

## ASSOCIATED FACIAL, VOCAL AND RESPIRATORY COMPONENTS OF EMOTIONAL EXPRESSION: AN EXPERIMENTAL STUDY\*

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AMONG the topics which Kinnier Wilson<sup>1</sup> has selected as representing some modern problems in neurology is that presented by the clinical picture of dissociation of the voluntary and emotional innervation of the facial muscles. It has long been known that patients suffering a paralysis of volitional movement of the facial musculature, as a result of supranuclear cortical or capsular lesions, may retain an activity of these muscles in the expression of emotion. Conversely, cases have been reported in which voluntary activation of the facial muscles has been unimpaired, while emotional excitement failed to produce the appropriate facial expression.

In his review of this subject, Kinnier Wilson<sup>2</sup> has suggested in explanation that the voluntary and emotional innervations of the facial nuclei are effected by different systems within the brain. Enlarging upon this suggestion, Wilson has postulated a brainstem mechanism which subserves the synkinesis of the facial, vocal and respiratory activity observed in emotional behaviour. Further elucidation has been provided by Bard<sup>3</sup> in a consideration of facial and vocal activity from the point of view of his<sup>4,5</sup> recent studies of the brainstem mechanisms involved in the expression of emotion.

Our interest in this problem has developed from a series of investigations of these brainstem mechanisms (Ranson et al.<sup>6-13</sup>), in the course of which we have repeatedly observed coordinated facial and vocal responses obtained as specific reactions to stimulation of localized areas within the brainstem of experimental animals. It seemed desirable to make a special study of these effects, and we wish now to report the results of an investigation of such responses obtained from systematic electrical stimulation of the brainstem of the lightly anæsthetized cat and monkey and of the acutely decerebrate cat.

### METHODS

Data were obtained from eight monkeys (*Macaca mulatta*), from 14 normal cats, and from six cats decerebrated through the caudal part of or

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just behind the diencephalon. Of the eight monkeys, one was a normal animal, while each of the others had been the object of a previous study on the effect of restricted lesions in the hypothalamus or thalamus. No significant variation could be detected in comparing the results from the operated monkeys with each other or with those from the normal monkey.

The monkeys and normal cats were given nembutal (16 to 20 mg. per kilo body weight, intravenously) to preserve a light anæsthesia, and under supplementary ether the skin was incised, the appropriate region of the calvarium was removed, the dura reflected, and the Horsley-Clarke instrument adjusted to the animal's head. The decerebrate cats were prepared by the transection method under ether which was discontinued after decerebration. All brain tissue ahead of the plane of transection was removed at operation in the decerebrate animals, the level of section was described and drawn at autopsy, and in two instances was determined by microscopical examination of serial sections of the intact end of the brainstem.

In one monkey kymographic records of the respiratory changes associated with the responses were made, and it may be emphasized that this was the only animal of the series in which a tracheal cannula was employed. Reactions from this animal were checked for vocal effects, however, by stimulation of each point concerned either before insertion of the tracheal cannula, or after its removal and closure of the trachea by inserting and tying in a short length of glass tube to divert the air once more through the larynx.

All stimulation of the brainstem was performed with the aid of the Horsley-Clarke instrument, the use of which has been described in detail by one of us.<sup>14</sup> The short distance, approximately 0.2 mm., between the electrodes used, together with the weak faradic current from one dry cell attached to a Harvard inductorium the secondary coil of which was set at 9 cm., permitted restriction of the stimulation to a localized area surrounding the tips of the electrodes.

The region explored extended in the monkey from the transition between thalamus and midbrain, through the midbrain, to the upper part of the medulla, and included the entire left half of the brainstem and the medial portion of the right side, all or a large part of this region being explored in each of the animals. In some, stimulation was begun rostrally and extended caudally; in others the reverse procedure was followed. Stimulation of the brain in the normal and decerebrate cats was in each case begun rostrally and extended caudally, exploration being made of the left side of the brain and the medial portion of the right side. In the normal cats the anterior part of the cerebral hemispheres and the diencephalon were explored in some animals and the diencephalon, midbrain and pons in others. In the decerebrate cats, exploration was necessarily confined to the midbrain, pons and upper part of the medulla.

Extensive written records of the responses were made throughout the course of each experiment, and the site of each focus of stimulation was

determined by subsequent microscopical examination of serial sections of the explored area of the brain prepared for histological study by the Weil method. This location of the reactive points was first determined for each animal on projection drawings of sections through the explored areas. Representative levels were then selected and the data from all of the animals explored in these planes were plotted upon them. Four such levels shown in figs. 2-5 illustrate the localization of reactions in the monkey, and those shown in figs. 6-14 the localization in the normal and decerebrate cats.

### OBSERVATIONS

*Description of responses from the monkey.*—Vocalization in the monkey occurred rhythmically with each expiratory phase of a greatly accelerated respiration. It has most commonly been manifest as cries of a wide variety of intensity and pitch, ranging from soft and plaintive sounds, through moderately loud and high-pitched notes, to loud shrill shrieks or screeches. Another large number of responses may be described as barking of a chirruping or chattering nature. Occasionally cooing or whistling sounds have been encountered. With the exception of these rare cooing or whistling noises, the sounds as a whole have impressed us as resembling those which connote the expression of unpleasant affective states, and a large number of the responses have closely simulated examples of the rather extensive repertoire of vocal expressions exhibited by the normal monkey in the emotional behaviour of its daily life.

The play of the facial muscles, which was an accompanying feature of the majority of these vocal responses, also resembled closely that seen in the activity of the normal monkey, with the difference that it was usually present only on one-half of the face, that contralateral to the side of stimulation. Much less commonly bilateral or ipsilateral contractions of the muscles of expression were encountered. In addition to the accompanying opening of the mouth and dilatation of the nostrils, the responses of barking and crying were most commonly associated with a contraction of the facial muscles producing a retraction of the angle of the mouth, an elevation of the upper lip, and to some extent the side of the nose. As a result of these contractions the teeth were exposed and the face assumed a snarling expression. Less commonly the forehead was wrinkled, and the ears retracted and flattened against the side of the head. These facial contractions were not tonic ones but occurred phasically and in definite patterns with each expiration and cry, being partially or completely relaxed during inspiration. The less frequent whistling sounds and some of the soft, chirruping barks were not accompanied by movements of this sort, but instead were associated with a contraction of the lips to produce a rounding of the mouth-opening, which appeared not so much a grimace as an aid to phonation.

Irrespective of the specific nature of the vocalization or facial expression

two general types of responses have been obtained. In the first of these, the vocal effects did not occur at the onset of stimulation, but appeared only after the stimulus had been continued from one to several seconds, there often being an initial apnoea. Vocalization began with soft and low-pitched cries or barks, and the succeeding sounds, occurring with each expiration, became increasingly louder and higher pitched as excitation was continued. At the cessation of stimulus, there was usually one, but sometimes several cries or barks still louder and higher pitched than those elicited during stimulation.

A kymographic record of the respiratory changes associated with this type of response is shown in fig. 1A. Before stimulation in this record, the

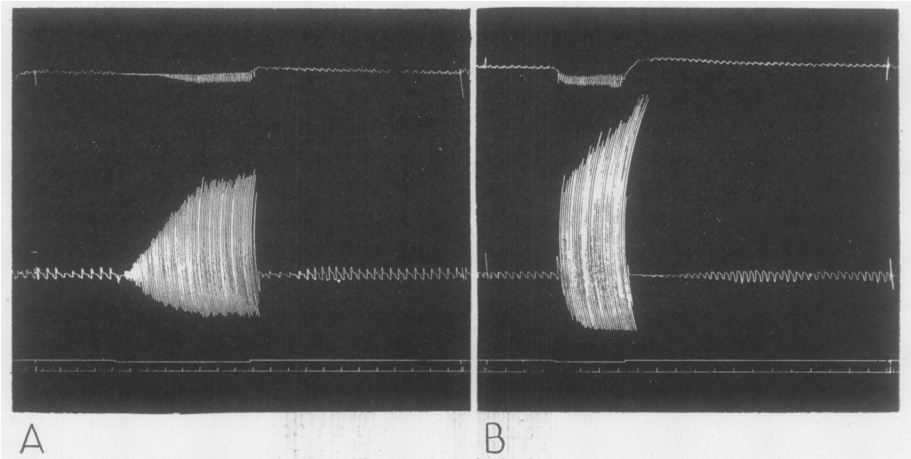


Fig. 1.—Kymographic records of respiratory changes associated with vocal responses from the monkey. The tracings from above downward represent : chest movements with expiration as a downstroke ; air exchange from tracheal cannula with expiration as an upstroke ; a signal-marker with the dip indicating the period of stimulation ; and the time in three-second intervals. Record A illustrates the response to stimulation of a point in the central grey matter of the aqueduct ; record B the response to stimulation of a point in the lateral part of the mesencephalic tegmentum.

respiratory rate was 48 per minute. Respiration was partly inhibited for the first second of stimulus, and then began and continued for the duration of stimulus at a rate of 224 per minute, gradually increasing in amplitude during the first half of the period of stimulation. After faradization was stopped there occurred one respiratory excursion comparable to those seen during stimulation. The vocal effects elicited from stimulation of this same point before insertion of the tracheal cannula appeared shortly after the beginning of stimulus, starting with low cries. The succeeding cries, occurring with each expiration, became increasingly louder and higher pitched as stimulation was continued, and at the cessation of stimulus there were one or sometimes two cries still louder and higher pitched than those obtained during faradization.

Reactions of this type are characterized in brief by an initial apnoea, a

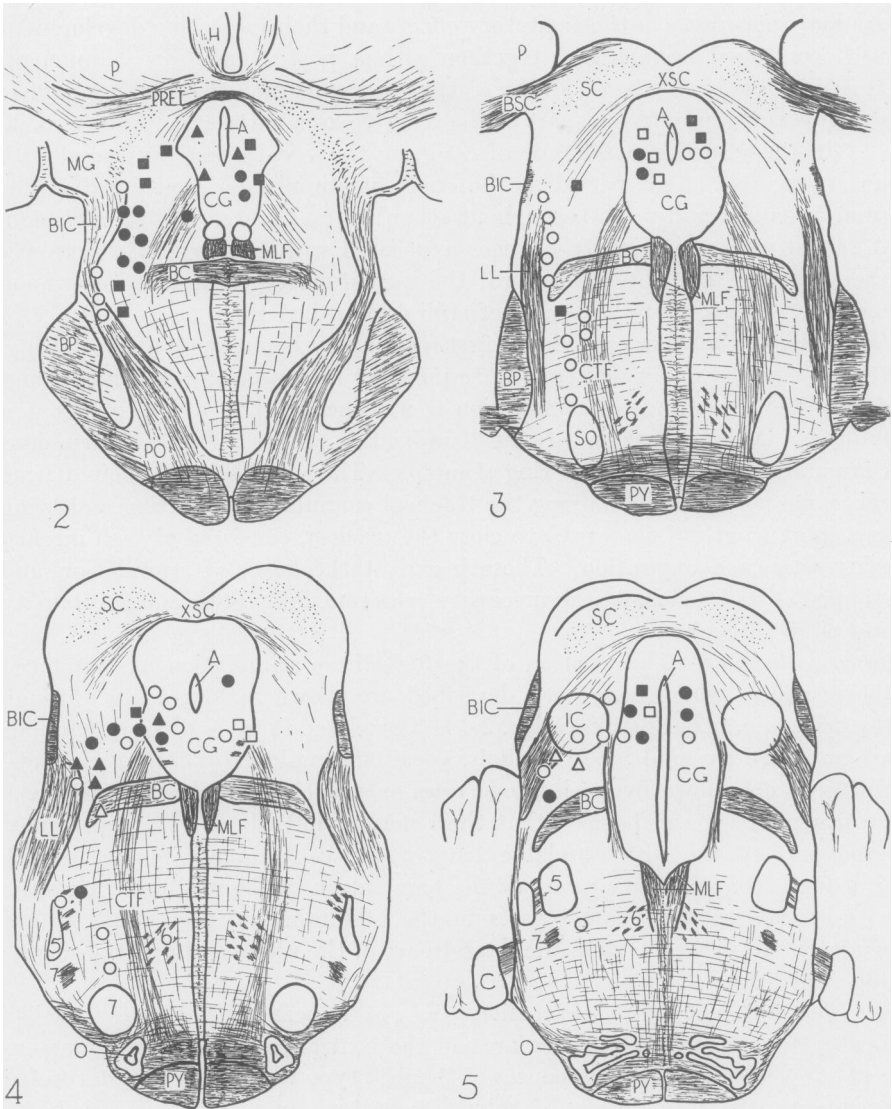
gradual appearance of the excitatory effects and their increasing development with continued stimulation, together with a post-stimulatory component. It will be made clear below in the section on localization that these responses were obtained only from a part of the reactive area within the brainstem.

In the second general type of reaction, the vocal effects appeared with no appreciable latent period at the onset of stimulation, continued at the same intensity and pitch throughout stimulus, and ceased at its conclusion. A record of the respiratory changes associated with this type of reaction is shown in fig. 1B. In this record, the amplitude of respiratory excursion increased throughout the period of stimulation, but there is no evidence of the inhibitory influence which the first record may be interpreted as showing. Before stimulation in fig. 1B, the respiratory rate was 53 per minute, and during the 11 seconds of stimulation it was increased to a rate of 188 per minute. After cessation of the faradization there were no excursions comparable to those seen during stimulus. The vocal effects, elicited from this same point after removing the tracheal cannula and inserting and tying in a short length of glass tube to close the trachea, consisted of high pitched cries with each expiration. These began at the onset of stimulation and stopped at its conclusion, the successive cries remaining of the same intensity and pitch throughout.

*Localization.*—The location of the foci whose stimulation has produced the responses which have been described are shown in four levels through the brainstem of the monkey (figs. 2–5). Correlated facial and vocal reactions are indicated by solid black symbols, vocal effects alone by outline symbols. Soft cries are shown by circles, loud cries or screeches by squares, and barks by triangles. It can be seen that the reactions have been obtained from a large part of the rostrocaudal extent of the central grey matter of the aqueduct, from the dorsal part of the tegmentum of the midbrain, together with its lateral and ventral parts in the midbrain and pons, and further caudally and ventrally from the lateral part of the reticular formation of the upper medulla.

The different vocal expressions do not appear to have any specific localization within the reactive area in the central grey matter and mesencephalic tegmentum, but responses of the first type which may be interpreted as due to the stimulation of mixed excitatory and inhibitory elements (fig. 1A) have been obtained only from the central grey matter or the immediately adjacent dorsal portion of the mesencephalic tegmentum. The reactions from this region were not exclusively of this type, however, for responses of the second type (fig. 1B), which show only an excitatory effect, have been obtained in part from the central grey matter and the adjacent tegmentum. Reactions of this second type are the only ones obtained from the ventrolateral part of the tegmentum and its continuation in the reticular formation of the medulla.

Changes in facial expression are seen to have had a fairly regular distribu-



**Figs. 2-5 illustrate the location of points whose stimulation produced faciovocal effects from the lightly anesthetized monkeys. The four levels through the brainstem are in the vertical plane of the Horsley-Clarke coordinates and extend serially from the most rostral to the most caudal plane. These planes are oblique from the transverse because of the angle given to the caudal part of the brainstem by the cephalic flexure of the monkey brain. Each level shows the data from three animals. Correlated facial and vocal effects are indicated by solid black symbols, vocal effects alone by outline symbols. Soft cries are shown by circles, loud cries or screeches by squares, and barks by triangles. Abbreviations for figs. 2-13 are as follows :**

- |            |  |
|------------|--|
| <b>A</b>   | <b>aqueduct</b>                        |
| <b>BC</b>  | <b>brachium conjunctivum</b>           |
| <b>BIC</b> | <b>brachium of inferior colliculus</b> |

tion among the responses through the midbrain, but were not frequently elicited from the pons and never from the upper part of the medulla. It has already been noted that these changes were seen predominantly in the crossed side of the face. The data, however, do not furnish any information as to the site of the crossing. Direct stimulation of the facial nucleus or the facial nerve, anywhere along its devious course through the brainstem, yields only a coarse clonus or subtetanus of all or several of the ipsilateral facial muscles, the rate of contractions apparently being related to the frequency of induction shocks. Such responses may be readily distinguished from changes of expression, the latter being predominantly or entirely of the crossed side of the face, of a rate synchronous with respiration, and selectively involving definite groups of facial muscles to produce characteristic grimaces.

Systematic stimulation of the transition area from thalamus to midbrain in the monkey, rostral to the level shown in fig. 2, has not yielded any facio-vocal effects. Exploration of the thalamus or hypothalamus has not been attempted in these experiments. There appeared to be a definite dropping out of the responses as the upper part of the medulla was reached, though no comprehensive exploration of the remainder of the medulla was attempted in these animals. In considering the significance of such negative data, the possibility should be kept in mind that areas which are non-reactive may contain functionally important cells or fibres which are too scattered to be effectively activated by the localized stimulus employed.

These facio-vocal responses obtained from the monkey cannot be considered as isolated phenomena peculiar to this animal alone, for comparable

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BP	brachium pontis
BSC	brachium of superior colliculus
C	cochlear nucleus
CG	central grey matter
CTF	central tegmental fasciculus
H	habenula
IC	inferior colliculus
IV VEN	fourth ventricle
LL	lateral lemniscus
LM	medial lemniscus
MG	medial geniculate body
MLF	medial longitudinal fasciculus
O	inferior olive
P	pulvinar
PE	basis pedunculi
PO	pons
PRET	pretectal region
PY	pyramidal tract
RN	red nucleus
SC	superior colliculus
SN	substantia nigra
SO	superior olive
XIC	commissure of inferior colliculus
XSC	commissure of superior colliculus
5	fifth nucleus or nerve
6	sixth nerve
7	seventh nucleus or nerve

effects have been elicited from stimulation of a similar region of the brainstem of the cat.

*Description of reactions from the cat.*—Two general groups of responses were obtained from the cat, the first being made up of cries and the second consisting of spitting reactions. The cries obtained varied widely in pitch, and ranged in intensity from soft and almost sighing effects to loud wails and howls, or intense screams. The prolonged duration of each cry was a characteristic feature. These cries were successively repeated during the period of stimulation, sometimes regularly with each expiration, but usually with from one to three silent respiratory excursions, or a period of respiratory inhibition between cries. Commonly also, they occurred alternating with from one to four spitting responses. While these effects sometimes appeared only after latent periods which could be estimated in periods of seconds, they have usually been manifest with no appreciable latency at the onset of stimulation. Only rarely has an increase in intensity or pitch of the cries during the period of stimulation been observed.

Even the most vigorous of the cries from the cat have characteristically been obtained with a minimum of noticeable alteration in the musculature of the face and mouth. With rare exceptions, they definitely were not accompanied by any emotional play of the face. Usually the mouth was opened slightly, and sometimes the tip of the tongue was retracted with each expiration and cry. Rarely a slight tensing or tremor of the lips was observed.

The spitting reactions from the cat exhibited, on the other hand, a minimum of vocalization associated with vigorous contractions of the muscles of the face, jaw and tongue. In these spitting reactions the mouth was opened widely, the back of the tongue was elevated, and its sides were tipped upward to form an elongate trough of the anterior portion. The angles of the mouth were retracted and the upper lips elevated, exposing the formidable canine teeth. The muscles on the side of the nose were contracted to pull the tip of the nose upward and the skin of the forehead downward. Occasionally the ears were retracted and flattened against the head. All of these contractions were performed phasically and in a coordinated manner with each expiration, which was audible as a short and often explosive hiss. They were partially or completely relaxed during inspiration. The facial contractions were sometimes bilateral and equal, but were often more marked on the half of the face opposite the side of stimulation, and were sometimes exclusively contralateral. The respiratory rate was usually accelerated.

The contrast in the emotional play of the face during the crying and the spitting reactions was strikingly illustrated when the two occurred on alternating expirations during stimulus. With the cries the face remained still and expressionless, while with the spitting it exhibited the activity just described.

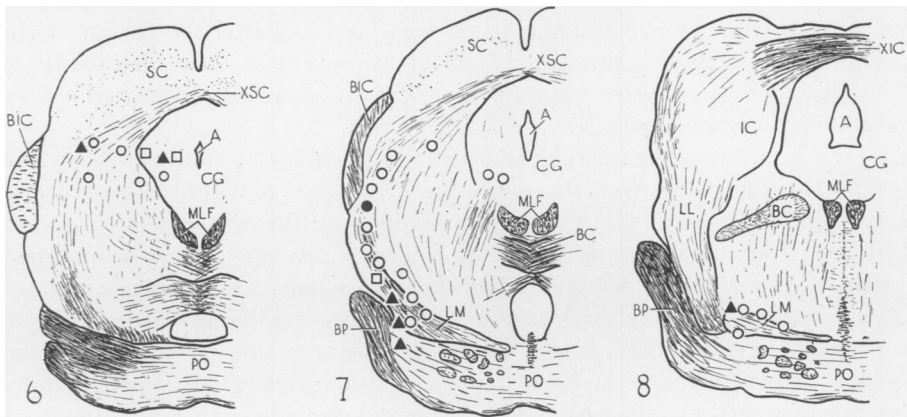
The responses from the cat, like those from the monkey, have impressed



us as resembling those which connote the expression of unpleasant emotions. Also, as in the case of the monkey, a large number of reactions from the cat have so closely resembled the facial and vocal activity of the normal animal during emotional behaviour in its daily life as to appear identical with it.

*Localization.*—The location of the points whose stimulation has produced the responses from the normal cats is shown in three levels through the brainstem of that animal (figs. 6–8). Correlated facial and vocal effects are indicated by solid black symbols, vocal effects alone by outline symbols. Weak cries are shown by circles, loud cries or screams by squares, and spitting by triangles.

The responses have been obtained from the rostral portion of the central



Figs. 6–8 illustrate the location of points whose stimulation produced facio-vocal reactions from the lightly anaesthetized cats with intact brain. The three levels through the brainstem are in the vertical plane of the Horsley-Clarke coordinates, 6 being the most rostral level and 8 the most caudal. Figs. 6 and 7 each show the data from three animals, level 8 that from two animals. Correlated facial and vocal effects are indicated by solid black symbols, vocal effects alone by outline symbols. Weak cries are shown by circles, loud cries or screams by squares, and spitting responses by triangles.

grey matter surrounding the aqueduct, and the reactive area extends from this region through the dorsal portion of the mesencephalic tegmentum to its lateral part (fig. 6). At a more caudal level (fig. 7), reactions have been obtained from the areas just described and in addition from the extent of the lateral and ventrolateral boundaries of the mesencephalic tegmentum. Still further caudally (fig. 8), responses were elicited only from the region of the fibre-bundles forming the ventral boundary of the tegmentum.

The different vocal expressions do not appear to have any specific localization within the reactive area, but responses in which there was a period of respiratory inhibition between cries were obtained only from the lateral edge of the central grey matter and the adjacent dorsal portion of the mesencephalic tegmentum.

Mention has been made in the introduction that responses comparable

to those just described have often been encountered before in investigations in this laboratory ; but in many of these investigations, particularly in those on the forebrain, use of a tracheal cannula has precluded any possibility of studying vocal activity. In the present experiments without a tracheal cannula the opportunity was taken, therefore, of reexploring the more rostrally situated parts of the brain for associated facial and vocal reactions. Stimulation of a large number of points in the anterior part of the cerebral hemisphere, including the anterior limb of the internal capsule, the septal region and a large part of the corpus striatum, did not yield any such responses.

A reactive region was encountered, however, in the anterior part of the hypothalamus from about the level of the supraoptic commissures to that of the ventromedial hypothalamic nucleus, and included the region of the lateral hypothalamic area, the subfornical component of the medial forebrain bundle, and the nuclei supraopticus diffusus, perifornicalis and hypothalamicus dorsomedialis.

From this region spitting responses were elicited which were identical with those obtained from the midbrain. Stimulation within this area also produced a variety of cries entirely comparable to but generally of less intensity than those obtained from the midbrain. In one animal, stimulation within this portion of the hypothalamus produced purring, a response we have never encountered from the midbrain. There has been no specific localization of the different reactions within the responsive area, and the situation from which the variety of responses has been obtained in these experiments is identical with that found to yield spitting reactions in earlier investigations (Ranson and Magoun,<sup>8</sup> Kabat<sup>13</sup>). This location has been well illustrated in fig. 9 of the paper by Kabat,<sup>13</sup> to which reference is directed. Aschner<sup>15</sup> and Karplus<sup>16</sup> have previously induced crying by stimulation of the hypothalamus, and Gibbs and Gibbs<sup>17</sup> have elicited purring from electrical stimulation of the infundibular region. The vocalization reported by Bechterew<sup>18, 19</sup> from thalamic stimulation in the guinea-pig, rabbit, cat and dog has little localizing value, since the entire diencephalon was often enclosed between the electrodes.

Stimulation of the caudal portion of the hypothalamus in the present series of experiments yielded no facial or vocal reactions and no connected chain of responses could be traced from the hypothalamus into the reactive area in the midbrain. Here, again, the possibility should be kept in mind that negative results may be due to such factors as scattered pathways or the effects of anæsthesia.

The responses to electrical stimulation within such a complex part of the nervous system as the brainstem cannot be distinguished a priori as being due to the activation of afferent or efferent pathways or systems. Reference to neuroanatomical information concerning the reactive structures is often of help in deciding this, but when applied to the site from which

faciovoical reactions have been obtained from the midbrain and pons of the cat and monkey in these experiments it is of little aid, for the reactive area as a whole does not correspond to the distribution of any well-defined anatomical pathway or system familiar to us. The relation of some of the responses on the ventral and ventrolateral aspects of the tegmentum (figs. 7, 8) to the medial lemniscus, in association with which the spinothalamic fibres ascend, suggests the possibility that the responses were produced by stimulating afferent fibres coursing through this region to the thalamus. In an effort to explore this possibility, the midbrain and pons were stimulated in six cats in which the attempt was made to eliminate any participation of such afferent fibres by transecting the brainstem just behind the diencephalon. This procedure also eliminated afferent arcs relayed to the cerebral cortex.

*Reactions from the decerebrate cat.*—In only one of these cats could the diencephalon be considered entirely eliminated, its caudal and ventral parts remaining intact in the other five. We observed the occurrence of typical faciovoical responses to stimulation of the midbrain and pons in all of the decerebrate animals. The reactions consisted of cries and spitting reactions so identical in every respect with those elicited from the lightly anæsthetized cats with intact brains, as described above, that a second description would be superfluous. A slightly larger number of the more intense responses, as the screaming cries, were obtained from the decerebrate cats, but this difference was not marked and might be explained by the absence of anæsthesia in the decerebrate animals.

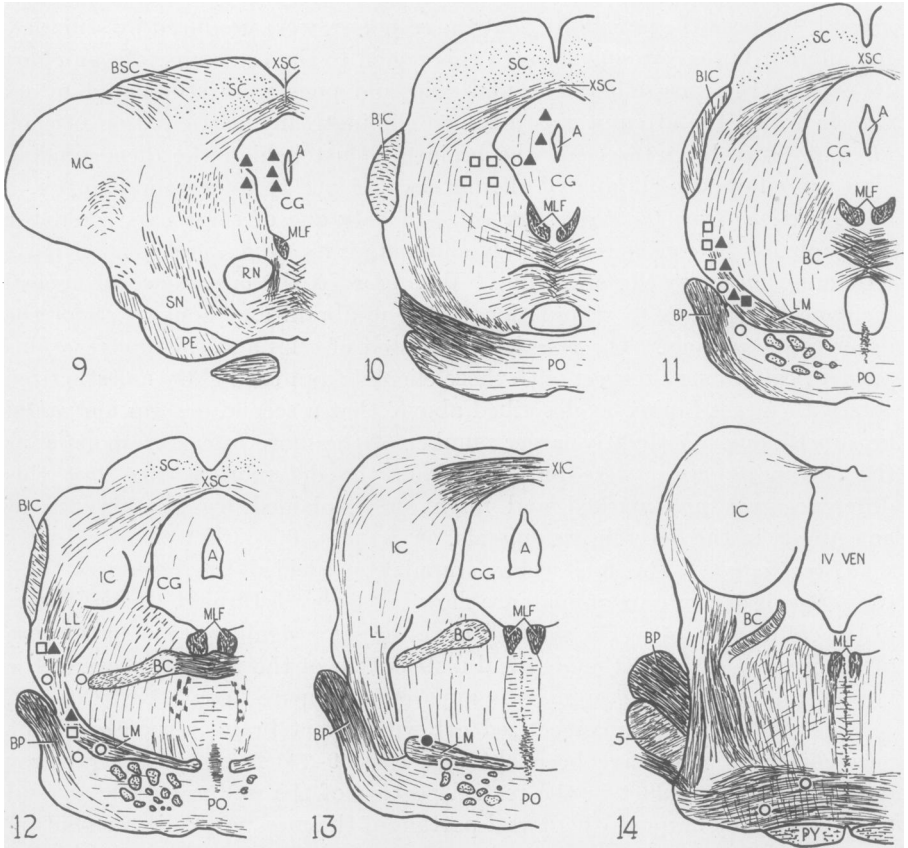
*Localization.*—The foci whose stimulation yielded the responses from the series of decerebrate animals are shown in six levels through the brainstem of the cat (figs. 9–14). The symbols have the same significance as in the case of the normal cat, and the identical distribution of the reactive areas in the normal and decerebrate animals is apparent (compare figs. 6–8 with 9–14).

As in the lightly anæsthetized cat with intact brain, responses of the decerebrate animals have been obtained (figs. 9–14) from the central grey matter of the aqueduct in the rostral portion of the midbrain, and extend from this region through the dorsal portion of the mesencephalic tegmentum to its lateral part. A number of responses are situated along the lateral boundary of the tegmentum, and at more caudal levels this reactive area becomes situated more ventrally and medially, so that in a plane through the inferior colliculus and rostral portion of the medulla it has assumed a position in the fibre-bundles on the ventral border of the transition from the tegmental region to reticular formation.

Responses from the lateral and ventral portion of the mesencephalic tegmentum whose possible relationship to spinothalamic fibres has been referred to above, have been obtained from all six of the animals of the decerebrate series, including one in which all diencephalic tissue was lacking, and a second in which the section passed from just behind the habenulæ to just in front of the mammillary bodies, and in which, therefore, only

the most caudal portion of the diencephalon remained attached to the midbrain.

Reactions from the central grey matter of the aqueduct and the dorsal portion of the mesencephalic tegmentum were not obtained from the two animals just described, nor from one animal decerebrated through the



Figs. 9-14 illustrate the location of points whose stimulation produced faciovocal responses from the decerebrate cats. The six levels are in the vertical plane of the Horsley-Clarke coordinates and extend serially and caudally from the most rostral level, 9, to the most caudal, 14. Figs. 9 and 10 each show the data from two animals; levels 11 and 12 each show the data from three animals; levels 13 and 14 each show the data from one animal. The symbols represent the same responses as in figs. 6-8.

habenulae dorsally and the infundibulum ventrally. They were elicited in abundance, however, from another animal transected through the habenulae and infundibulum, and from a second animal in which the transection was adjacent to but slightly more anterior to this plane. They were also obtained from the central grey matter and dorsal tegmentum on both sides of the midbrain of a third animal in which the section had passed from just in

front of the superior colliculus on one side and a little farther forward through the caudal part of the thalamus on the other, downward and forward to just behind the optic chiasma ventrally.

Responses have been obtained from the central grey matter and dorsal tegmentum, therefore, in animals in which varying portions of the caudal part of one or both sides of the thalamus and hypothalamus have been present, but they have not been obtained from other animals in which the caudal part of the diencephalon has remained intact or in which the transection has passed just behind the diencephalon. These variable negative data should not be overlooked, but it may be questioned whether they are significant beyond indicating that the extent to which nervous tissue adjacent to a transection recovers its excitability may vary in different animals.

#### DISCUSSION

In considering the reactions obtained during these experiments, it should be pointed out that while cries have been obtained from both monkey and cat, these cries have not been identical in inflection and tone in the two animals. Each animal has, furthermore, yielded vocal responses specifically characteristic of its group alone, for barking has been elicited only from the monkey, and spitting only from the cat. Such differences are not, however, greater than might be expected of reactions from two widely separated species of animals, each of which has certain characteristic modes of emotional expression. In our opinion both the vocal and the facial reactions from the two animals represent components of a fundamentally similar response. A comparison of the regions of the brainstem from which the reactions have been obtained in the two animals permits one to go further and ascribe them to the stimulation of an essentially similar collection of neurons or their processes.

The fact that Graham Brown<sup>20</sup> obtained an apparently related type of reaction from stimulation of the cut surface of the central grey matter surrounding the transition from third ventricle to cerebral aqueduct in the decerebrate chimpanzee, in which all but the most dorsal and caudal part of the diencephalon had been removed, suggests that a similar mechanism for facio-vocal responses may exist in higher primates.

There is little information concerning the nature of the reactive area. The fact that responses have still been obtained after elimination of the diencephalon by transection demonstrates that afferent connexions to the thalamus or higher centres are not essential. Such results from decerebrate animals do not exclude the dependence of these reactions on possible ascending pathways completing their afferent arcs at a mesencephalic level, and other investigators have reported reflex vocalization, in some instances with associated facial changes, occurring in acute and chronic midbrain preparations (Woodworth and Sherrington,<sup>21</sup> Bazett and Penfield,<sup>22</sup> and Keller<sup>23</sup>).

Such observations, however, attest the presence of an efferent mechanism of this type in the brainstem below the diencephalon, and it seems clear that within the reactive area delimited in these experiments there is contained an efferent pathway or system capable of producing facial and vocal responses during emotional excitement.

While the faciovocal reactions obtained from the midbrain and pons during these experiments have often been accompanied by such manifestations of general emotional excitement as pupillodilatation, pilomotor activity, urination, struggling, and, when it has been recorded, by rises in blood pressure, they have often occurred without any noticeable associated effects, or in association with responses whose emotional connotation is remote, such as the tegmental response of the limbs and trunk. It seems probable that a correlation of the faciovocal component with other features of emotional expression in the behaviour of the normal animal involves the activity of the more rostrally situated diencephalon or cerebral cortex.

#### SUMMARY

Coordinated facial and vocal activity, on the whole closely resembling that seen and heard during the expression of unpleasant emotion by the respective normal animal, has been obtained in response to electrical stimulation of a localized area in the midbrain and pons of the lightly anaesthetized monkey and cat, and of the acutely decerebrate cat. The anterior portion of the hypothalamus has also been found to be reactive in the lightly anaesthetized cat.

In both the cat and the monkey the reactive area in the midbrain includes the central grey matter of the aqueduct and a bridge of tissue extending from this region through the dorsal part and into the lateral and ventral portions of the tegmental area.

Responses from the decerebrate cat demonstrate that the effects are, in part at least, independent of afferent projections to the thalamus or cerebral cortex, and the conclusion seems justified that within the reactive area is contained an efferent pathway or system for eliciting coordinated facial, vocal and respiratory activity during the expression of emotion.

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