This early outward current might occur predominantly in the soma and have a persistent component which could augment the late outward current. (iv) There may be differences in these membranes which are not interpretable on the basis of currently known mechanisms. Although the late current ratios are disturbed by the addition of TTX, their order of distribution remains practically the same. Individual variations may be attributed to variations in the measurements, but the possibility that TTX is affecting some current component during the late phase is not excluded.

The results appear to support the view that the axon spike is due largely to sodium ions and the soma spike largely to calcium ions. Additionally, it appears that the soma of the giant cell cannot be considered to be a homogeneous membrane throughout.

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Predatory Attack, Grooming, and Consummatory Behaviors Evoked by Electrical Stimulation of Cat Cerebellar Nuclei

Abstract. *Electrical stimulation at single sites in the rostral fastigial nucleus elicits hypertension, grooming, feeding, and attack behaviors in the cat. The stimulus intensity and availability of suitable goal objects determines the behavior. Bilateral lesions of the area fail to produce motor deficits. The rostral fastigial nucleus may be a cerebellar area for behavioral and autonomic regulation.*

Traditionally, the fastigial nucleus has been viewed as sharing in the general function of the whole cerebellum in the regulation of movement and posture (*1*). However, there have been reports that electrical stimulation in or near the fastigial nuclei may produce cardiovascular (*2*) and even behavioral (*3*) responses. Several questions have been raised by these observations. Does the fastigial nucleus participate in the regulation of visceral and behavioral activities? If so, are such activities independent of the motor function of the nucleus? And, finally, are there anatomically distinct areas of the nucleus that mediate these activities?

Electrical stimulation of the ventromedial portion of the rostral pole of the fastigial nucleus in several species elicits a highly reproducible, stereotyped, and differentiated activation of the sympathetic nervous system (*4–6*). The response, termed the fastigial pressor response (*5*), is characterized by a marked elevation of blood pressure, heart rate acceleration, and vasoconstriction, an autonomic pattern simulating the reflex cardiovascular responses to assumption of an upright posture (*6*). The fact that such stimulation fails to produce evident changes in motor activity (*4, 5*) raises the possibility that this region of the fastigial nucleus may influence visceral activity apart from its participation in somatomotor regulation.

To further evaluate the function of this area of the fastigial nucleus, we examined the effect of electrical stimulation and small lesions in unanesthetized cats on behavioral and motor performance and the relation of these responses to evoked activity. Our results suggest that a restricted portion of the fastigial nucleus may be primarily involved in visceral and behavioral control.

Nine adult mongrel cats of both sexes were studied; it had been shown before surgery that these animals did not spontaneously kill rats. The animals were anesthetized with α-chloralose (50 to 60 mg per kilogram of body weight, intravenously). Under sterile conditions, a Silastic rubber cannula was inserted into the common carotid artery, brought out through a stab wound in the back of the neck, and connected to a strain gauge transducer for blood pressure and heart rate recording by standard methods. Stainless steel electrodes, insulated to within 0.5 mm of the tip, were then inserted stereotaxically into regions of the fastigial nucleus from which blood pressure responses could be elicited (*5, 6*). After the electrodes were implanted, the incision was closed and the cannula was plugged.

Several days later, when fully recovered from anesthesia and surgery, the animals were placed in an observation cage. The arterial cannula and wires from the stimulation electrodes were attached to one end of a swivel device located on top of the cage. The strain gauge transducer and wires from a constant current stimulator were connected to the other end of the swivel. In each session, we examined the effects of graded electrical stimuli on behavioral and cardiovascular responses. Various combinations of animal chow, water, and live or dead rats were used for goal objects in the behavioral tests. Animals were observed for several weeks. After a suitable number of testing sessions, a lesion was made at each electrode site by passage of an anodal constant current (150 μa for 40 seconds). Over the ensuing days, the animals were tested for changes in the evoked autonomic and behavioral responses. In addition, each animal was carefully examined for abnormalities of posture and gait, disturbances of visual and tactile placing, hopping and deep tendon reflexes, and changes in the defensive responses to tail pinch or attack by another cat. After 1 to 2 weeks of testing, the animals were anesthetized with pentobarbital (60 mg/kg, intravenously) and perfused through the aorta with 10 percent formalin for subsequent histological identification of lesion sites.

Electrical stimulation of the rostral fastigial nucleus in these unanesthetized cats produced a prompt elevation of the systolic and diastolic arterial blood

pressure and an elevation of the heart rate (Fig. 1). Electrical stimulation (*7*), at the threshold for cardiovascular responses did not produce any overt changes in behavior (Fig. 1A). Stimuli strengths of 1.2 to 1.5 times the threshold for the cardiovascular responses elicited marked behavioral changes (Figs. 1 and 2). At the threshold for behavioral activation, the animal would alert and, if reclining, sometimes rise to a sitting or standing position (Fig. 2A). Slightly higher stimulus intensities produced increased cardiovascular responses (Fig. 1B) and stimulus-bound grooming in all animals which was indistinguishable from the spontaneous behavior.

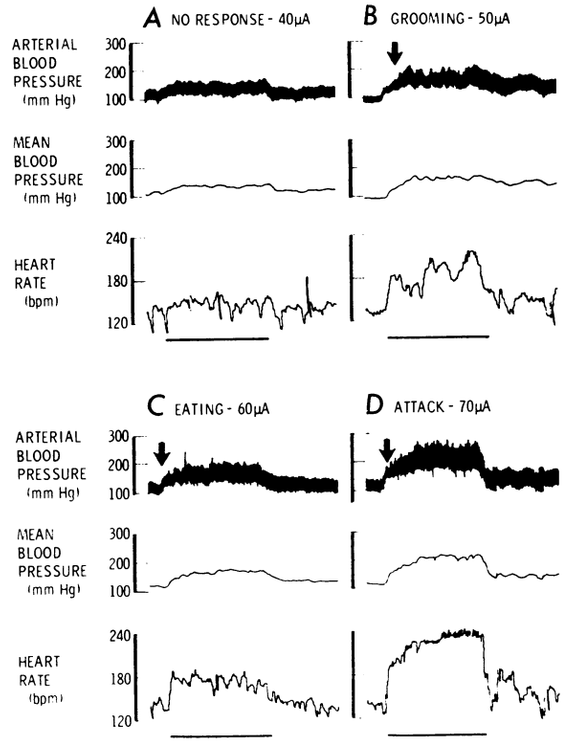

Fig. 1. Relation between stimulus intensity, cardiovascular response, and behavior elicited by electrical stimulation at the same site in the rostral fastigial nucleus of an individual cat. In each frame the upper trace is blood pressure recorded from the carotid artery, the middle tracing is mean blood pressure, and the lower tracing is instantaneous heart rate. The black bar represents the stimulus train (50 hertz for 40 seconds). The arrow represents onset of designated behavior. Increasing the stimulus intensity elicits different behaviors and augments the cardiovascular responses; *bpm*, beats per minute.

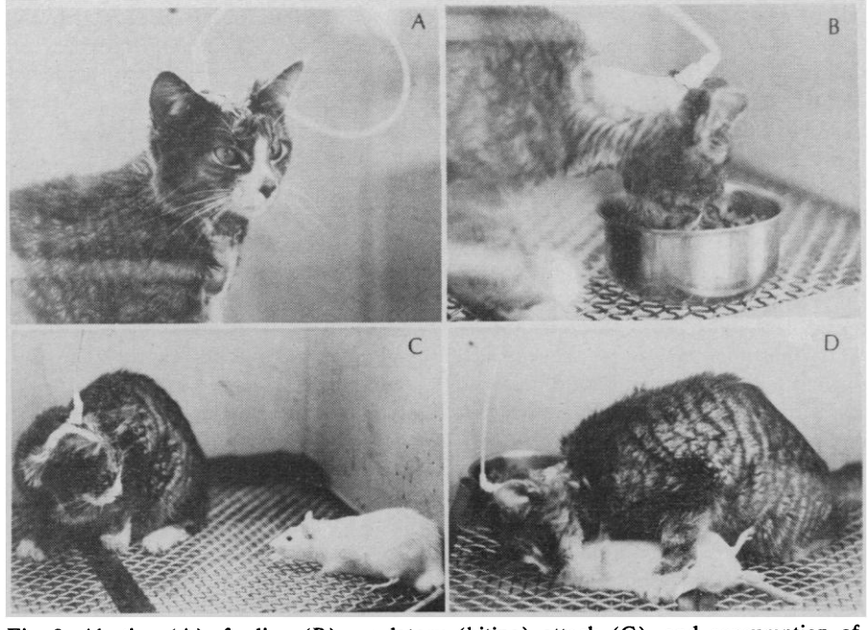

Fig. 2. Alerting (A), feeding (B), predatory (biting) attack (C), and consumption of prey after attack (D) evoked by electrical stimulation of the rostral fastigial nucleus in an individual cat. This behavioral sequence was produced by increasing stimulus intensity at a single electrode site.

At still higher stimulus intensities, feeding and even larger cardiovascular responses were evoked in five of the nine cats (Figs. 1C and 2B). The animal approached, energetically chewed, and swallowed food placed nearby, and occasionally lapped water.

The behavior with the highest threshold was predatory attack and was elicited in seven of nine animals (Figs. 1D and 2D). Attack on a live or dead rat had a latency of several seconds. The animal would visually fix on the prey, growl or intensely meow, crouch (Fig. 2C), and suddenly bite the head and neck of the rat (Fig. 2D). The cat did not assume any of the postures or autonomic stigmata (such as pupillary dilatation or piloerection) characteristic of the defense reaction (*8*). The biting attack was savage and would persist during stimulation. If stimulation was repeated, the animal would, after killing the prey, devour its head, tail, and paws. In five of the nine animals, all three of these behavioral patterns (grooming, feeding, and attack) were evoked from a single electrode site.

The determinants of which behavior was elicited were related to stimulus intensity and, in part, to the availability of the goal object. Thus, if a rat and food were both available, stimulation at intensities eliciting killing would produce only that behavior. The animal would eat after removal of the rat and would groom after removal of food. In two cats, however, the thresholds for attack and eating overlapped. The animals would preferentially attack if both food and prey were available. In the absence of prey, the animals would eat. All cats showed an increased propensity for biting or chewing any object placed near or touching the mouth.

Stimulation at sites from which behavior was evoked always elicited cardiovascular changes. Conversely, stimulation at any site from which a cardiovascular effect was elicited always evoked a behavior. However, cardiovascular changes were not essential for the appearance of evoked behaviors. Blockade of the pressor response by phentolamine (1 mg/kg, intravenously) did not affect the threshold or form of the behavioral responses.

Stimulation of the ventromedial pole of the fastigial nucleus evoked changes in posture or movement that were al-

ways associated with behavioral and cardiovascular responses. Electrodes placed at adjacent sites in the dentate nuclei elicited motor, but not behavioral or visceral changes.

Bilateral lesions at the effective sites in the fastigial nucleus abolished the behavioral and cardiovascular responses to stimulation. Thus, the evoked responses were not the result of current spread. A mild truncal tremor and hindlimb ataxia that disappeared 2 days after placement of the lesions was seen in only two cats. The defense response of all animals elicited by tail pinch or threat by another cat were unaffected by the lesions.

The present study demonstrates that electrical stimulation restricted to the rostral and ventromedial pole of the fastigial nucleus can elicit grooming, feeding, and predatory attack in cats, all behaviors heretofore considered to be primarily represented in the hypothalamus and limbic systems. The evoked behaviors are integrated, appropriately goal-directed, and not associated with alterations in movement or posture inappropriate for the behavior. The behaviors are specifically related to stimulation of a restricted area in the fastigial nucleus, since they cannot be elicited after coagulation around the electrode tip or by stimulation of adjacent cerebellar nuclei. While others have noted that electrical stimulation of deep cerebellar nuclei may produce emotional "behaviors" (*3*), the earlier studies failed to show whether such behaviors were differentiated, were independent of motor activation, or had a discrete localization. This study would, therefore, appear to be the first in which clearly defined behaviors could be evoked independently of any motor activity from a highly localized site within the cerebellum.

The range of behaviors evoked from a restricted locus in the fastigial nucleus is notable. While it is not possible by the use of fixed electrodes to ascertain whether there is anatomically discrete representation of grooming, feeding, or attack within this limited zone of the fastigial nucleus, there are several reasons to conclude that the behavior is not organized topographically. First, the fact that all three behaviors were elicited in five animals and two were elicited in seven animals with an identical gradation of stimulus thresholds suggests a considerable overlap for the representation of each behavior at a single fastigial site. Thus, it is the intensity of the stimulus and not the location of the electrode which is one of the determinants of the identity of the behavior. Second, the observation that the nature of the behavior evoked from a single electrode at a fixed stimulus intensity could be changed by altering the availability of goal objects (such as food or prey) is another demonstration that the locus of the electrode is not critical. Thus, our findings suggest that the behavioral responses from fastigial stimulation are probably not due to excitation of discretely organized neural pathways. Rather, they appear to result from a general activation of neurons subserving discrete fixed-action patterns, the resultant behavior being determined, in part, by the intensity of the activation and the presence of suitable goal objects.

This interpretation of the organization of behavior within the rostral fastigial nucleus parallels and supports the view of Valenstein regarding the organization of behavior within the hypothalamus of the rat (*9*). It would strongly support his view that the central neural organization of some behaviors is not fixed, but is plastic and subject to environmental control.

This study has demonstrated an inextricable relation between behavioral and cardiovascular responses from electrical stimulation of the rostral fastigial nucleus. The various evoked behaviors were all associated with increased blood pressure and heart rate. The pattern of the autonomic responses elicited from this site in the rostral fastigial nucleus is stereotyped (*6*). Only the magnitude of the response varies as a function of stimulus strength. However, the nature of the behavioral responses depends on stimulus strength, and frequently all of the behaviors are elicited from the same stimulation site. These findings contrast with the relation between cardiovascular responses and behavior evoked from the hypothalamus in the cat, for which different evoked behaviors (such as feeding or defense) are associated with particular cardiovascular responses characteristic of the behavior (*10*) and depend upon the stimulation site. The stereotyped set of autonomic adjustments common to each of the different evoked behaviors from the fastigial nucleus might represent activation of the cardiovascular responses associated with assumption of an upright posture (*6*) possibly in anticipation of movement, a common factor shared by all of the behaviors reported here.

It is not possible to define the pathways that mediate the behavioral responses to stimulation of the rostral fastigial nucleus. We have shown that the cardiovascular responses are relayed via the fastigiobulbar tract (*5*) to the paramedian reticular nucleus in the medulla and thence through as yet undefined pathways to the spinal cord. It is possible, however, that the behavioral components may be due to orthodromic excitation of other pathways projecting centrifugally from the fastigial nucleus to other brainstem nuclei or to antidromic excitation of axon collaterals projecting onto the fastigial nucleus. However, the fact that behavior and cardiovascular activity can be elicited from electrical stimulation that does not evoke any alteration in motor activity and that lesions of this restricted site of the fastigial nucleus fail to result in a motor deficit suggests that this restricted region of the cerebellum may primarily function as a modulator of emotional and visceral behaviors.

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