal tract and thereby produce changes in motor effects.

**BLOOD CHEMISTRY**

Rise of blood sugar on stimulation of all the limbic structures in monkeys and all except the anterior cingulate in cats was obtained in the present study. Cats after anterior cingulate stimulation showed a fall in blood sugar level. This fall in blood sugar level was often associated with vicious and violent behaviour and convulsions. The degree of fall in blood sugar level alone cannot be held responsible for such convulsions. Is there any relationship between the behaviour of these cats and their blood sugar levels, or is the fall in blood sugar only a result of their behaviour, yet remains to be solved.

The rise of blood sugar obtained from caudal and lateral hypothalamic and a fall from medial parts of rostral regions were interpreted in terms of sympathetico-adrenal and vagoinsulin activities (Anand & Dua, 1955a). As the different parts of limbic system are interconnected and are also connected to the hypothalamus, they possibly mediate their autonomic visceral control through the hypothalamus. A similar rise observed after electrolytic and surgical lesions of different frontal and limbic structures may also be interpreted in terms of autonomic effects. Since the rise in blood sugar was often associated with rise in sodium one may consider the possibility of endocrinal involvement in such a response.
Increase in blood sodium observed in majority of the animals after frontal and temporal lesions, substantiates the reports of Allot (1939), Sweet et al. (1948) and Tokay (1931) who observed retention of sodium after frontal lobe damage and stab wounds of caudate nucleus. Heath (1954) on the other hand reported a gradual fall in the sugar and sodium levels of blood after lesions in septal regions. In the course of the present study, stimulation of the different frontal and temporal lobe structures produced variable changes. In general stimulation of most of the temporal lobe structures led to fall in serum sodium and rise in serum potassium, whereas rise in serum sodium without any change in serum potassium was observed from frontal regions.

Thus the changes produced in sodium and potassium contents of blood after stimulation and ablations of different limbic structures are suggestive of some regulatory influence of these areas on these electrolytes of the body. It would be worth investigating whether such a change produced is mediated through some endocrinal influence, possibly the adrenals, or the renal functions are implicated. Recently Gupta (1960) has shown that involvement of limbic areas alters the renal haemodynamics and urea clearance.

Variable changes in serum proteins without any consistent change in albumin: globulin ratio were obtained both after stimulation and ablation of different frontal and temporal limbic structures. Kitani et al. (1959) and his associates have observed that "liver insufficiency factor" or liver resection and "hyperammonemic factor" can influence brainstem
reticular activity and limbic system structures. It would be reasonable to assume that limbic system should also be influencing liver functions. Changes in serum proteins may be visualised as a result of derangements in liver functions. It would be interesting to study liver functions after stimulation and ablation of these limbic regions and see if such relationship exists. Metabolic and endocrinal involvement after the experimental ablations and various clinical conditions give further support to such a possibility.

Alteration in blood chemistry accompanying emotions of rage and fear (Cannon, 1939) and emphasis on interaction between pituitary with its tropic hormones, and the adrenal cortex in such changes (Selye, 1950) have been advanced.

It seems that the changes in blood chemistry thus observed may be the overall picture of involvement of cellular and glandular metabolism, which the limbic system might be regulating through its autonomic and endocrinal control besides its influence on the affectively determined behaviour.

**ENDOCRINAL ACTIVITY**

(1) ACTH Secretion

Stimulation of different limbic regions led in general to various degrees of eosinopenia both in 1 and 4 hour's count. The eosinopenic response obtained on giving a stress persisted after ablation of different limbic regions (except amygdala). In view of these results it may be tentatively suggested that the general eosinopenic response observed
after stimulation might be a result of stimulation acting as a general stressing agent rather than leading to a specific response from a particular area.

On the other hand, the marked eosinopenic response obtained from posterior orbital surface and amygdala might be of significance in implicating these regions in release of ACTH. Since there was an abolition of eosinopenic response after ablation of amygdala this lends further support to some more important role of amygdala in release of ACTH secretion. Amygdaloid nuclei possess rich projection system extending into the hypothalamus. There are grounds for believing at this stage that such a response from Amygdala is possibly mediated via the hypothalamus.

The response from hippocampal region has been quite interesting. There was actually a rise observed in the circulating eosinophils on stimulation of this region in the cats. There is quite a possibility that the rise might be due to its inhibitory influence on hypothalamic regions mediating ACTH response. Porter (1954) has put forward that hypothalamic centres may be excited or inhibited by impulses arising in the central nervous system. There is also a likelihood that this increase in eosinophils might be a sympathetic effect mediated through hypothalamus. There has been a rise in eosinophils observed on stimulation of lateral part of posterior tuberal region (Anand and Dua, 1953) of hypothalamus and it was suggested that such an increase might be due to a sympathetic effect causing contractions of the spleen (McDermott et al. 1950).

It thus seems that limbic system has an influence
The final common pathway to the anterior lobe is probably through the hypophyseal portal system. Recently Harris (1956) has put forward that the endocrine response to a great variety of stimuli referred to as "stress stimuli" - increased secretion of adrenaline, A.D.H., ACTH and decreased secretion of TSH - might be mediated by the reticular activating system. We know that the limbic system is well connected to structures of reticular formation and hence the ACTH responses from the limbic regions may be explained on basis of these connections.

Physicians have always known that the emotional life had something to do with illness. In this era of stress and strain when psychosomatic medicine is getting on a firm footing to treat these illnesses wholly or in part, a proper understanding of the various higher nervous regions taking part in such emotions and the outcome of that, is very essential. Since body as such is a self preserving and self regulating mechanism, it seems to be a joint effort of nervous and endocrinal factors to bring about a co-ordinated response into play whenever the body is exposed to any kind of stress. The ACTH secretion in response to any kind of stress leading to adrenocortical enlargement was taken by Selye to play a useful part in the systemic, non-specific, adaptive reaction and called this as the alarm reaction.

Since the various regions of limbic system are well known for the integration of emotional behaviour of animals and human beings, their role in influencing the endocrinal activity is self obvious.
(ii) Gonadotrophic Secretion.

The abnormal sexual behaviour observed by G.J. Chinna in this laboratory (Chinna, 1960) after lesions in different limbic structures indicate that these regions are implicated in sex behaviour of the animal. The "hypersexual" response can be produced in monkeys after lesions involving a wide range of nervous structures like amygdala, hippocampus, temporal tips and anterior perforate substance ventral to the head of the caudate.

It was further observed in that study that the sexual pattern developed after lesions of different limbic regions does not change after castration showing thereby that the activity of the gonads is not responsible for such a behavioral change. Could it be then, that the behavioral change observed is a result of mediation of some nervous influence and not the result primarily of some endocrine disturbance. This is supported by Green et al. (1957) who showed that injecting excessive amounts of gonadal hormones did not produce the hypersexual response. According to him the hypersexual response is due to initiation or destruction of the nervous tissue.

It is evident from these and other studies on limbic system done during the present work that topical representation of separate functions is not the pattern of organisation in limbic system. Perhaps some sort of balanced and integrated activity of all these regions at some level is responsible for normal sex behaviour. Maybe the destruction of some region tends to upset the balance and to release the
activity of some part of the brain which brings about the exteriorization of affective behaviour. That such area could possibly be located in hypothalamus is supported by observations of Harris (1958). He demonstrated that the area posterior to the mamillary region and adjoining the reticular formation produced all the manifestations of sexual behaviour in castrated animals when tiny amounts of sex hormones were implanted in it.

It may thus be put forward with some amount of certainty that hypothalamus executes these abnormal responses, and these are possibly mediated through the reticular formation. The projections and reciprocal connections between limbic system and hypothalamus and reticular formation provide an anatomical basis for explaining such responses. Also the limbic system through hypothalamus might be finally influencing pituitary hormones thereby regulating the endocrinial activities.

The abnormal sexual behaviour could not be observed in all the monkeys with similar lesions. Also such responses were conspicuous by their absence in cats. These observations are in contrast to those reported by Shreiner and Kling (1956) but are in agreement with the findings of Shealy and Peele (1957) and Bard (1958). Thus we find that the limbic system structures influence sexual behaviour differently in different species and also in a most flexible and unfixed manner in the same species.

**OTHER VISCERAL AND SOMATIC RESPONSES**

Interactions between somatic and autonomic mechanisms
must not be overlooked. It has been shown as a result of the present studies, that these interactions are not only present but are exceedingly important. The visceral and somatic responses observed during the course of stimulation studies in the unanaesthetised animals have been similar to those reported by other workers (Kaada, 1951; MacLean, 1953; Gastaut, 1952; MacLean and Delgado (1953) and others). The visceral responses were both of sympathetic and parasympathetic nature while the somatic usually involved ipsilateral facial, eyelid, orbital and oral muscles. Most of the visceral and nearly all of the somatic responses were obtained from all the areas of the limbic system. In the temporal lobe, responses were easier to elicit from the amygdala than from the pyriform cortex, hippocampal formation and temporal tip, which required slightly higher voltage stimuli. Most of the somatic responses like blinking, closure of eye, raising of nasolabial fold, retraction of head etc. always began on the same side as that of stimulation. They appeared on the opposite side as well, as the stimulation was continued. This may be explained on the large number of inter-connecting fibres between the two sides, which may be involved as the stimulation is continued. Frost et al. (1958) could record the after discharge from the anterior commissure and the amygdaloid complex of the contralateral side when the face movements became bilateral on stimulation of amygdala of one side. Such a response disappeared after cutting the anterior commissure suggesting the presence of inter-amygdaloid connections. The contraversive turning of the head, stressed by Kaada (1953) as a response from
the Amygdala and suggested as of diagnostic importance in temporal lobe epileptic seizures (Magnus et al. 1952) was obtained on stimulation of posterior orbital gyrus, anterior cingulate and amygdala. The piloerection and sneezing observed on stimulation of anterior cingulate and amygdala confirm the observations of Hoff and Green (1936); Smith (1945); Ward (1948); Kaada (1951); Showers and Crosby (1958); Gastaut (1952); MacLean (1952); MacLean & Delgado (1953). Coordinated oral responses relating to eating were also produced by stimulation of all regions of this system. Most of the cats showing eating automatisms also had different degrees of salivation. The monkeys on the other hand did not show any salivation. The eating automatisms observed from the limbic regions were not associated with increased food intake as that obtained from the hypothalamus. MacLean and Delgado (1953) reported eating automatism from the temporal regions and suggested that this part of the brain is concerned with the organization of the oral activities of the animal as they pertain to feeding and to the vocalization, defence and attack involved in obtaining food. The motor responses observed from various limbic structures particularly the amygdaloid and periamygdaloid regions are probably mediated over connections to basal ganglia and tegmentum of the mid brain. The masticatory movements may be mediated by important connections known to exist with alimentary reflex centers in septal and preoptic areas as described by Hess & Magnus (1943). Some of the visceral sensorimotor responses may involve these pathways in addition to projections to the
anterior hypothalamus. It may be mentioned here that some of the facial responses like raising of the nasolabial fold, facial spasm and jaw movements etc. which form an important background for the emotional expression of the monkey, were more easily elicited in monkey than in cat—monkey being highest in the phylogenetic scale. The exteriorization of such emotional responses from the hypothalamus needs no more emphasis. Since the same response can be elicited from a number of temporal and frontal limbic structures, it is probable that a discharge starting in any of these areas is relayed to other structures.

Hill (1949), Feindel and Penfield (1954) and Golués et al. (1951), describe the eating automatism and other manifestations of the fully developed attack as the postical phenomenon dependent upon the spread of discharge. The anatomical basis for such a spread and complexity of responses has been explained by many workers (Falconar, 1954; Feindel & Penfield, 1954; Marsan and Tost, 1951; Meyer and Allisson, 1949) by demonstrating physiological inter-connections between various frontal and temporal limbic structures. Feindel & Penfield (1954) remarked that amygdala may play a most important part in the production of sensory seizures and automatism.

Some of the visceral responses like pupillary changes, lachrymation, urination and defecation etc. are also recorded from the amygdaloid nuclei. Similar responses are reported from stimulation of hypothalamus. The extensive projections of the amygdala upon the subcortical structures as revealed
by the electrophysiological studies of Gloor (1955) explain how it is possible that such a confusingly great number of responses can be elicited by amygdaloid stimulation. Some of these responses like micturition and defecation (Hess, 1946; Kabat et al. 1936) mastication (Hess 1943) are reported to result from stimulation of stria terminalis the main efferent connection of the amygdala. This suggests that this bundle might be taking part in mediating these responses although it does not exclude the existence of alternate pathways. Koikegami and his collaborators (1952, 1953, 1955) on the other hand think that these responses are mediated via direct ventral amygdalohypothalamic pathways. Whatever may be the route of mediation one thing is clear at least that these somato-visceral and viscero-somatic circuits are greatly modulated by influences from the higher regions. This modulation may be tonic or may be brought into play by ascending impulses arising in these circuits.

CONCLUSIONS

The observations presented above clearly show that certain fronto-temporal limbic regions have a definite modulatory influence on the various visceral, autonomic, metabolic and endocri-nal activities of the body. For the sake of convenience the responses have been described under the headings of various systems. It should not, however, be overlooked that these systems form part of the whole and are linked with each other in a circular process of transaction just as the total organism is related to its environment.
Each system is influenced by the so called visceral brain and serves as the environment of the other. This co-ordinated response leads towards the maintenance of homeostasis of the biological unit of life. Any type of stress on any of these systems disturbs the target violently and from it ripples of effect gradually spread as if in a circle with decreasing intensity and speed at the periphery. Other systems respond as internal emergency mechanisms, intensifying input or substituting for output. These emergency mechanisms are affected by nervous discharge - autonomic (both sympathetic and parasympathetic) and voluntary. Enough of evidences are there in the literature to establish the mediation of these sympathetic and parasympathetic impulses from the hypothalamus. Present study is a step forward to demonstrate that though the hypothalamus is there to execute these activities it is the limbic system which is responsible for the integration of such responses. It influences the lower regions in such a way so as to bring about a response most suitable for any particular moment. In short, the limbic system aims at the maintenance of "milieu interieur", by mediating its influence through changes in the autonomic, endocrinal and behavioral activities of the individual.