BEHAVIOR DISTURBANCES RELATED TO DECOMPOSITION OF REFLEX ACTIVITY CAUSED BY CEREBRAL INJURY. AN EXPERIMENTAL STUDY OF THE CAT

A Review

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INTRODUCTION

Unusual changes in behavior have been noticed following removal of the frontal pole of both cerebral cortices of the cat. They result in apparent dementia. Habits of eating and lapping milk show marked deterioration. The cats no longer clean themselves and the fur becomes matted and dirty. Activity is greatly increased; the animals tend to follow moving objects and to be easily distracted. They display undue emotion in contact with other cats, and in relation to feeding. The experimental animals occasionally become frozen in an attitude of immobility, suggesting catalepsy. The sexual activity of the males is altered. There is a loss of the personality traits characteristic of cats as individuals.

This bizarre behavior of the animals lends itself to analysis on the basis of a breaking down of reflex activity. The present report attempts an explanation of the altered behavior of the animals related to a loss of normal control from the cerebral cortex, and the release of less complicated reflex behavior controlled by lower centers in the nervous system.

PLAN OF PRESENTATION

In the discussion of behavior disturbances related to decomposition of reflex activity the abnormalities will be broken down and considered under the following headings: difficulties in lapping and chewing, increased spontaneous activity, abnormalities of posture and walking, loss of the cleaning reflex and abnormalities in licking and biting, changes in sexual activity in the male, disturbances due to involvement of autonomous activity, abnormal emotional responses, and catalepsy. It is necessary at the same time to consider the manner in which reflexes are conditioned and elaborated in new-born and young kittens as the nervous system matures.

EXPERIMENTAL BASIS FOR THE OBSERVATIONS

The author’s studies bearing on the development and decomposition of the reflex activity in cats have extended over a number of years. In 1926 Weed and Langworthy reported the results of stimulating the electrically responsive motor cortex of the adult cat and the development of responses to electrical stimulation of this same area in new-born and young kittens. The motor responsive area in the cat lies near the anterior pole of the cerebral cortex surrounding the cruciate

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suleus. Stimulation near the midline and anterior to this sulex gave rise to phasic movements of the opposite foreleg whereas stimulation more laterally produced contractions of the facial and muscles of mastication. Electrical stimulation posterior to the sulex elicited responses in the opposite hindleg.

Electric stimulation of this same portion of the cortex in the new-born kitten produced movements of the foreleg alone. There were no contractions of the facial and masticatory muscles and no movements of the hindleg. When the kittens were two weeks old responses began to be obtained in the contralateral facial muscles and in the hindleg. It appears, therefore, that only the foreleg area in the cerebral cortex is responsive at birth, and later the areas for the face and hindleg mature and become responsive to electrical stimulation.

The development of a myelin sheath upon the axones gives some indication of the degree of maturity of nerve fibers in the brain. The process of myelinization in the central nervous system of the young kitten was studied (Langworthy, 1929). At the time of birth there are few myelinated fibers in the brain of the kitten above the level of the midbrain. There is some evidence to show that pathways become functional at the time when the axones acquire their myelin sheath.

The process of myelinization in the human fetus and baby was also studied in connection with the development of reflex behavior (Langworthy, 1933). Again, in the new-born baby the forebrain gives little evidence of myelinated fibers, although the pathways to the level of the midbrain show considerable myelinization. It is possible in a rough way to correlate the development of myelinization with the maturation of pathways and the development of new reflex activities.

The earlier experiments had to do with the stimulation and delimitation of the cerebral motor cortex. Later studies were concerned with the defects noted in adult cats after removal of the electrically responsive and other portions of the motor cortex. The motor cortex of the cat lies very close to the frontal pole of the cerebral hemisphere. Only a small area of rather undifferentiated cortex lies in front of the motor area. The large pyramidal cells characteristic of the motor cortex extend anterior to the area from which responses can be obtained upon electrical stimulation. This is true of all mammals including primates and man. We designated this anterior area as the area frontalis, and described the arrangement of nerve cells in this region and in the electrically responsive areas (Langworthy, 1928).

Removal of the cerebral motor cortex on one side produced some increased tone of the muscles in the contralateral extremities. This was noticed particularly when the cats were held in the air with the legs unsupported. The legs of these animals tended to assume odd postures in standing and locomotion was somewhat disturbed. The extremities sometimes turned under at the wrist and ankle, so that the animals stood upon the dorsal surfaces of the feet. The suggestion was made that removal of the anterior portion of the motor cortex which is not responsive to electrical stimulation was responsible for the change of tone in the extremities.

After removal of the cerebral motor cortices on both sides the cats showed a
great change in their behavior, and this formed the basis for further observations including those discussed in this paper (Langworthy and Kolb, 1935). It was customary to remove the cerebral motor cortex first upon one, and then upon the second side. In performing this operation the small portion of cortex anterior to the motor area was also cut away; in other words the frontal poles of the cerebral cortex were removed. The anterior portion of the cerebral cortex was exposed under aseptic precautions, and an area including the entire cerebral motor cortex was ablated either with a knife or a suction apparatus. In some cases there was a moderate injury of the olfactory bulb and the olfactory cortex, but usually the olfactory system was left intact. In most operations the cerebral ventricle was not opened, and there was no damage to the caudate nucleus. At a second operation the opposite cerebral motor cortex was removed in a similar way. Many of these animals lived for months and their unusual activity could be studied during this period.

One other finding in connection with stimulation of the cerebral motor cortex in the cat has a bearing upon the abnormalities in feeding observed after injury of this region (Langworthy and Kolb, 1935). Stimulation of the lateral portion of the anterior cruciate gyrus, lateral to the area from which responses in the facial and muscles of mastication could be obtained and close to the rhinal fissure gave rise to rhythmical lapping and chewing movements. These continued as long as the stimulus was applied, and their rhythmicity distinguished them from the movements of the muscles of mastication obtained from the more mesial area already described. This lateral area was removed in the operations.

Disorganization of lapping and chewing reflexes

Tilney and Riley in 1924 discussed the behavior of new-born kittens as related to the myelinization of tracts in the nervous system. In the kitten the sucking reflexes are operative immediately after birth. Stimulation of a large perioral area will cause the head to be turned in the direction of stimulation, and the sucking movements develop. The insertion of a small object into the mouth will likewise elicit sucking. This is true even though the object placed in the mouth has a bitter taste. They grouped the feeding activity of new-born kittens into the following components: 1. Movements in seeking the nipple. 2. Movements in grasping the nipple by closure of the mouth which results in sucking. 3. Movements in swallowing. 4. Movements of the hind and forelegs. During the periods of nursing flexor and extensor movements of the forelegs occur; they serve to keep the kitten in contact with the nipple.

During the first few days of life stimuli which will elicit the sucking reflex become much more circumscribed and show a marked conditioning. Stimulation of the face a distance from the mouth will not elicit a response, but only stimulation of the lips. Moreover, the kitten will reject a foreign body placed in the mouth.

As the kitten grows older it begins to lap milk, and eat solid food. It may be assumed that the earlier feeding reflexes are further differentiated for these purposes. The licking reflex by means of which the cat cleans its fur may be considered as closely correlated with and developing from the feeding reflex, inasmuch as it involves movements of the tongue and mouth. Finally in the male cat the biting reflex has a sexual function, inasmuch as the male cat bites the neck of the female cat during sexual activity.

The disorganization of the adult lapping and chewing reflexes was profound after removal of the frontal pole of the cerebral cortices bilaterally. There was a reappearance of certain behavior characteristic of the kitten sucking at the nipple. The cats not only
showed difficulties in the ordinary functions of eating, but new types of activity appeared in relation to the feeding reflex. In some ways these cats showed abnormalities similar to those found in patients with pseudobulbar palsy due to bilateral injury of the corticobulbar tracts in the brain. In making the preparation it is customary to remove the frontal pole of the cerebral cortex first on one side, and then on the other. After unilateral extirpation the cats showed no changes in the feeding reflexes; these appeared immediately after the second frontal pole was removed.

For the first few days after both frontal poles of the cerebral cortex had been excised the cat made no attempt to eat spontaneously, and had to be fed by stomach tube. If the mouth was opened passively and food placed far back at the base of the tongue, it was often swallowed, although more often it was extruded from the mouth. After a few days most of the cats ate spontaneously. Their appetite was greater than normal. They lost the delicate manner of eating characteristic of normal cats. They were never satisfied unless they placed their forepaws in the feeding dish. The forelegs showed alternate pawing movements during the period of feeding. The food was taken into the mouth in large mouthfuls and the cat never swallowed until the mouth was bulging with meat. In obtaining food the head was lowered and raised with quick darting movements. While eating meat the cat would often grasp the metal edge of the dish with the teeth, as if it was impossible to differentiate metal or glass from the food.

Loss of ability to lap milk was more severe than inability to eat solid food and persisted for a longer period. Lapping fluid is a very precise function requiring exact coordination of the tongue. The abnormal preparation lost this power of tongue movement for a considerable period. For a time the cats did not drink at all. They placed the whole mouth in the milk and tended to inhale and exhale into the dish. They were unable to take the milk into the mouth.

Later the power to lap milk gradually returned. The cats often interrupted the lapping to bite at the edge of the dish. Sometimes lapping continued outside of the dish, so that the cat lapped into the air. If the dish was moved a few inches forward and away from the cat, the animal often had difficulty in finding it again. There was a continuous effort to place the forepaws in the dish of milk.

Richter and Hawkes (1939) observed perseveration in rats after removal of the frontal poles of the cortex. This was especially noticeable when they ate or drank. Chewing movements continued for some time after they had swallowed their food. In the same way when drinking water from an inverted bowl, they continued to lap the lip of the bottle long after their tongues no longer came into contact with the water.

When the animals began to eat meat they would not only bite upon the food but also upon any object close by the food. Thus, they would seize the glass or metal dish with their teeth and attempt to bite it. They would continue this biting of unsuitable objects and ignore the food close at hand. When the cats were stimulated to eat they seemed unable to distinguish between edible and nonedible material.

In some cases it was difficult to induce the animals to eat. This was dependent partially on the fact that the cats were so distractible. It will be shown later that scratching of the skin anywhere over the body induced licking and biting movements which were poorly oriented in relation to the point stimulated. Scratching in the midline of the back at the root of the tail caused the cats to bite into the air directly in front of the body. If a dish of food was placed in front of the animal and this reflex elicited the cat would begin to eat.

Following removal of both frontal poles of the cerebral cortex, the cats became dirty and unkept. Cats normally clean the fur by licking. This activity was absent or poorly directed; consequently the animals gave no care to the fur. During sexual activity the male cat bites and grasps the skin of the female’s neck with his teeth. This ability was lost in the experimental male cat. The bite was poorly directed and poorly maintained.

Throughout the lifetime of these animals the cats showed alternate pawing movements of the forelegs on attempting to eat solid food, or to drink milk. They always endeavored to place their forelegs in the dish of food. These movements of the forelegs suggest the movements of the young kitten in nursing. This tendency is not found in the adult cat.
During the period of feeding, the cats showed undue emotional responses. Often they would growl and snap at the food. After they began to eat, purring or growling became marked and often interfered with the feeding reflex. It might be said that these animals were unduly emotional in regard to food.

Some years ago we described the abnormalities in feeding observed in these cats with bilateral removal of the frontal lobes of the brain as similar to the phenomenon of pseudobulbar palsy in man after injury of the corticobulbar pathways upon both sides (Langworthy and Kolb, 1935). Individuals with pseudobulbar palsy show difficulties in eating, speaking and emotional instability. They tend to laugh or cry on the slightest stimulus. The jaw jerk is overactive. In order to produce these changes in man the pathways from the cerebral motor cortex, controlling the bulbar nuclei, must be injured bilaterally. The analogy is quite clear in the cats which show difficulty in chewing and swallowing. Eating was interrupted by outbursts of growling and more often purring. Difficulty in drinking was even more profound due to the loss of the ability to lap, and there was incoordination of breathing with the drinking.

Increased spontaneous activity

After removal of both frontal poles of the cerebral cortex, the cats became overactive, continually walking around the cage. This overactivity sometimes developed immediately after the animals recovered from the anesthetic, but in other cases it did not appear for several days after the removal of the second cerebral motor cortex.

It was possible to measure quantitatively the change in activity after operation. The cat was placed in a cage where its movements were recorded by means of cyclometers. There was often some increase in activity after removal of the first frontal pole, but this became markedly accentuated after ablation of the second cortex. In general it may be said that after the frontal cortex was removed bilaterally the animals were twenty to eighty times as active as they were before the operation. Some of the animals actually died either directly or indirectly from over-exhaustion resulting from the constant activity (Langworthy and Richter, 1939).

Previously Richter and Hines (1938) found increased spontaneous activity in monkeys after removal bilaterally of portions of the frontal cortex. In these cases there were some injuries of the caudate nuclei, and it was thought that over-activity was not present unless the caudate nucleus was injured. Kennard, Spencer and Fountain (1941) produced similar hyperactivity in monkeys after lesions in the frontal lobes of the brain alone without damage to the caudate nuclei. They believed injury to the caudate nuclei was not essential for the production of this activity. Richter and Hawkes (1939) produced overactivity in rats after similar cortical injuries.

There has been considerable speculation concerning the cause of increased activity. The cats become abnormally excitable and distractible. Many of them were ravenously hungry. It has been suggested that the increased activity is related to increased peristalsis of the gastrointestinal tract. Kennard, Spencer and Fountain (1941) found that their monkeys were very distractible, and suggested that the activity was related to visual stimuli. Schaltenbrand and Cobb (1939) noticed that their decorticate cats were more active during the day and tended to be quiet at night. They attributed the activity to auditory stimuli.

Abnormalities of posture and walking

After injury of the cerebral cortex of the cat upon one side there is an increased tone in the muscles of the opposite extremities (Langworthy, 1928). Removal of both cortices increases the tone in all the extremities of the body. This extensor rigidity is of mild degree and only can be observed when the animals are held in the air or placed upon their backs. Although the increased tone is not as readily demonstrable when the animals are upon their feet, it leads to abnormal positions of the extremities and the gait is bizarre.

The abnormal postures of the legs were described in a somewhat different way by Bard
in 1933. He stated that following removal of the cerebral motor cortex upon one side there was a loss of hopping and placing responses in the legs of the opposite side. When the normal cat is blindfolded and the dorsal side of the feet brought in contact with the table they will be flexed and placed in a standing position upon the table. After removal of the cerebral motor cortex, placing will not occur in the contralateral extremities. The loss of placing and hopping reflexes may be demonstrated in several other ways.

Similar motor abnormalities could be demonstrated in the animals described here. The fore and hindlegs were extended rigidly on suspending the cat by the head and tail and the animal was forced by the increased tone to remain immobile. At most there were alternate rhythmic movements producing flexion and extension of the wrist and claws of the forelegs.

There was some dulling of sensibility in the affected extremities. A stronger pinch had to be applied to the paw to induce flexion of the extremity on the abnormal side of the body. These extremities were not as reflexly responsive to noxious stimuli.

Due to changes in tone and diminution in sensory perception the extremities were held in strange positions. They often were hyperextended in front, behind, or at the side of the body. This was particularly true of the hindlegs, which would shoot forward between the forelegs or be extended posteriorly. The paws were often flexed at the wrist and ankle so that the cat stood on the dorsal surfaces of the feet. If the cat was held by the back of the neck, with only the hindlegs in contact with the ground, the forelegs were abducted against the side of the body and flexed at the elbow. The hindlegs were hyperextended and somewhat abducted in walking. If the head was suddenly flexed or flexed as in eating, the hindlegs would fly up into the air. On attempting to overcome this difficulty, the hyperextended hindlegs would fly forward past the forelegs and the cat fell backwards. When the animal was placed upon its back it lay quietly. The hindlegs were maximally extended, the forelegs abducted and flexed at the elbow.

On the day following removal of the second motor cortex the cats were able to stand, and walked continually. During the first few days the cats did not turn from a straight line to avoid objects. Within two weeks after the operation they avoided obstacles fairly well. The remarkable persistence in following a straight line without regard to obstacles was a real threat to the life of the cat in the first few days after operation. The cats would continue to push their heads against solid objects until they were likely to tear open the wound. Every precaution had to be taken to put the cats in a place where they could not injure themselves. Since removal of both cortices at the same time made the cats so active, one cortex and then the other were removed. Using ether as an anesthetic allowed the animals to awaken soon after the operation and they were extremely overactive. Substitution of nembutal for ether prolonged the anesthesia so that the cats regained consciousness more gradually. They remained relatively inactive for several hours, and were less likely to injure themselves.

Laboratory stools seemed to have some fascination for these active cats and they would push ahead until their extremities were entangled in the rungs. They were unable to extricate themselves from this position. When they reached a corner of the room they continued to push their heads into the corner and seemed unable to turn either to the right or the left.

A certain number of animals either after unilateral or bilateral operations tended to move in circles. After operation upon one cortex the animal circled toward the paralyzed side. The normal extremities on the same side were used more efficiently and caused the cat to circle in the direction away from the sound legs. Those that circled after the second operation walked away from the side of the most recent lesion. This is understood if it is realized that the legs first paralyzed showed considerable recovery while those involved by the second operation were the weaker. One animal which had walked in circles away from the side of the second operation was induced on the fifth day to walk toward the side of the lesion in pursuit of food. The legs on this side were so ataxic that the cat lost its balance and fell. The tendency to circle interfered with eating in that the cat had to circle correctly in order to reach the plate of food.
Another unusual response was obtained from many animals. If they were free to wander in the laboratory, they followed close at the feet of anyone walking around, duplicating every turn of the person whom they were following. This following reaction continued for weeks after the removal of both motor cortices. Bard in 1934 described similar behavior in cats with removal of all the cerebral cortex on both sides. He thought the cats responded to noises in this following response since his cats were blind. The animals described here were very restless and distractible, and probably were stimulated by any visual or auditory stimulus. They perhaps reacted more to vision than to sounds.

Richter and Hawkes (1939) found that many rats after removal of the frontal pole of the cerebral cortex showed changes in behavior in that they bit at everything within reach and made violent efforts to escape. Following bilateral cortical ablation they showed a high degree of distraction, reacting to the slightest noise, sometimes with a leap of several feet.

Loss of the cleaning reflex and abnormalities in licking and biting

After the frontal pole of the cerebral cortex was removed bilaterally, the animals no longer took care of their fur which became matted and dirty. In addition there were unusual responses of licking and biting on stimulation of the surface of the body. When an area upon the skin was stimulated a scratch reflex might develop, and then movements of licking and biting. The licking and biting were often the only responses to skin stimulation. These movements were poorly directed, and did not reach the area of stimulation with any precision. Scratching of the back in the midline near the tail would often cause the animal to lick the air in front of the body or the ground between the forelegs. If the animals did not eat spontaneously, stimulation in the region of the tail would produce licking movements, so that they would eat food placed in front of them. Often the stimulation first produced biting of the skin which would change into licking.

Bard (1934) observed these same abnormal biting reflexes after removal of the entire cerebral cortices and part of the diencephalon bilaterally. One cat developed an ever increasing tendency to bite herself in response to the slightest irritation.

The abnormal responses may be described as seen in one of our animals. "The biting and licking movements were first obtained on scratching at the root of the tail, and the animal tended to direct the biting toward the left side of the body. If stimulation was strong, the cat would bite, but if it was weak licking movements would occur. The reflex could also be obtained by rubbing or stroking over the back, flanks, or even the hindlegs. The cat often licked the neck or forelegs. Occasionally he could be made to direct the movements farther back toward the area stimulated. Sometimes the neck was so strongly flexed in an endeavor to lick over the chest that the animal lost its balance and fell forward. Even on licking to the side, the force of the movement made the cat lose its balance. The response continued as long as the stimulant was active. After this stimulus had been applied several times the cat seemed emotionally upset and often growled. At times the cat would lick into the air. For a period of ten days at one time, licking movements appeared whenever the animal scratched himself with a hindleg. The movements were purposeless as the cat barely applied the tongue to the body, but licked into the air. With the cessation of scratching, the licking stopped."

Abnormalities of sexual function in the male cat

It is clear that certain diseases producing destruction of the central nervous system lead to a loss of sexual potency. In males coordination of sexual activity is represented at all levels of integration in the brain, including the cerebral cortex. Recent studies have tended to stress the amount of destruction which may occur in the nervous system with possibility of traces of sexual functions, rather than with the abnormalities produced by destruction of different reflex pathways.

The sexual activity of the male cat may be divided for discussion into: a deep characteristic cry, biting at the neck of the female, mounting and treading, intromission and
almost immediate ejaculation. This is recognized by another throaty cry on the part of the female.

All but one of the seven experimental animals performed sexually after removal of the frontal pole of the cerebral cortex, first upon one and then upon the second side. There seemed to be an increase of libido following the operations and erection and ejaculation were normal. Abnormalities appeared in the actual performance. The initial cry was quite normal. The biting reflex was greatly impaired after bilateral operation. The biting was poorly oriented, so that the male cat would bite at the side of the female's neck. Often the biting response was broken down into a rhythmical biting or licking response. Mounting and orientation of the body was defective after injury of the cortex upon the one side, and even more abnormal following the second operation. Several of the animals showed a cataleptic-like state on sexual excitement which will be described in a later section. In one case these cataleptic manifestations prevented the animal from copulation after removal of the second frontal area. Whenever this cat was aroused sexually he became fixed in one position and seemed unable to move.

Disturbances of autonomic activity

There are indications that certain autonomic activities are controlled in the frontal poles of the cerebral cortex close to the electrically responsive motor area so that bilateral removal of the frontal poles of the brain will produce disturbances of autonomic function. Fulton suggested that the overactivity described is dependent on increased gastric peristalsis.

Many of the cats appeared to have an increased appetite and ate greedily, large quantities of food. One gained markedly in weight but most of them showed no weight increase. No attempt was made to measure the changes in food intake quantitatively. However, Richter and Hawkes (1939) using quantitative methods found that removal bilaterally of the frontal poles of the cerebral cortex in rats not only produced overactivity but there was also an increase in food intake; there was no change in water intake and a decrease in body weight.

Using a balloon-tambour, air-water system, Hesser, Langworthy and Kolb (1941) made graphic studies of gastric activity in normal cats and after removal of the frontal pole of the cortex upon one and both sides. Definite alterations in gastric activity followed removal of the motor cortices. They were demonstrable as greater consistency and strength of stomach contractions, along with increased tone throughout distention. This was interpreted as evidence of release from a regulating influence in the motor cortex. A marked stretch reflex with delayed relaxation of the stomach wall after sudden distention was also apparent.

Similarly studies were made of the behavior of the vesical muscle (Langworthy and Hesser, 1938). It was found that micturition was induced by filling the bladder with smaller quantities of fluid after extirpation of one cerebral cortex. Following removal of the second cortex even less distention was required to bring on micturition. The muscles of the bladder showed an increase of the stretch reflex.

These results suggest that the smooth muscle of the body is controlled by reflex arcs involving the cerebral cortices and its function becomes abnormal after removal of the cerebral motor cortex bilaterally.

Emotional responses in these animals

Patients with bilateral involvement of the fibers from the cerebral motor cortex show difficulty in speaking and swallowing, and emotional instability. The cats undoubtedly have difficulty in eating and displayed some emotional instability. There is greater emotional response connected with feeding than is observed in the normal animal. Often when food was offered to the abnormal cats they would begin to growl and purr, and these expressions of feeling interfered with and interrupted their eating. In general it was thought
that the cats were more friendly with the investigator and more antagonistic to other cats than before removal of the frontal poles of the brain. When placed with other cats they became angry easily, and prepared for battle. Occasionally they endeavored to fight, but their movements were so poorly coordinated that they were ineffective.

This emotional instability seen after removal of the frontal poles of the cerebral cortex bilaterally is not similar to the sham rage described in cats by Bard (1928). Bard removed both cerebral cortices completely and also portions of the diencephalon to release the manifestations of sham rage.

Catalepsy

In 1937 Barris observed that bilateral, one-stage removal of the rostral portions of both cerebral cortices of cats resulted in a group of symptoms closely resembling catalepsy. The cats could be made to assume unusual postures and hold them for a considerable period of time. Barris stated that a high degree of plasticity of the muscles characterized this condition.

Magoun and Ranson (1938) repeated these experiments and did not notice the catalepsy described by Barris. They observed that the animal was likely to hold the legs in unusual positions when quiet, due to the loss of the sensorimotor responses described by Bard. However, they found it impossible to pose the animal in any unusual position.

The present series of cats has been observed to stand for periods of time in unusual positions with the hind-legs thrust anteriorly between the forelegs or with the forelegs strongly abducted or even crossed. This is undoubtedly due to the loss of sensorimotor control from the cortex. In addition periods of suspended activity have been observed, which may be described as catalepsy. When the cats were aroused or frightened, they tended to freeze into one position, which they held for seconds or minutes. The eyes stared straight ahead. The legs which no longer demonstrated the normal placing responses were held in an abnormal attitude. While the findings have not demonstrated it in the same way, this abnormality may be related to catalepsy as described by Barris.

The one male which did not show normal sexual activity after removal of both cerebral motor cortices appeared to be prevented by the onset of catalepsy. When the animal was placed with the female in heat he appeared to be aroused and gave the characteristic cry. However, when excited he stopped short in a fixed cataleptic attitude, which he held for a considerable period. Anger at other cats or sexual interest would bring on these periods of catalepsy.

Indeed the animals seldom were able to mobilize themselves for aggressive activity against other cats even though they showed distinct signs of rage. They would growl and show erection of the hair over the body but at the same time they became set in one posture with the eyes staring straight ahead.

DISCUSSION

The most important change noticed in the animals after removal of the frontal poles of the brain has not been considered. Normal cats have very definite traits in reacting to humans. Thus, many of them are tame, enjoy being petted, and rub against the body, while others are wild and unruly. Bard in 1937 pointed out that after removal of the cerebral cortices and portions of the diencephalon, there was a complete loss of preoperative personality. This was also true of the animals with the frontal poles of the cortex removed. They never showed any traces of affection for persons thereafter and reacted as automata. After the motor pathways from the cerebral cortex were lost the animals were apparently unable to express themselves. They seemed dazed and their behavior was mechanical and free from all spontaneity.
Those characteristics of the individual known as personality are dependent primarily upon integrations elaborated in the cerebral cortex. Personality is highly developed in man but is also noticeable in animals. Individual cats and dogs develop definite traits of character which are readily appreciated by their owners. These personality traits must be expressed through motor channels. The cerebral motor areas give rise to the cortico-fferent pathways which permit the cerebral cortex to control the body musculature. After the entire cerebral motor cortex has been removed bilaterally there can be no motor expression of cortical activity. The cats appeared stunned, showing only stereotyped behavior. Feeding became a reflex mechanism lacking the dainty and precise characteristics of eating in the normal cat. The animals no longer reacted as personalities but rather as automata. Catalepsy was an expression of the loss of the ability to respond, due to removal of the motor pathway.

The preparations described here presented a marked deterioration in behavior after removal of the frontal poles of the cortex, including the entire motor area. These changes centered around abnormalities in chewing, lapping, licking and biting. Many of the strange types of behavior shown by these animals can be directly related to the difficulties in using the mouth properly. Cats drink liquids by means of complicated movements of the mouth and tongue, known as lapping. Licking movements are used to keep the fur clean. Biting is utilized in altercations with other animals and by the male cat to preserve his position during sexual activity. It seems logical to believe that the nursing reflex of the kitten at birth is modified by developing centers in the cerebral cortex to control the more complicated activities of the adult. The abnormalities seen in the animals after bilateral removal of the motor cortices may be considered partially as release phenomena due to the loss of control from the region of the cerebral cortex.

Bard has given exact and careful descriptions of the behavior of his cats after removal of the cerebral motor cortices and portions of the diencephalon. It is interesting that his animals differ from the ones described here in only a few ways. The sham rage described in Bard’s experiment, but not in the present one, is an important difference. His cats were blind due to the removal of the occipital cortex. They responded reflexly to sounds, even though the auditory cortex was removed. He thought that animals with injury of the olfactory pathways had less inclination to eat than animals with these structures intact.

The findings may be considered as they apply to man and to medical problems. Senile patients and other individuals with organic disease of the nervous system may show psychotic disturbances having an organic basis. In these individuals there has been some attempt to explain the findings on the basis of injury of specific reflex pathways. The great loss of voluntary movement and the increased tone in the muscles following injury of the cerebral motor cortex on one or both sides in man tends to mask these reflex abnormalities and to render them difficult of analysis. This is not true of the cat where the cerebral cortex does not have as dominant a control over motor activity. Removal of the cerebral motor cortex in the cat produces only a moderate increase of tone in the peri-
pheral muscles and only a partial loss of motor activity in the extremities. Thus, other changes in behavior become more obvious.

Patients with diffuse degenerative changes in the central nervous system may show behavior disturbances which are an accentuation of normal personality trends. Other symptoms can be related specifically to damage of definite areas in the central nervous system. This may be illustrated in the case of patients with disseminated sclerosis (Langworthy, Kolb and Androp, 1941). These individuals often manifest a marked euphoria and late in the disease attacks of forced and irresistible laughing and crying occur. This emotional instability can be related partially at least to a release of lower centers from the cerebral cortex. On the other hand a number of patients with disseminated sclerosis have to be confined to a mental hospital because of obsessions, delusions or sexual indiscretions. These symptoms cannot be correlated directly with organic changes in the nervous system, but pertain more to personality defects characteristic of the individual. The patients were able to handle these traits while they were well, but they became accentuated when the individual was incapacitated.

Possibly more of the unusual traits of patients with organic disease of the nervous system will be attributed to damage of specific areas in the central nervous system as our knowledge and understanding increases. Symptoms which appear incomprehensible may have a logical explanation in terms of reflex disturbances. The following example illustrates this point. A woman was confined to a local chronic hospital because of diffuse cerebral arteriosclerosis. Each day she was lifted and placed in an arm chair near her bed. When the attendants in the evening attempted to place her in bed, she grasped the arms of the chair tightly, so that she pulled the chair into bed with her. It was assumed by the orderlies that this patient was contrary because she did not wish to go to bed; on the other hand a well developed grasp reflex could be demonstrated in both hands. Once the patient grasped an object with her hand she was unable voluntarily to let go. This grasp reflex is due to the release of lower centers by cortical injuries.

Many children with mental deficiency show restlessness, and in some cases morbid hunger. Levin (1936) suggested that these children suffered from a congenital failure of development of the frontal lobes of the cerebral cortex. This conclusion was based upon the evidence that removal of the frontal lobe in animals gives rise to the same symptoms. The cats which are described here showed restlessness, distractibility and appeared to have abnormally large appetites.

To understand the manner in which reflex activity may break down after injury of the cerebral motor cortex in the adult, it is helpful to keep in mind the evolution of this activity after birth. There are certain types of reflex activity manifest in the new-born infant which begin to be conditioned during the first few days of life. Later they are further modified and are taken over for the accomplishment of more complex patterns of movement. They then disappear in their original form. However, localized injury of the cerebral cortex may interfere with more complex function, and cause the primitive reflex to reappear in
somewhat its original form. It may be assumed that the original reflex activity in the new-born is controlled through lower levels of integration in the central nervous system, possibly in the brain stem. With the assumption of cerebral control the activity of the lower centers is placed in subordination. Loss of cerebral function may later permit the lower level response to reappear. This reappearance may be thought of as a release phenomenon of the type discussed by Hughlings Jackson.

The grasp reflex may serve as an illustration. The new-born baby shows a grasp reflex of the hands. If the finger is placed in the palm of the baby, the hand closes upon it with sufficient force, so that the infant can be lifted, and will hang for a period of several seconds, supporting its own weight. This grasp reflex is retained for weeks and months, usually disappearing toward the end of the first year of life.

However, it will be realized that the reflex is not lost, but becomes controlled through higher reflex levels in the nervous system to form a more complex pattern of movement of the hand. In the new-born baby the forebrain and particularly the cerebral cortex are immature and probably nonfunctional. Activity at birth is dominated by centers in the brainstem and the grasp reflex as seen in the baby is dependent upon reflex pathways below the level of the forebrain. As the forebrain and cerebral cortex become mature they take over and change the pattern of activity of the hand, modifying the grasp reflex. Thus, the extremity is used in reaching out and holding objects and finally for all the complex activities observed in the adult. Injury of the premotor area (area 6) in the adult will cause the grasp reflex to reappear. The patient tends to close the fingers over any object stimulating the palmer surface of the fingers or the palm, and finds it difficult to let go.

Another example of the development and differentiation of reflex activity may be seen in the feeding reflex. A new-born baby has available a mechanism for nursing and swallowing food which is controlled by lower levels in the nervous system. During the first few days of life, this reflex can be set into operation by stimuli that are non-specific. Stimulation of any area over the face will cause the baby to turn its mouth to that place and begin sucking movements. Soon however, the operation of the reflex becomes conditioned.

This reflex also becomes modified rather than lost. Gradually the reflex activity becomes further differentiated to permit chewing, and finally the eating of solid food. Adult eating habits gradually become established. In certain senile patients with extensive injuries of the cerebral cortex the primitive reflex of the new-born baby reappears. Any perioral stimulation will give rise to sucking movements of the lips. The primitive sucking reflex of the infant has been elaborated and controlled from higher reflex centers into the more elaborate feeding reflexes of the adult.

**SUMMARY**

Cats with both frontal poles of the cerebral cortex, including the motor areas, removed show marked deterioration in behavior. They no longer manifest the
personality traits of individuals but react as automata. Overactivity and distractability are marked. The animals lose the dainty methods of eating characteristic of normal cats and show abnormal responses to food. Movements of the mouth used for eating, lapping, biting and licking are poorly coordinated and the different responses are performed inappropriately, with one substituted for another. Due to disturbance of licking, the cats no longer keep themselves clean. There is evidence of increased emotional response in relation to food and to contact with other cats. Emotion sometimes gives rise to cataleptic-like responses. Tone is increased in the muscles, there is a heightened threshold to nocuous stimuli and the extremities tend to assume abnormal positions. The animals may be considered to show a dementia dependent on the loss of the motor pathways from the cerebral cortex. The means of expression through cortico-efferent pathways is removed. Reflex patterns coordinated at lower levels in the nervous system are released. These preparations show most of the abnormalities which Bard described after removal of all the neocortex and portions of the diencephalon. They do not exhibit sham rage.

BIBLIOGRAPHY


