A DIENCEPHALIC MECHANISM FOR THE EXPRESSION OF RAGE WITH SPECIAL REFERENCE TO THE SYMPATHETIC NERVOUS SYSTEM

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At various times "the seat of the emotions" and the central mechanisms responsible for emotional behavior have been sought in the cerebral cortex. While it is reasonable to suppose that the neural processes underlying emotional consciousness are indeed cortical, it does not follow that the bodily changes which make up emotional behavior are due to a nervous discharge of cortical origin. The behavior attending the major emotions, fear and rage, is called forth by the urgency of certain definite circumstances and it is plainly directed toward the preservation of the individual. It constitutes a reaction which is primitive, energetically purposive and common to the divergent members of the vertebrate series. This consideration certainly suggests that the reaction is dependent upon older divisions of the nervous system. There is considerable evidence to show that this is actually the case.

Not only may the expression of one strong emotion, namely, anger, occur in the mammal deprived of its cerebral hemispheres, but in such an animal the tendency to exhibit this emotion is especially marked. The affective behavior of Goltz' dog (1892) was confined to a reaction, capable of regular elicitation, which closely resembled the rage of a normal dog. The same was true of the dog described by Rothmann (1923) and of the two hemisphereless cats prepared and studied by de Barenne (1920). The trivial and often irrelevant nature of the conditions which would evoke the reaction in these animals is noteworthy. A display of anger could be produced in Goltz' animal by pinching the skin or by taking it from its cage. The latter procedure invariably caused a violent protest in spite of the fact that it was the usual signal for feeding and would have been quite agreeable to a normal dog. In Rothmann's dog snarling and growling were obtained by gentle scratching of the back, and the presence of a fly on the creature's nose sent it into a fit of rage. De Barenne reports that his cats showed a similar emotional response to various disturbances, innocuous as well as painful; merely lifting them caused energetic movements of defense and those reactions which are so characteristic of the angry cat—spitting, growling and erection of the hair of the back and tail. The picture presented by these animals implies the unrepressed activity of certain primitive subcortical mechanisms.

From the earliest times it has been recognized that emotional excitement is accompanied by profound visceral changes, and Cannon (1915) has stressed the fact that in fear and rage the viscera are dominated by a discharge of impulses over the sympathetic division of the autonomic system. Although this aspect of emotional behavior failed to receive any attention in the observations of Goltz, Rothmann and de Barenne, the knowledge that cortical ablation renders the mammal excessively prone to a display of anger led Cannon and Britton (1925) to use a decorticate preparation in the study of one important consequence of the emotional activation of the sympathetic, namely, medulliadrenal secretion. In acute experiments on cats they found that after disconnecting the cortex from the brain stem there appeared upon removing the anesthetic "a group of remarkable activities such as are usually associated with emotional excitement—a sort of sham rage." A prominent feature of this quasi-emotional state consisted of signs of widespread sympathetic activity; it was attended by erection of hair, profuse sweating from the toe pads, a high arterial pressure and, provided the adrenal glands remained intact, notable increments in the rate of the denervated heart. Bulatao and Cannon (1925) described the high glycemic percentages associated with the sham rage and showed that medulliadrenal secretion plays a major rôle in their production.

A hint as to the locus of the subcortical level responsible for this emotional activity of decorticate animals can be gained from the results of experiments in which cerebral ablation has not been followed by such behavior. In 1904 Woodworth and Sherrington gave the name "pseudaffective reflexes" to certain responses, expressive of affective states, which they obtained in decerebrate cats (hemispheres and diencephalon removed) on stimulating an afferent nerve. Similar reflexes were noted by Bazett and Penfield (1922) in their chronically decerebrate cats; lashing of the tail, kicking, running, even biting, and, very occasionally, growling occurred when the animals were disturbed. It is, however, important to distinguish between the pseudaffective activity of these midbrain preparations and that of decorticate animals. In the former, as exemplified by the experiments of Bazett and Penfield, it consists of isolated items of behavior, never attains a general affective state and is typically brought forth by a stimulus which is connected with some habitual mode of response. And although in the experiments of Woodworth and Sherrington these reflexes, evoked by strong afferent stimulation, had a certain "width of coördination," it was pointed out that "they never amounted to an effective action of attack or escape." On the other hand the sham rage of the decorticate animal in the chronic (Goltz, Rothmann, de Barenne) as well as in the acute (Cannon and Britton) condition is elicited by trifling disturbances of any kind, it is astonishingly intense and possesses a width and energy of expression that makes it unmistakably the counterpart of intense fury in the normal animal. The level responsible for this more general and more energetic quasi-emotional behavior must lie above the mesencephalon.

The central source of the sympathetic discharge is primarily important in a study of the neural basis for emotional expression. In this connection it may be said that a central representation of certain fractions of the sympathetic system can be discerned at several points along the cerebrospinal axis, especially in the medulla oblongata. It is not unreasonable to regard the vasoconstrictor center, the bulbar cardio-accelerator mechanism and that portion of the medulla involved in Bernard's sugar puncture as sympathetic mechanisms, for the activation of each results in a discharge of impulses over certain groups of preganglionic sympathetic neurones. But it has been pointed out by Cannon (1915) that, in accord with the extensive distribution of its fibers and their arrangement for a diffuse discharge, the sympathetic, unlike the other divisions of the autonomic system, tends to discharge as a whole. This consideration in itself implies the existence of some dominant central coördinating mechanism which when active will produce a discharge of impulses over the entire series of sympathetic connector neurones. Cannon has further emphasized that the conditions under which this widespread discharge occurs are those which demand a vigorous response to ensure the maintenance of an essential condition or even of life itself. Foremost among these are the major emotions, fear and rage.

The present investigation was undertaken with this point in mind and was directed toward the delimitation of the part of the brain stem responsible for the sham rage of the decorticate cat. It was felt that not only would this elucidate the neural basis for this emotion but might yield some evidence for the existence of that predominant central mechanism which is so clearly implied by the tendency of the sympathetic to discharge vigorously and as a unit under conditions of stress.

The experimental procedure which was adopted as being the simplest and most direct method of realizing this delimitation was that of ablation of varying portions of the brain stem after removal of the hemispheres.

METHOD. Directly after etherization a tracheal cannula was inserted and the carotids ligated in the neck. After laying bare a large area of the parietal and a small part of the frontal bones, a trephine hole was made to one side of the mid-line and enlarged so as to expose the dorsal surfaces of the two hemispheres. Diploic bleeding was arrested by the application of pledgets of cotton. The mid-line was not crossed until the opening on one side had been completed and, as a rule, hemorrhage was slight provided care was taken not to injure the dura and underlying vessels. On passing across the mid-line the longitudinal sinus must necessarily be ruptured and therefore the rest of the operation was carried out with the greatest dispatch while an assistant compressed the vertebral arteries. After incising the dura the occipital pole of one hemisphere was raised so as to bring into view the posterior colliculus of the same side. A flattened and somewhat curved blunt dissector was inserted toward the base and brought to a position just lateral to the inferior quadrigeminal brachium. Holding the handle of the instrument toward the opposite side it was then possible by means of a single forward movement to remove the entire cortex and medullary center of one hemisphere. The procedure was repeated on the other side and this resulted in the ablation of the entire cortex except a small medial portion of each pyriform lobe. Immediately, the desired extent of brain stem was removed by making a frontal transection or, as in a number of experiments, by slicing away the dorsal parts of the diencephalon after removal of the corpora striata. A large sharp knife was used in order to produce a clean-cut surface with minimal traumatization of adjacent tissue. The cut surface was packed lightly with cotton moistened with warm Ringer-Locke's solution. When bleeding was persistent, small strips of muscle were applied. Then, after gradually releasing the pressure on the vertebrals, hemostasis was usually complete.

The entire operation was done as rapidly as possible. It was found that better results were obtained by working rapidly with vertebrals compressed than by proceeding slowly and attempting to check hemorrhage at each step. The respiration afforded a good index of the degree of cerebral anemia. As a rule the operation could be completed before any marked respiratory disturbance developed.

Since all parts of the cortex which subserve sensation, including pain, were removed, the ether was discontinued as soon as the cerebral ablation was completed. The development of the sham rage was thus made possible. The cat was placed on an animal board in the dorsal position and secured by all four feet with the head slightly elevated. While it was recovering from the anesthetic a femoral artery was cannulated and connected with a mercury manometer.

A detailed record of the behavior of the animal was kept throughout each experiment. Changes in the heart rate and arterial pressure were shown by the tracings; the respiratory rate was taken and all symptoms of significance were noted. These records and notations were made at varying intervals of time depending upon the changes in behavior. The temperature of the animals, as shown by a rectal thermometer, was maintained as nearly as possible within a degree Centigrade of the normal level. At the end of each experiment the remaining portion of the brain was carefully removed from the cranium, fixed in formalin and preserved in 70 per cent alcohol. A careful gross examination of these brains was supplemented by a study of the frontal sections of the cat's brain shown in Winkler and Potter's (1914) book. In this way it was possible to determine the extent of the ablation with a reasonable degree of macroscopic accuracy. In addition an histological study, still incomplete, has been made of sections cut from a number of these brain stems.

During the initial stage of the investigation the pseudaffective state was first produced by decortication, and then later the brain stem was cut across in an effort to determine the level of transection necessary to abolish the activity. Experience taught, however, that a second intervention was hazardous, especially in the face of the high arterial pressure which accompanies the activity. Therefore, in general, the method adopted was to determine the behavior following a single definite ablation. In a few of the earlier experiments the vagi were cut in the neck and the stellate ganglia removed; in the acute experiment this denervation renders the heart an indicator of medulliadrenal secretion (Cannon, Lewis and Britton, 1926). But in the majority of the experiments the nerves were left intact.

RESULTS. Records of behavior following cerebral ablation were obtained in 52 cats. Because of early death, hemorrhage or inadvertent injury of the remaining parts of the brain, 6 of these failed to be of any service in the localization of the region responsible for the sham rage. The following report is, therefore, based upon the results of 46 experiments.

The pseudaffective phenomena which occurred in these experiments were quite similar to those described by Cannon and Britton (1925). They developed spontaneously or could be evoked by the slightest disturbance; they usually appeared in fits which lasted from a few seconds to several minutes. They included struggling, attended by movements of the head and arching of the trunk with thrusting and pulling of the limbs; clawing movements of the fore legs with protrusion of the claws; waving and lashing of the tail; a snarling expression; and very rapid panting with mouth open and movements of the tongue to and fro. In addition to these activities were signs denoting a vigorous sympathetic discharge: erection of the tail hairs; sweating from the toe pads; retraction of the nictitating membranes; exophthalmos (separation of the lids); large increments in arterial pressure and heart rate. These activities sometimes appeared in incomplete combinations, two or three of them being absent during the whole or a part of an experiment. Pupillo-dilatation was noted in some cases, but since it may be brought about either by sympathetic activity (cervical sympathetic impulses or circulating adrenin) or by inhibition of the tonic discharge over oculomotor fibers supplying the sphincter of the iris, it cannot be taken as a certain indicator of the former. A similar difficulty is encountered in connection with the acceleration of the innervated heart. This might be attributed to a sympathetic discharge acting directly by way of the accelerators or indirectly through humoral factors; on the other hand, it might be due to central inhibition of the tonic vagal discharge. No attempt has been made to determine the relative importance of these three factors, but in view of the generalized sympathetic activity under these conditions it is certain that accelerator impulses play a rôle in the production of these more rapid rates. Cardiac acceleration frequently occurred simultaneously with the rises in arterial pressure and during the fits of sham rage there was never the slightest tendency to obey Marey's law.

All experiments were acute. The length of life was variable; but, in general, the more active the animal the shorter the survival. One of the inactive preparations survived over 19 hours and was finally killed while still in good condition, but in the whole series, the average duration of life was 4 hours. It was found that whenever the true pseudaffective behavior (sham rage) made its appearance it did so within 35 minutes of the completion of the cerebral ablation. There was only one exception to this rule, experiment 21, in which the activity did not appear until 65 minutes had elapsed; but in this case a moderate hemorrhage intervened and this may have temporarily postponed the development of activity.

The testimony of all who have studied decerebrate cats is consistent in showing that the decorticate sham rage never occurs in these preparations. Decerebration is commonly carried out by transecting the midbrain at a level passing between the superior and inferior colliculi dorsally and the roots of the third nerves ventrally. Often, as in the majority of Bazett and Penfield's animals, the ablation is extended to the most caudal parts of the midbrain. In this enquiry, therefore, the exploration of the brain stem has been confined to the diencephalon, the cranial part of the mesencephalon and, especially, to the zone of transition between these two divisions. Winkler and Potter (1914) have been followed in considering as diencephalon that part of the brain stem, "which is limited frontally by the anterior commissure and the chiasma n. optici, and caudally by the epiphysis and corpus mammillare."

The sham rage occurs after ablation of hemispheres, corpora striata and the cranial half of the diencephalon. This was especially well demonstrated by seven experiments in which decortication was followed by frontal transections, at various levels, through the diencephalon. In each of these there occurred the same vigorous quasi-emotional behavior which Cannon and Britton (1925) produced by decortication. Since these experiments are especially important in the delimitation of the central region responsible for the behavior, they will be described in some detail.

Experiment 1. After removal of the hemispheres the brain stem was transected through the cranial part of the thalamic region; the section was frontal and struck the base at the chiasma. Twenty-four minutes later, at 2:47, the first activity appeared quite spontaneously. It consisted of a fit of struggling with lashing of the tail, marked erection of the tail hairs, protrusion of the claws, snarling and a rapid rise in arterial tension from 130 to 160 mm. Hg. The denervated heart beat at a rate of 244 per minute. Four minutes later the animal was lying quiet; the hairs remained unruffled after being smoothed and the heart rate had dropped to 226. From 2:51 to 3:19 similar fits appeared at intervals. The tail hairs were erected with the onset of activity and they became smooth during the intervening periods of quiet. Similarly the arterial pressure and heart rate increased roughly in proportion to the activity and fell when the animal became quiet. During one intense struggle biting occurred while the head was thrown from side to side. At 3:19 the activity became continuous. From 3:19 to 3:26 the pads of the hind feet were moist with sweat.

At 3:27 a second transection was made, this time through the midbrain. Dorsally it shaved the cranial borders of the superior colliculi and ventrally it passed just behind the roots of the third nerves. Following this the animal remained quiet until its death at 7:05; the tail was still and the hairs down, the claws were never protruded, the pulse rate gradually fell from 288 at 3:26 to 186 at 6:53, and the arterial pressure remained nearly constant and above 90 mm. Hg until just before death. At 4:32 rough handling induced lashing of the tail which ceased as soon as the animal was left alone; there were no other reactions. This transection was followed by strong decerebrate rigidity.

Experiment 4. The only transection was made at the time of decortication. This passed more caudally than the first transection of experiment 1. It struck the base between the optic chiasma and the stalk of the hypophysis. For 35 minutes after removal of the ether the animal remained quiet and exhibited decerebrate rigidity. It then proceeded to show more and more spontaneous activity and for the next two hours presented much the same behavior as did the cat of experiment 1. There was struggling, lashing of the tail and protrusion of the claws. It failed to sweat, but the tail was bushy throughout; there were marked rises in arterial pressure (e.g., 112–152 mm. Hg) whenever activity occurred; the heart was denervated and its rate varied from 200 per minute during a long period of quiet to 254, the rate recorded at the time of maximal activity. During the quiet periods the most intense sham rage could be induced simply by loosening the thong binding one of the legs. Toward the end of the experiment, as the spontaneous activity became less and less, the extensor tone of the limbs became conspicuous.

Experiment 26. Transection at mid-thalamic level; the cut passed from a point 3–4 mm. in front of pineal body to the middle of the tuber cinereum. Heart not denervated and sympathetic innervation of eyes left intact. From 1:54, the time of the transection, until 2:29 slight passive movements evoked struggling, protrusion of claws and rises in arterial pressure (e.g., 110–144 mm. Hg), but eyes remained closed and covered with relaxed membranes; there was no sweating. At 2:29 there was a strong brief and spontaneous fit of activity: struggling, protrusion of claws, simultaneous rises in heart rate (296–302 per min.) and arterial pressure (112–138 mm. Hg). At this time sweat appeared on the toe pads. Similar periods of activity, more prolonged and frequent, appeared up to 4:00. During one intense fit the head was thrown from side to side and the mouth opened in a typical snarl. During the few periods of quiet the eyes were closed and the nictitating membranes relaxed, but with the onset of activity the palpebral space was widened and the membranes completely withdrawn; similarly the arterial pressure diminished and remained constant. From 4:00 to 5:30 the animal remained quiet unless disturbed, when a typical strong fit of activity immediately developed. Sweating ceased at 3:26. The respiratory rate was above normal from the first, and typical panting set

TABLE 1

(*Experiment 34*)

TIME	RECTAL TEMPERATURE	HEART RATE PER MINUTE	ARTERIAL PRESSURE	RESPIRATIONS PER MINUTE	NOTES
			mm. Hg		
2:05					Decortication and transection completed; ether off. Heart not denervated
2:24	36.3	170	162	40	Quiet; hairs down; claws in; eyes closed; pupils moderately dilated; nictitating membranes far over eyes; rigidity
2:37	37.2	198	180	44	Tail waving; hairs erected; head movements; eyes half open; membranes partly retracted
2:42	37.3	178–216	210–240	52	Slight spontaneous struggle; head moved; hairs further erected; tail still. Bending neck caused the rises in arterial pressure and heart rate recorded
2:47	37.2	174	175	34	Quiet; hairs erected; claws in; eyes half closed; pupils much wider; membranes far out over eyes; rigidity
2:57	37.2	220	208–222	28	Spontaneous struggle; tail waving
3:05	37.3	192	185	30	Quiet; hairs slightly erected
3:20	37.3	186	164	28	Quiet since 3:13. Tail still; hairs same; eyes closed; membranes far out over eyes; pupils wide; claws in; rigidity
3:28	37.2	204	185±	30	Spontaneous struggle with rise in arterial pressure; further erection of hair; opening of eyes; retraction of nictitating membranes; claws in
3:47	37.1	192	169±	32	Continuous spontaneous struggle; claws out; tail waving; hairs up; eyes wide; membranes retracted; sweat on toe pads
3:56	37.0	200±	118–133	26	The same
4:05	37.1	194	137	34	The same
4:20	37.1	228–240	122–140	34	Spontaneous struggling at intervals; claws out; tail waving; hairs up; sweat on pads
4:37	37.3	210–216	138–160	44	Tapping leg with pencil causes struggle with rises in heart rate and arterial pressure; widening of eyes and retraction of membranes. Claws out; pads damp
5:24	36.7	183	134–160	36	Slightest touch evokes activity as before; pads damp
5:30–11:28	37.6–36.5	242–196	115–53	56–34	No activity either induced or spontaneous. Arterial pressure gradually fell; above 88 till 7:45
11:54					Killed

TABLE 2

(*Experiment 13*)

TIME	RECTAL TEMPERATURE	HEART RATE PER MINUTE	ARTERIAL PRESSURE	RESPIRATIONS PER MINUTE	NOTES
			mm. Hg		
2:26					Decortication and transection completed; ether off. Heart not denervated
2:39		302	136	172	Quiet; hairs up slightly; panting; claws in; rigidity
2:44	37.0	228	128	240	Same; tail waving
2:48	37.0	244	120–144	216	Spontaneous struggle; hairs further erected; claws out; panting slower and deeper with struggle
2:54	37.0	256	110–128	200	Vigorous spontaneous struggle; tail lashing and bushy; claws maximally protruded; movements of vibrissae; snarling expression; panting tongue to and fro
2:58	36.8	256–264	102–130	240	Continuous activity, more intense; eyes very wide
3:03	36.8	256–268	116–144	200–240	Continuous maximal activity; pulling and tugging; claws maximally protruded; tail lashing and bushy; arterial pressure and heart rate up and down with activity
3:11	36.7	262	87–100	204	Slight struggle; tail waving and bushy; claws out; panting with mouth open and tongue to and fro. Sweat on toe pads
3:15		256	83	232	Continuous activity; but not so intense as at 3:03
3:17	36.5	246–256	74–90		Intense struggling from moment to moment; more moderate activity during intervals; no periods of quiet; no rigidity
3:22	36.3	246	55–62	160	The same; pupils and eyes very wide; pads moist
3:28	36.2	244	65	170	Quiet followed by one slight struggle with protrusion of claws. Wide pupils; panting; continuous waving of tail and hairs erected after smoothing down; rigidity
3:31	36.2	246	65	180	Strong struggle with increased respiratory rate; movement of vibrissae; no rigidity
3:40–3:45	36.0	236	44	200	Struggling from time to time; claws maximally protruded; tail waving and bushy; pupils very wide; panting at increased rate, mouth open and tongue to and fro
3:55					Cat died; respiratory failure and falling arterial pressure

in at 2:50, attaining a rate of 160 per minute toward end of experiment (5:30). Animal lacked tail; no observations on hair.

Experiment 5. Same ablation as in experiment 26 and showed essentially the same behavior.

That the sham rage will develop after a still more caudal truncation of the brain stem is shown by experiments 34 and 13. Figures 1 and 2 indicate that in cat 34 the transection struck the base a trifle behind the level represented by experiment 26, but dorsally it is distinctly more caudal. Reference to Winkler and Potter (1914) shows that the distal half of the thalamus, a corresponding portion of the hypothalamus and a small portion of the geniculate bodies remain in the diencephalon. The corpora striata were completely removed. The behavior of this animal, described in detail in table 1, was intensely quasi-emotional. Besides the changes involving skeletal muscle there were the usual signs of a vigorous and widespread sympathetic discharge. In this experiment, as well as in experiment 26 and all which follow, the heart was not denervated. Accordingly, with stellate ganglia and cervical sympathetic trunks intact, widening of the eyes, retraction of the nictitating membranes and sweating from the fore feet were among the sympathetic symptoms which appeared during the active periods. In this instance sweat appeared on the toe pads of all four feet, but only after prolonged activity. In almost every case in which this symptom appeared it was characterized by a certain latency and it usually disappeared before the other signs of sympathetic discharge abated. In experiment 13, the brain from which is shown in figures 3 and 4, the transection passed in the same frontal plane as in 34, but the level is about a millimeter more caudal. Nevertheless, as indicated in table 2, this cat spontaneously exhibited all the signs of extreme rage. It was the most intense activity encountered in the entire investigation and it continued with only one brief interruption for over an hour. Its vigor brought about an early death from reactionary hemorrhage. This was the most caudal truncation of the brain stem that was followed by a spontaneous exhibition of the pseudaffective state with its full complement of activities.

Experiment 33 is of some special interest. Here the transection was made at about the same level as in the two experiments just described, but it ran a markedly oblique course. Judged by experiments 34 and 13 enough tissue to the right of the mid-line was spared to permit the development of the sham rage, but at a point 2 mm. to the left of the mid-line the cut attained a level which other experiments have shown produces a quiet decerebrate animal. In spite of this somewhat unilateral ablation, table 3 reveals the fact that for over 7 hours the cat exhibited the activity typical of sham rage. And it may be added that there were no indications of any differences in the motor activities of the two sides of the body.

Observations of the behavior following transections of the diencephalon

TABLE 3

(*Experiment 33*)

TIME	RECTAL TEMPERATURE	HEART RATE PER MINUTE	ARTERIAL PRESSURE	RESPIRATIONS PER MINUTE	NOTES
			mm. Hg		
2:01					Decortication and transection completed; ether off. Heart not denervated. No artificial heating till 5:00
2:19	38.8	166	165	28	Quiet; tail bushy; claws in; pads dry; eyes closed; pupils narrow; nictitating membranes out; rigidity
2:29	38.7	178	174	20	Tail lashing, bushy; claws out; eyes open; membranes retracted
2:35	38.5	188	170	28	The same
2:42	38.4	192	154–180	18	Spontaneous struggle with rise in arterial pressure; claws out; tail lashing, bushy; eyes wide; membranes retracted
2:49		198–228	158–177	26	No struggle; otherwise the same. (Release of leg induces struggle with increase of heart rate and arterial pressure)
2:58	38.2	174–210	150–156	22	Strong spontaneous struggle with rises in arterial pressure and heart rate; claws out; tail lashing, bushy; eyes wide; membranes back; sweat on toe pads
3:04	38.4	186	115	28	Quiet; tail quiet, bushy; otherwise as before
3:13	38.3	192	118	24	The same
3:29–3:40	38.3	198–202	138–158	28	Tail waving, bushy; claws maximally protruded; eyes wide; pupils very wide; membranes slightly out; pads moist; slightest touch evokes intense activity
3:50	38.2	202–222	133–150	24	Spontaneous struggle with rises in arterial pressure and heart rate; tail lashing; claws out
4:00	38.0	202	123	24	Quiet; intermittent waving of tail, bushy; claws out; eyes half closed; membranes over eyes; membranes quickly and completely retracted on releasing leg
4:08	38.2	204–240	125–156	20	Quiet; release of foreleg causes struggle, waving of tail, further erection of hairs, fresh retraction of nictitating membranes, definite dilatation of pupils, rises in arterial pressure and heart rate
4:30–4:48	37.8	210–232	130–170	30	Quiet; tail still but bushy; claws out; rigidity; moving leg or thermometer evokes struggle, tail waving; further protrusion of claws, separation of lids, abrupt retraction of membranes, simultaneous rises in arterial pressure and heart rate

TABLE 3—*Concluded*

TIME	RECTAL TEMPERATURE	HEART RATE PER MINUTE	ARTERIAL PRESSURE	RESPIRATIONS PER MINUTE	NOTES
			mm. Hg		
5:00	37.6	230	144	34	The same. Heating pad applied for first time
7:25	38.5	210–240	117–187	40	(Next observation.) Intense spontaneous struggling from time to time with rises in arterial pressure and heart rate as indicated, lashing of tail, further protrusion of claws and erection of tail hairs, retraction of nictitating membranes, opening of mouth and snarling. Panting; mouth open, tongue to and fro
7:38	38.6	222–240	118–160	40	The same intermittent spontaneous activity
9:01	37.7	240	124–158	56	The same. Pads dry
9:16–9:25	37.6	238–248	100	36	Quiet; tail still but bushy; claws out; eyes half closed, membranes over eyes
9:43	37.5	248	86	28	Brief spontaneous struggle; slightest disturbance evokes activity
10:22	38.0	252	68	26	Quiet since 9:43, but tail bushy and claws partially protruded. Rigidity. Cannot induce any activity by manipulating animal
10:30					Killed

between the levels represented in experiments 1 and 34 were obtained in six other animals. In each of these the typical activity made its appearance and ran the same general course as in the seven experiments detailed above. In the light of the results obtained when more caudal transections were made, the appearance of the sham rage in thirteen out of a total of thirteen experiments is a result of outstanding significance.

The sham rage fails to develop after transecting the caudal extremity of the diencephalon or the cranial portion of the mesencephalon. Because of a certain interlocking of diencephalon and mesencephalon in the cat's brain, it is not possible to divide one from the other along any frontal plane. Yet a transverse section which passes downward from the cranial borders of the superior colliculi to reach the base just behind the mammillary bodies will separate them approximately (Winkler and Potter, 1914). Cranial to it will lie the entire hypothalamus except the distal extremities of the corpora subthalamica which are about to give place on each side to the substantia nigra. Behind it there will remain a small caudal portion of the ventral and posterior nuclei of the thalamus and the greater mass of the geniculate bodies which embrace the mesencephalon dorso-laterally.

On the other hand this section will just cut off the cranial ends of the mesencephalic red nuclei which extend forward between the nuclei of the hypothalamus.

A number of experiments were devoted to the exploration of this zone of transition between diencephalon and mesencephalon. In none of them did a true decorticate sham rage develop, nor could it be induced by disturbances which invariably evoke it in animals retaining the caudal half of the diencephalon. Protocols of some of these experiments follow.

Experiment 52. Frontal transection made at 10:02 a.m. Figures 5 and 6 show that it passed through the pineal body dorsally and cut away the cranial two-thirds of the mammillary bodies ventrally. Animal observed for 6 hours. Remained in excellent condition, arterial pressure averaging around 95 mm. Hg. Showed decerebrate rigidity and no spontaneous activity of any kind. Respiration suddenly became rapid at 11:40 and remained around 150 per minute thereafter; this high rate persisted after reducing body temperature from 38.0° to 35.0°C. Mouth kept closed and no true panting. Moving or inserting rectal thermometer caused brief struggling, with tail waving, slight protrusion of claws, moderate increments in arterial pressure (e.g., 94–106 mm. Hg) and heart rate (e.g., 202–220 per minute). Moving limbs or whole cat or pinching evoked nothing. Tail hairs became slightly erected with the induced activity, but no other signs of sympathetic activity appeared; nictitating membranes remained out over partially closed eyes; there was no sweating.

Experiment 40. Brain shown in figures 7 and 8. Transection struck base through caudal third of mammillary bodies; above, it passed more cranially than in experiment 52. Animal killed in good condition after 19 hours of observation. During first five hours release of legs caused slow head movements and protrusion of claws with rise in arterial pressure and, occasionally, a small increase in heart rate—nothing else. During next nine hours only tail waving could be induced. For remainder of experiment moving legs passively brought on movements of progression. Toward end of experiment kicking and tugging with protrusion of claws followed application of hot-water bag; this was attended by huge rises in arterial pressure (e.g., 85–160 mm. Hg). This activity was not accompanied by any ocular changes, erection of hair or sweating. The pulse rate decreased as arterial pressure rose. Immediately after the cerebral ablation the heart rate was slow, 112 per minute, but it soon became more rapid and for the rest of the experiment vacillated back and forth between 160 and 212; no marked accelerations occurred at any time. The respiratory rate varied from 34 to 56 per minute. Strong decerebrate rigidity persisted throughout the 19 hours.

Experiment 51. A clean cut was made across the brain stem at 10:15 a.m. It passed down the cranial borders of the superior colliculi and severed the mammillary bodies through their caudal third. From 10:15 to 11:50 the animal showed no activity except very slight struggling with waving of the tail and trifling rises in arterial pressure (e.g., 138–145 mm. Hg) on moving thermometer in rectum. Only once did this cause cardiac acceleration (204–236 per minute). The claws were not protruded, the eyes were partly closed and the nictitating membranes remained relaxed and immobile; there was no sweating, but from the beginning the hair of the tail was slightly erected. Between 11:50 a.m. and 12:18 p.m. the central end of one crural nerve was stimulated electrically at three different times. It regularly produced waving of the tail, weak struggling, acceleration of the respiration (40–60 per minute), erection of the tail hairs, abrupt retraction of the nictitating membranes, pupillo-dilatation and increased arterial tension, the maximal rise being from 115 to 175 mm. Hg; only once did cardiac acceleration occur (260–280 beats per minute). The pads remained dry and the claws were never protruded. The activity immediately subsided after the stimulation ceased. From 12:30 until the animal was killed at 3:00 p.m. it remained quiet except for weak waving of the tail from time to time. Rigidity was present in all four legs throughout.

The brain stem was transected at this level, i.e., at the caudal extremity of the diencephalon, in a total of seven experiments. In the other four the results were precisely the same as those described in these three protocols. At no time in any of these animals did there develop either spontaneously or as a consequence of stimulation a behavior which even approximated the picture of intense fury which regularly occurs after retention of the caudal half of the diencephalon. It is quite true that a few of the reactions which make up the sham rage were obtained in these cats by such disturbances as moving the limbs or rectal thermometer, but they were limited in extent and vigor. It is also wholly apparent that they lack the spontaneity and easy elicitation of the sham rage. Even the widespread reaction obtained in cat 51 by direct stimulation of an afferent nerve could not measure up to the fits of sham rage invariably seen after the more cranial transections.

In five animals the brain stem was cut across through the cranial part of the mesencephalon. In experiment 1, already described, such a transection put an end to the strong activity which had followed decortication and ablation of all of the brain stem cranial to the chiasma. Typical of these were experiments 46 and 31. Protocols of these follow.

Experiment 46. The transection shaved the cranial borders of the superior colliculi and reached the base just behind the mammillary bodies. The observation covered 4 hours and 35 minutes; it was terminated by killing the animal. No struggling, tail waving, widening of the eyes, retraction of the nictitating membranes or sweating occurred either spontaneously or in response to the usual disturbances. Tail hairs slightly erected throughout. Arterial pressure and heart rate were variable, but changes developed slowly and without apparent cause. On several occasions passive movement of legs induced moderate rises in arterial pressure curve (e.g., 93–115, 107–129 mm. Hg). Heart rate varied from 212 at beginning to 292 beats per minute at end. Respiration normal during first two hours; it then quickened and reached rate of 72 per minute, but there was no true panting. Decerebrate rigidity was present throughout.

Experiment 31. Brain shown in figures 9 and 10. Observed from 3:17 to 7:00 p.m. No spontaneous activity; slight waving of tail was the only symptom that could be evoked by moving the legs or rectal thermometer. Claws never protruded, mouth closed and no panting. Respiratory rate increased from 33, at beginning, to 58 per minute at end. Rigidity was present throughout. Tail hairs very slightly erected, eyes remained closed and covered by relaxed nictitating membranes. No sweat. TraubeHering waves appeared in pressure tracing; there was a gradual fall in arterial pressure from 120 mm. at 3:38 to 76 mm. at 5:53, and finally to 62 at 7:00. Until 5:15

the heart rate varied between 132 and 148 per minute; at 5:53, in the absence of any other bodily changes, it mounted quickly to 228 per minute and remained there to the end of the experiment. Strong rigidity of the limb extensors persisted throughout.

The sham rage may occur after ablation of the dorsal parts of the diencephalon. The experiments cited thus far have shown that if the caudal half of the diencephalon remain connected with the lower divisions of the brain stem a stage of sham rage will develop. They fail to show specifically whether the part essential for the activity is located dorsally or ventrally in this region. The apparently well-established relation of the hypothalamus to the sympathetic system suggested that the basal part of the diencephalon might be the source of this quasi-emotional behavior with its sympathteic discharge. Therefore in a large number of animals an attempt was made to leave only the hypothalamus connected with the midbrain. While twelve cats survived this more difficult operation for periods of sufficient duration to determine whether the sham rage would develop, only four exhibited it. A microscopic examination of their brains has shown that the desired separation was never wholly effected; in each a little of the ventral and caudal parts of the thalamus remained intact. Nevertheless these experiments are of some service in attaining a more precise delimitation.

Experiment 44 represents the most extensive dorsal ablation which was followed by the sham rage. A lateral view of the brain from this cat is presented in figure 11. A microscopic study of serial sections cut from it has shown that there remained in the diencephalon all of the hypothalamus which lies behind the chiasma except the cranial ends of the corpora subthalamica, a thin lamina of the ventral part of the thalamus, and all of the caudal extremity of the thalamus except the pulvinar. Table 4 gives some impression of the intense quasi-emotional behavior of this animal. The visceral changes which were such a prominent feature of the activity can leave no doubt as to the general involvement of the sympathetic system. The extraordinarily high rate of the innervated heart, the profuse sweating and the marked ocular changes warrant special notice.

Similar ablations were made in experiments 21 and 37, and each gave positive results. Again, histological examination of the brain remnants from these animals revealed small ventral and caudal fractions of the thalamus and the greater part of the hypothalamus. In both animals vigorous struggling occurred spontaneously and could be induced by the slightest disturbance, but for the most part the activity involving skeletal muscle was confined to a constant protrusion of the claws, incessant lashing of the tail and an occasional expression of snarling. These activities were accompanied by maximal changes in organs innervated by the sympathetic system. In short there seemed to be a preponderance of

TABLE 4

(*Experiment 44*)

TIME	RECTAL TEMPERATURE	HEART RATE PER MINUTE	ARTERIAL PRESSURE	RESPIRATIONS PER MINUTE	NOTES
			mm. Hg		
9:50					Decortication, transection at level of chiasma and ablation of dorsal part of diencephalon
10:09	37.2	208	167	32	Quiet; hairs up; pads dry; claws in; eyes half closed; nictitating membranes over eyes; rigidity
10:18	37.2	232–248	182–194	28	Slight spontaneous struggle with rises in arterial pressure and heart rate; tail waving
10:22		262	184		The same; claws out continuously; fore feet wet with sweat
10:28–10:35	37.7	290–296	187–215	32	Continuous struggling; tail lashing and bushy; maximal protrusion of claws; fore feet dripping with sweat, hind pads moist; with struggling, eyes and pupils widen, membranes retract and heart rate and arterial pressure rise rapidly
10:45	38.0	308–320	160–189	44	Intense fits of struggling accompanied by tail lashing, protrusion of claws, widening of eyes and pupils, retraction of membranes, rises in arterial pressure and pulse rate; tail bushy; fore feet dripping with sweat, hind pads moist
10:50	38.0	308	115–143	38	The same
11:05	38.0	300–308	90–106	40	Spontaneous struggling less frequent, but slightest touch induces maximal activity
11:20	37.8	310–318	90–122	40	Spontaneous activity as before. Sweating not so profuse
11:35	37.6	302	76–90	40	The same
11:55 12:45	37.0	296–300	95±	36–30	Quiet; tail bushy; claws out; pads dry; eyes partly closed; nictitating membranes relaxed
1:30	37.9	296–300	93–117	30	The same; passive flexion of leg induces struggle with tail waving, protrusion of claws, rises in arterial pressure and heart rate; slight rigidity
2:56	37.6	300	89–148	32	The same
3:27	37.4	290	76	30	The same; can induce activity by slightest disturbance
3:45					Killed

sympathetic over cerebro-spinal discharge. At the same time the character and coördination of the activity left no doubt in the observer's mind as to the type of behavior it represented; it was unquestionably a sham rage. The very absence of strong body and limb movements, except when the animals were disturbed, made the behavior of these animals very like that of a normal cat which is feeling savage. In both conditions the body and limbs are kept still, but the bristling hair, the ready claws, the lashing of the tail, the wide eyes and pupils afford unmistakable evidence of an intense affective state. In both cases a slight disturbance evokes vigorous movements of attack.

The inactivity of eight out of the twelve preparations which belong to this series is not difficult to account for. Examination of the brains from four of these negative experiments showed that the ablation had extended so close to the base over the mammillary bodies as to make them essentially midbrain animals. In the other four, however, the ablation was no different than in experiments 44, 21 and 37. The reason for their inactivity may be due to the fact that the longitudinal slicing of the diencephalon plainly exerts traction on the brain stem and it is only too likely that this might disrupt the mechanisms which are essential for the development of the sham rage. But, whatever the explanation, these particular negative results may be legitimately disregarded; the really significant fact is that positive results were obtained after making comparable ablations.

These experiments make possible a still further restriction of the central region which must be left intact if the decorticate sham rage is to develop. The method of frontal transection showed that the behavior is dependent upon mechanisms which lie within the caudal half of the diencephalon, but in view of the results of these dorsal ablations it becomes apparent that it is the ventral and caudal parts of this half which are essential. This delimitation is illustrated in figure 12 which presents a sagittal view of the brain stem of a cat. The lines represent the extent of the ablation in three representative and important experiments; in 34 and 44 the sham rage developed; in 40 it failed to do so, and, as will be remembered, in no case did the typical behavior appear after sections at or behind this level.

The transitional type of behavior obtained after transecting the caudal part of the diencephalon. There remain to be considered the results of an exploration of that segment of the brain stem which lies between the levels of transection represented by experiments 13 and 52 (see pp. 499 and 502). It has been shown that the presence or absence of this part of the diencephalon determines whether the sham rage does or does not follow removal of the higher parts of the cerebrum. Successful transections were made through this region in 9 cats. Since some fraction of the essential part remained in each, it is not surprising that 6 out of the 9 exhibited a type of behavior which was distinctly transitional between the sham rage of the decorticate animal and the relatively weak and less definitive reactions of the midbrain preparation. The activity of the remaining 3 was confined to reactions of the latter sort. Two experiments afford fair examples of this intermediate type of behavior. Ventral views of the brains from these cats are shown in figures 13 and 14.

Experiment 47. Transection at 11:00 a.m. It began dorsally at precisely the same point as in experiment 13 (see fig. 4) but ventrally it passed about a millimeter behind the level of that transection and struck the base at the cranial border of the mammillary bodies. On the left side lateral slicing removed part of the cerebral peduncle and some of the overlying tissue. This animal remained in excellent condition up to 5:40 p.m. when it was sacrificed, but showed no spontaneous activity. When undisturbed it remained motionless with tail hairs erected, claws in, eyes closed, nictitating membranes relaxed, and showed decerebrate rigidity. During the 90 minutes which immediately followed the operation such disturbances as manipulating the legs or moving the rectal thermometer caused only a short brief struggle accompanied by waving of the tail, protrusion of the claws, head movements from side to side and rises in arterial pressure and heart rate. Later these same disturbances had a more pronounced effect; they induced more vigorous and longer continued struggling and, in addition, facial movements suggestive of snarling, widening of the palpebral spaces, brisk retraction of the nictitating membranes and greater rises in arterial pressure (e.g., 166–204 mm. Hg) and heart rate (e.g., 206–256 beats per minute). Sweating did not occur nor did the respiratory rate rise above the normal. The arterial pressure remained above 140 mm. Hg and the quiet heart rate averaged around 210 beats per minute.

Experiment 50. Clean frontal transection at 9:53 a.m. It shaved the cranial borders of the superior colliculi and passed through the cranial part of the mamillary bodies. No spontaneous activity occurred at any time, but the toe pads were moist with sweat from 10:53 a.m. to 12:02 p.m. From 10:21 until the animal was killed at 2:30 p.m., moving the rectal thermometer or passively flexing a leg evoked a brief but strong fit of struggling accompanied by opening of the mouth, snarling, waving of the tail, widening of the eyes, brisk retraction of the nictitating membranes and increments in arterial pressure (e.g., 120–157 mm. Hg) and pulse rate (e.g., 230–252 per minute). When undisturbed the cat lay quietly with lids partially closed and eyes covered by relaxed nictitating membranes and showed decerebrate rigidity. The tail hairs were moderately erected throughout. The respiratory rate varied only between 22 and 27 per minute, the arterial pressure was at all times above 120 mm. Hg and the quiet heart rate gradually increased from 180, at the beginning, to 246 per minute at the end of the period of observation.

It is obvious that this sort of behavior falls short of the sham rage of such animals as cats 34 and 13 in being less vigorous and entirely dependent upon stimulation. At the same time it possesses a latitude which is absent from the reactions which can be similarly induced after more distal ablations. It is somewhat more expressive of an affective state. Particularly noticeable is the greater sympathetic activity; for example, the ocular symptoms of cervical sympathetic discharge were readily induced and sweating occurred in two experiments (38 and 50) of this series. These changes were not seen when the transection passed more caudally. It is suggested that the basis of these differences is the presence, in the brains of these cats, of a small but definite fraction of that part of the diencephalon which has been shown to be requisite for the development of the sham rage.

Discussion. The work of a number of investigators, to which reference has been made, has established the fact that the decorticate cat or dog, in the chronic as well as in the acute condition, is capable of displaying a type of behavior which is commonly regarded as expressive of anger. From this it may be inferred that the nervous mechanisms for the expression of this emotion are subcortical. The results which have been presented in this paper support that view. They show that the remarkable activity which develops almost immediately after decortication in the cat and which is best described as a sham rage, is dependent upon the integrity of a definite part of the brain stem. Thus it regularly appeared after ablation of the hemispheres and all parts of the brain stem cranial to the middle of the diencephalon. But when, in addition, the caudal half of the thalamic region was removed the typical sham rage invariably failed to develop. By combining the results obtained from frontal transections with those which followed ablation of the dorsal part of the thalamus it becomes possible to state that the discharge of nervous impulses which evokes this extraordinary motor activity is conditioned by central mechanisms which lie within an area comprising the caudal half of the hypothalamus and the most ventral and most caudal fractions of the corresponding segment of the thalamus.

The consistency of the results obtained in these acute experiments is worthy of emphasis. In no case did the true quasi-emotional behavior occur when the area defined above was removed. In the great majority of those experiments in which it was left intact that behavior appeared in its full vigor. The consistency is further demonstrated by the observation that when a fraction of the active region remained the result was frequently a behavior transitional between that of the fully active animals and that exhibited by the quiet midbrain preparations.

Anyone who has ever tied an unruly cat to an animal board will agree that the sham rage shown in these experiments closely resembles the behavior of the infuriated normal animal. It has been pointed out that this is essentially different from the "pseudaffective reflexes" obtained in cats after section of the midbrain. The latter are less intense, less generalized, less easily invoked and far less expressive of an affective state. They appear to take their origin from a background of neural inactivity whereas the phenomena shown in the decorticate or diencephalic preparation suggest hyperexcitability of the central mechanisms involved. A part of the central arrangements for emotional expression are of course situated below the level of the diencephalon. Certain elements of affective behavior may even be induced in the spinal cat, and still more in the bulbo-spinal or midbrain preparations, but the results of this investigation indicate that it is only when the diencephalic mechanisms are present that these elements can be readily welded together to form the rage reaction.

The question of the genesis of the decorticate rage cannot be answered with any assurance. Its spontaneity has been stressed, but it is realized that such a description is merely relative and serves to distinguish it from the less easily evoked "pseudaffective reflexes" of the decerebrate cat. Under the conditions of these acute experiments afferent impulses from the incised areas may be continually impinging upon the centers; and the restraint imposed upon the animal by tying it in the dorsal position is very probably a disturbing factor. The excessiveness of the activity as well as its easy elicitation gives it the appearance of a "release phenomenon." Thus it might be explained on the basis of the view first advanced by Hughlings Jackson (1884) and elaborated by Head (1921) to the effect that the cortex normally holds in check those activities of the lower and more archaic centers which would seriously interfere with its more discriminative reactions. The expression of emotional excitement is just this sort of activity and in the case of chronically decorticate animals release from cortical control must be the chief if not the sole factor in producing the tendency to react excessively; there the chronicity of the behavior precludes its being due to any sort of "irritation." But in acute experiments the latter may play a rôle. In these the widely opened cranium obviates the chance that the activity is, in any way, due to increased intracranial pressure. Nor could it be due to a cerebral anemia resulting from occlusion of the carotids, for it is recognized that in the cat the vertebral arteries are alone capable of maintaining an adequate cerebral blood flow.[1] Whatever the cause may be, it is one which activates a limited region in the brain stem.

The quasi-emotional behavior consists of both somatic and visceral

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[1] This is implied in the demonstration by L. Hill (1896) that 60 per cent of cats will withstand ligation of both carotids and both vertebrals. Since no study seems to have been made of the results of occlusion of only both common carotids in cats, this procedure was carried out in four cats with aseptic precautions. These animals were watched carefully for six hours following the operation and were kept under observation for several days. In no case did any abnormal activity occur. One cat showed some mental dullness and slight ataxia during the first two days. The others appeared normal at all times after recovery from the ether.

activities and the latter are plainly due to a discharge of sympathetic impulses. Both appear to be the result of the activation of intimately related central mechanisms; they are not separable and together form an integrated reaction. The vigorous activity in skeletal muscle is difficult to account for on the basis of the present neurological status of the diencephalon, for, so far as is known, this part of the brain does not contain any definite somatic motor nucleus. Mesencephalic centers may in some way be involved, but this possibility is rendered unlikely by the fact that this division remained almost wholly intact in animals which did not exhibit the sham rage. On the other hand, there is good evidence that the sympathetic system possesses a definite diencephalic representation. Physiological evidence has been presented by Karplus and Kreidl. These investigators have found (1909, 1911) that in cats electrical stimulation of an hypothalamic point, lateral to the infundibulum, will produce maximal bilateral dilatation of the pupils, separation of the lids and retraction of the nictitating membranes. They showed that they were activating a true subcortical center (1910), that the ocular effects produced were mediated by the cervical sympathetic and that no other parts of the diencephalon except the hypothalamus yielded them (1909, 1910). They mentioned that the stimulation induced profuse sweating from all four feet and, in subsequent papers (1918, 1927), reported rises in arterial pressure. In their most recent investigation (1927) they found that the vascular effect persisted after removal of adrenals and hypophysis (which does not prove, as they seem to imply, that the stimulation does not affect the glands). Houssay and Molinelli (1925) have presented evidence that while weak electrical stimulation of the motor cortex, corona radiata, internal capsule and the thalamus has no influence on the adrenal medulla, the same current applied to the hypothalamus will cause a substantial secretion of adrenin. On the anatomical side the matter is less clear, but Greving (1925) has described nuclei in this region which he believes are related to the sympathetic system, and Dresel (1923) has offered some evidence that certain cell groups in the hypothalamus are connected with preganglionic neurones in the lateral horns of the thoracico-lumbar region of the cord.

Certain facts relating to the regulation of body temperature support the view that there is a diencephalic representation of the sympathetic. It is well known that erection of hair, ruffling of feathers, constriction of peripheral vessels and an increase in blood sugar occur when the homoiothermic animal is exposed to cold, and there is abundant evidence that medulliadrenal secretion is added to the blood under these circumstances (Cannon, Querido, Britton and Bright, 1927). These activities have an important place among the bodily changes which resist a lowering of body temperature. They are all due to a discharge of sympathetic impulses.

It is reasonable to suppose that this discharge has its source in the diencephalon, for it is this part of the brain which is essential for the maintenance of a constant body temperature. The labors of a large number of investigators (Isenschmid and Krehl, 1912; Isenschmid and Schnitzler, 1914; Rogers, 1919; Bazett and Penfield, 1922; Magnus, 1924) indicate that so long as this portion of the brain stem remains intact the processes of temperature control may proceed in a normal fashion.

Furthermore, exposure to cold and emotional excitement are attended by similar bodily changes. Restlessness, trembling and shivering, and especially those visceral activities that denote a widespread sympathetic discharge are prominent in both conditions. These reactions represent an effort on the part of the animal to cope with a critical situation and afford excellent examples of the emergency function of the sympathico-adrenal mechanism which has been emphasized by Cannon (1915, 1919). It now appears that in both instances they are dependent upon the activity of the diencephalon. This fact suggests that the diencephalic representation of the sympathetic presides over the emergency function of that system. The presumption is strong that it is not concerned in the simple reflex sympathetic discharges nor in the tonic discharge which occurs over certain fractions of the thoracico-lumbar outflow. Lower levels seem capable of subserving these functions; the pioneer work of Owsjannikow and Dittmar showed this to be true of the vasoconstrictor mechanism; Karplus and Kreidl (1918) admit that the integrity of their hypothalamic center is not necessary for the reflex activation of the cervical sympathetic; and Cannon and Rapport (1921) found that the reflex secretion of adrenin is not impaired by a midbrain section, but is wholly abolished by a transection just behind the inferior colliculi.

In view of these facts it is suggested that the present investigation has contributed evidence for the existence of a dominant central mechanism for the control of the sympathetic system, located in the diencephalon and responsible for the tendency of that system to discharge vigorously and as a whole under conditions of stress. In addition it is believed that the results obtained reveal the true significance of the various sympathetic effects which have been produced by stimulation of the hypothalamic region in narcotized animals. As isolated facts they possess little meaning; interpreted as the result of the activation of a dominant sympathetic mechanism they gain significance.

SUMMARY

An investigation has been made of the source, within the central nervous system, of a remarkable group of activities which follow decortication in the cat. This behavior simulates the expression of anger as seen in the normal cat and is best described as a sham rage.

The method used was that of ablation of varying portions of the brain stem after removal of the hemispheres. In acute experiments it was found that the typical sham rage regularly developed after removal of all parts of the brain cranial to the middle of the diencephalon, and after removal of the dorsal part of the thalamus. It invariably failed to appear after sections which separated the ventral and most caudal fractions of the lower half of the diencephalon from the midbrain. This leads to the conclusion that the expression of anger in the cat is dependent upon central mechanisms which are located in this part of the brain stem.

It is pointed out that the sham rage of the decorticate or diencephalic cat closely resembles the behavior of the infuriated normal animal and that it is far more readily elicited and is more expressive of an affective state than are the pseudaffective reflexes shown by decerebrate preparations.

The intense and widespread sympathetic discharge which is a prominent and invariable accompaniment of emotional excitement occurs during the sham rage. The relation of the diencephalon to the sympathetic system is discussed and the view is advanced that the diencephalic representation of the sympathetic consists of mechanisms which are responsible for the activation of that system under conditions of stress.

It is a pleasure to express my indebtedness to Dr. Walter B. Cannon who suggested this work and whose advice and encouragement carried it along.

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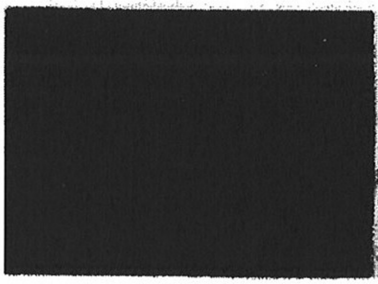

Fig. 1

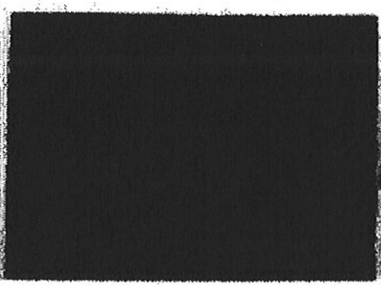

Fig. 2

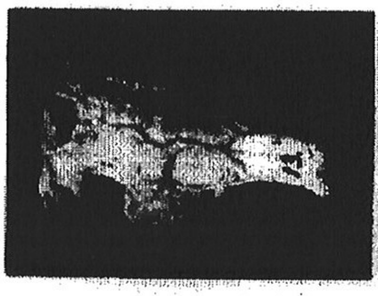

Fig. 3

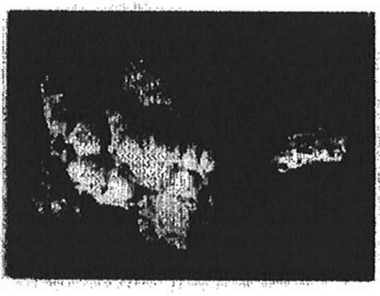

Fig. 4

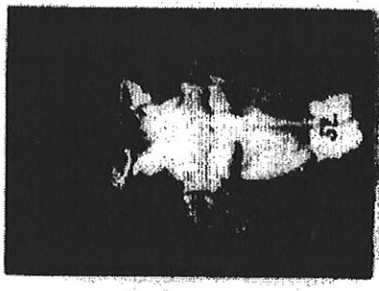

Fig. 5

Fig. 6

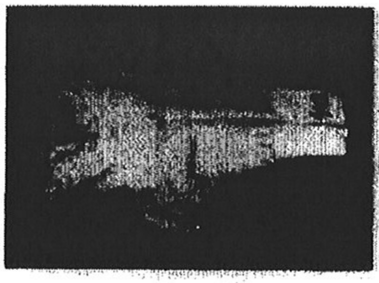

Fig. 7

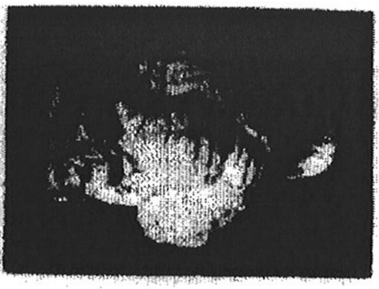

Fig. 8

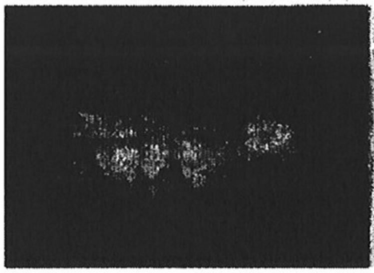

Fig. 9

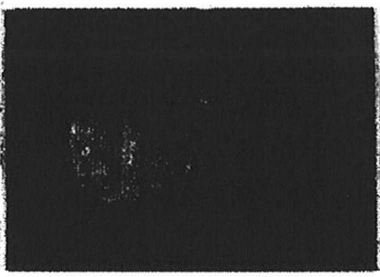

Fig. 10

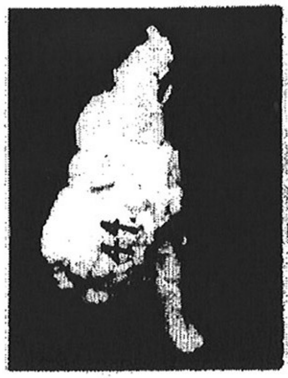

Fig. 11

Fig. 12

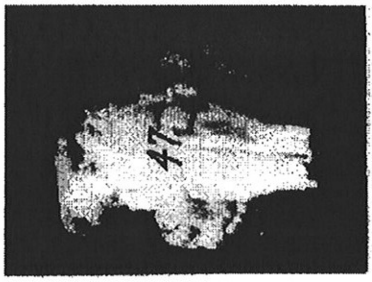

Fig. 13

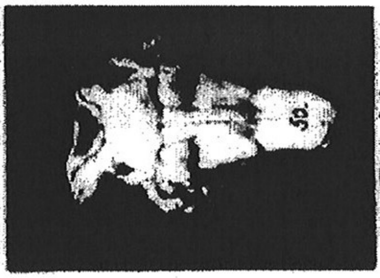

Fig. 14