CODING OF VIBRISSAE STIMULATION IN THE TRIGEMINAL GANGLION OF THE RAT

by

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER I. INTRODUCTION

Vibrissae are prominent structures of many mammals. Their number, size, and development are not proportional to the size of an animal; rather, their characteristics appear to be correlated with the mode of life of a species. Vibrissae occur in some species of every order of mammals (Pocock, 1914; Danforth, 1925).

Many specializations of locus and other characteristics of vibrissae have occurred. For example, they are found near the wrists of species that use forelimbs for climbing, digging or grasping; they are more prominent in pisciverous or insectiverous aquatic genera than in aquatic herbivora. In some aquatic species, the vibrissae have corrugated surfaces which apparently increase sensitivity to water currents. Vibrissae are conspicuous features of burrowing animals (Pocock, 1914; Lyne, 1959; Ling, 1966). Repetitive whisking movements of the mystacial vibrissae are seen in many but not all rodent species; such movements are absent in domestic cat and dog, raccoon and seal even though prominent facial vibrissae occur in all these animals (Welker, 1964). Vibrissae of the male of a species are often slightly more numerous and stronger than those of the female (Vincent, 1913; Ling, 1966).

A. The Role of the Vibrissae in the Behavior of the Albino Rat

Movement of the vibrissae plays a prominent role in "sniffing" behavior of the rat as it explores its environment. This behavior occurs in a precise spatio-temporal integration, involving movements of the head and snout, rapid respiratory movements (polypnea), and protraction and retraction of the mystacial vibrissae, all in a repetitive sequence at a rate of 6 to 8 per second. This characteristic pattern is elicited by mildly novel stimuli in any sensory modality. The descriptions of sniffing behavior that follow are based on the extensive cinematographic and observational analyses of Welker (1964).

The four components of sniffing behavior occur not only at the same rate, but also in a fixed temporal relationship to one another. As the nose contacts a surface, the vibrissae are maximally protracted and thus in contact with the surface. The tip of the snout is fully retracted, maximally exposing the nostrils, and inhalation is at its peak. Withdrawal then occurs, about twice as rapidly as approach; the head withdraws, the vibrissae are retracted, the tip of the nose is relaxed, and the animal exhales. This pattern occurs repeatedly at a rate of 6 to 8 cycles/sec., for periods from one to ten seconds long. The nose and vibrissae do not invariably contact a surface, and in such instances the sequence of movements occurs in mid air.

Figure 1. illustrates the sniffing sequence; Figure 2. shows a rat with vibrissae in the relaxed and protracted position.

In addition to describing this sniffing pattern in normal animals, Welker further analyzed the behavior after various types of neural damage. The sniffing sequence seems well-organized for optimal reception of both somatic sensory and olfactory stimuli. Nonetheless, selective deprivation of visual, olfactory, auditory or somatic sensory input did not significantly alter the cyclic, synchronous motor pattern of sniffing behavior. However, animals in which either the olfactory bulbs or the somatic snout afferents were destroyed showed some behavioral impairments; they had difficulty in discriminating noxious from innocuous substances until they were actually licked and were inefficient in finding their food.

Animals injected with an excitant drug (Ritalin) or a depressant (Nembutal) showed slightly higher or lower sniffing rates respectively;however, the rates were still within the range exhibited by normal animals, and the integration of the motor pattern was unaltered.

Ablation of both bilateral neocortex and olfactory bulbs disrupted the sniffing sequence, making it difficult to elicit and decreasing its rate, intensity and duration.

Welker also described the ontogeny of sniffing behaviors in normal infant rats. The various components of the pattern appeared at different ages; the sniffing rate also

exhibited a developmental course. Polypnea was the only component present during the first four postnatal days. At first it occurred at a rate only slightly faster than normal breathing but gradually increased. On the fourth day the vibrissae began to retract synchronously; prominent protraction of the vibrissae and nose became visible on day 7 and discrete head movements on the eighth day. These behaviors did not reach their full amplitude and rate until the fourteenth to eighteenth day. Although the behaviors matured at different times, when each did appear, it occurred at the same rate and in normal synchrony with those movements already present. Thus on day 8, all the behaviors occurred at a rate of about 4/sec. and on day 10 at 4/sec. From day 14 on, the adult rate of 6 to 8 cycles/sec. was observed. The temporal relationship of the various components as they emerged was similar to that of the adult rat.

The synchronous sniffing pattern is relatively immutable; it is essentially identical in the 18 day old infant, which is neither weaned nor has yet had its first period of intense exploration, and in the adult animal. Moreover only the most drastic interference with the nervous system has any substantially disruptive effects.

In an early study by Vincent (1912), the vibrissae were found to be important in maze learning and tactile discrimination by albino rats. In a sideless elevated maze, rats deprived of vibrissae from birth took longer to learn

and fell off the maze more frequently than normal subjects; they also kept their bellies flattened to the center of the pathway rather than running "high," on extended legs, as did the normal rats. Unilateral removal of the vibrissae resulted in the rat staying close to the edge of the maze on the side where the vibrissae remained. Such animals actually learned the maze more rapidly, since staying consistently to one side prevented most errors. The infraorbital nerve was sectioned bilaterally in some animals, so that the nose as well as the vibrissae was insensitive; these rats performed more poorly than those in which the vibrissae were simply removed. Blind animals with snout afferents intact learned at about the same rate as visually-intact animals with the infraorbital nerve sectioned, but the former suffered many fewer falls from the maze. Blind animals without vibrissae did not master the maze in almost two months of training. Vincent concluded that vibrissae are important in providing the rat with a sense of support, in delimiting the edges of a path, in defining right and left, and in providing a sense of equilibrium.

In a second experiment reported in the same paper (Vincent, 1912), rats were required to discriminate corrugated from smooth sides of an alley in order to obtain food and avoid punishment. Animals without vibrissae learned more slowly than normal or blinded rats; animals with bilateral infraorbital nerve section failed to reach criterion on

this problem in four months of training.

Vincent's results contrasted with those of Watson (1907), who reported no impairments in maze retention 48 hours after cutting the vibrissae. Many differences in procedure might account for this, such as Watson's use of rats that had already learned the maze and the use of a maze with sides versus the elevated maze employed by Vincent.

Koranyi, Endroczi and Lissak (1963) reported that following removal of vibrissae, rats showed a temporary impairment followed by rapid recovery of performance in a previously learned avoidance task. These results are similar to the findings of Watson on maze learning.

Richardson (1910) showed the importance of the vibrissae to the rat in learning a jumping task. Blind rats learned to jump from one platform to another much more readily if their snout or vibrissae contacted the second platform before jumping. When the second surface was out of reach of the rat's vibrissae, the experimenter could stimulate the animal to jump by touching the tips of its vibrissae with a pencil.

Zucker and Bindra (1961) found that rats deprived of vibrissae and vision spent more time exploring a novel environment, as measured by walking and rearing, than did control animals. With much of their sensory input thus

removed, the deprived animals did not adapt to novel stimuli as readily as the normal rats.

B. Anatomy of the Vibrissae and Associated Structures

1. General Description

Pocock (1914) has distinguished five categories of facial vibrissae, based on their position on the head of an animal: a) Buccal, which is subdivided into the mystacial vibrissae on the muzzle and upper lip and the submental, on the chin and lower lip; b) Interramal, behind the mandibular symphysis; c) Genal, rostral to the base of the pinna; d) Superciliary, above the eye; and e) Subocular, below the eye. Of these, the mystacial are by far the most conspicuous and numerous in the rat. The use of the term vibrissae, without further qualifications, will refer to the mystacial vibrissae in this paper.

The mystacial vibrissae are arranged in five rows along the lateral aspect of the face of the albino rat (Fig. 3). There are 30 to 35 relatively large vibrissae on each side. For convenience, in specifying any particular vibrissa, the rows have been designated V through Z, from dorsal to ventral, and the columns have been numbered 1 to 8, from caudal to rostral. The number of large vibrissae in each row varies; row V, the shortest, has only five, while rows

Y and Z, the longest, have eight large vibrissae. The longest and thickest vibrissae are located caudally; they become shorter and finer more rostrally, gradually tapering off into the small sinus hairs found adjacent to the lips and nares. The distinction between what are here termed "large vibrissae" and "small sinus hairs" is an arbitrary one. They are apparently structurally similar, with size being the only notable difference. The most caudal vibrissae (column 1) are about 5 cm. long; column 3 vibrissae are 3 to 4 cm.; those of column 5 are 1 to 2 cm. in length. It is not uncommon to observe two hairs emerging from a single large follicle. The vibrissae, when whisking, provide a rostral-to-caudal mobile span of as much as 5 cm. on either side of the face, thus greatly increasing the potential stimulus area an animal can contact from a given body position.

In genetic studies of mice, the number of mystacial vibrissae has been found to be an extremely invariant characteristic in most strains (Fraser and Kindred, 1962). Danforth (1925) found that less than 1% of mice showed any variability in the pattern of the mystacial vibrissae.

2. Morphology

The most extensive study of the morphology of vibrissae follicles was performed on mice by Melargno and Montagna

(1953). Less complete descriptions of the follicle of the albino rat (Vincent, 1913; Patrizi and Munger, 1966) and kangaroo rat (Webster, 1966) show a virtually identical structure; thus the following description is largely based on the more complete study on the mouse.

Hair itself is not a sense organ. The receptive organ is within the hair follicle, which is specialized in several ways which apparently promote sensory input. The vibrissae follicle (Fig. 4) is embedded in a dense capsule of fibrous connective tissue, which is attached to the dermal papilla at the bottom of the capsule and constricts at the top of the follicle into the conical body which encloses the sebaceous glands. Between the capsule and the follicle is found the large blood sinus which is the most distinguishing feature of tactile hairs as compared to pelage (coat) hairs. The lower part of the sinus is known as the cavernous sinus, due to the trabeculae of stellate cells and capillary plexuses which are found there. The upper or ring sinus is associated with the ringwulst, an umbrella-shaped thickening of connective tissue. The entire follicle is surrounded by a mesenchymal sheath, which is the source of both the traberculae in the lower portion and the ringwulst in the upper part of the sinus.

The blood sinuses provide a possible mechanism for altering pressure which may affect sensory reception

(Vincent, 1913; Patrizi and Munger, 1966). There is considerable speculation that the cavernous sinus may serve as an erectile organ, altering the input to the large ringwulst just above it. Presumably when the sinus is turgid, the vibrations of the hair in the follicle are altered, thus changing the afferent impulse pattern.

The internal root sheath, hair shaft and hair bulb of vibrissae are similar to those of coat hair. Some elaboration of the external sheath has occurred in the vibrissae follicle; there is a superior enlargement of the external membrane just above the ringwulst and a glassy membrane, a hyalin membrane of varying thickness which separates the external sheath and the mesenchymal sheath.

The dermal papilla is large and traversed by many small capillaries, as contrasted with papillae of coat hairs which are largely avascular. Scott (1955) contrasted the capillary network of the papilla with the blood sinuses found in the upper part of the follicle, saying that the capillary network serves the high metabolic demands of the papilla region required to maintain the constantly growing hair.

Oliver (1966) reported that the vibrissa follicle will regenerate as long as no more than the lower third of the follicle is removed. The hair will not grow until the papilla has regenerated. If a smaller than normal papilla regenerates, a smaller than normal vibrissa will

grow.

The hair itself acts as the transmitter of externally-applied tactile stimuli to the receptor endings. Sherrington (1900) said,

> "The short hairs of the skin much enhance the tactile sensitivity. On 9 sq. mm. of skin from which the hairs have been shaved the liminal stimulus was 36 mgms. whereas before it was shaved, 2 mgms. was the liminal stimulus... The hair is three to twelve times more sensitive than the (touch) spots. Each short hair is a lever, of which the long arm outside the skin acts at an advantage upon the touch organs at the root." (p. 926)

The vibrissae provide a much longer lever for this amplifying function.

Besides its greater length, the vibrissa hair is also specialized in that keratinization occurs very low in the hair follicle. Such stiffening provides a more efficient pathway for transmission of mechanical deformation. (Ling, 1966).

The muscular attachments of the follicle have not been described in detail, but a brief report has been made by Vincent (1913). Vibrissae follicles share in the general skin musculature, as well as having extensive muscular attachments of their own. Long cords of muscle run from the sides of the follicle into the subcutaneous tissue beneath it. There is also a flat muscle band on three sides as well as a muscular structure around the neck of the follicle and around the conical body. The latter are thought

to influence the level of damping of the vibrations of the tactile hair.

3. Sensory Innervation

The infraorbital branch of the trigeminal nerve provides the somatic sensory innervation of the vibrissae and mouth. It is relatively large in the rat, containing an estimated 15,000 to 20,000 fibers. Vincent (1913) provides the basis for the following description of the rich and complex sensory innervation of the vibrissae.

There are often 150 or more fibers entering one follicle of a large sinus hair. As the nerve bundle reaches the root of the hair, it divides into two parts which penetrate through opposite sides of the lower third of the dermal sheath. Both sections divide further, surrounding the follicle with parallel bundles of ascending fibers, many of which ascend to the neck of the follicle. Many axons preserve their myelin sheaths almost all the way to their terminations near Merkel disc cells. There are anywhere from 1 to 4 such discs per follicle. All the large fibers which terminate above the level of the ringwulst are forced to pass through it. In addition to this ascending innervation, a nerve ring is formed above the ringwulst by fibers descending from the dermal plexus.

In a brief report on the receptors of the mole, Quillam (1964) reported at least 40 neurons entering each vibrissa

follicle.

Patrizi and Munger (1966) studied the nerve terminations in rat vibrissae follicles with the electron microscope. They also found that most of the neurons ended at Merkel disc cells, after losing their myelin sheaths at the level of the ringwulst. They describe "neurite-Merkel cell complexes" which appear quite similar to those found in epidermal and coat hair innervation. The Merkel cells are filled with mitochondria at the point of association with the neurite. Their data did not permit them to determine whether there was one or more than one neurite per Merkel cell. They speculate that the specialized secretory nature of the Merkel cell might provide the mechanism for graded chemical changes in the production of receptor potentials.

C. Neural Circuits for Tactile Sensation of the Face

Somatic afferent impulses from the face activate neurons in the trigeminal division of the somatic sensory system. The primary afferent fibers travel in the trigeminal (Vth) cranial nerve to the semilunar (Gasserian) ganglion; they ascend in the trigeminal root and spinal tract largely to synapse in the trigeminal nuclear complex of the brain stem. Many fibers then project to the somatic sensory receiving areas of the thalamus and neocortex. The trigeminal circuit just described, along with the dorsal root, dorsal

column input from the trunk and limbs, constitute the classical sensory pathway for light touch stimulation known as the medial lemniscal system (Rose and Mountcastle, 1959). The following review will emphasize neuroanatomical and neurophysiological data concerning the peripheral neurons of the trigeminal-lemniscal system. The central receiving areas will be discussed more briefly.

1. The Semilunar Ganglion

a. Neuroanatomy

The semilunar ganglion has three divisions, each projecting with relatively little overlap to three trigeminal skin fields. The divisions are the ophthalmic, maxillary and mandibular (Head, 1894; Sherrington, 1898; Kerr, 1963; Darian-Smith, Mutton and Proctor (1965).

Cajal (1909) described the ganglion as composed primarily of monopolar cell bodies. As the unmyelinated axon leaves the cell body, it forms a tightly coiled glomerular structure and then bifurcates into an ascending and descending segment, each of which is myelinated. Histological examination of the ganglion in cat and monkey shows a cell mass running from anteromedial to posterolateral through the three divisions, irregularly interupted by fiber bundles (Kerr and Lysak, 1964; Darian-Smith et al., 1965) (See Fig. 5 & 6).

Electron microscopy has revealed the ultrastructure of the ganglion to be very similar in many species of animals; it is composed of nerve cells of various sizes, surrounded by satellite cells, and containing large central nuclei (Moses, Beaver and Ganote, 1965). Although some studies failed to report unmyelinated fibers (e.g. Gerard, 1923; Brookhart, Livingston and Haugen, 1963), both myelinated and unmyelinated fibers have been observed with the electron microscope (Dixon, 1963). The latter are presumed to subserve efferent sympathetic rather than sensory functions, which would account for their not being identified in the physiological studies, which employed afferent test stimuli.

Conduction time studies permit the inference that a wide spectrum of axon diameters exists among the myelinated afferent fibers. McKinley and Magoun (1942) found conduction velocities of 40 to 50 meters/sec in the trigeminal nerve of cat. Brookhart et al. (1963) reported conduction speed in the peripheral segment of axons innervating tooth pulp to be between 30 and 45 meters/sec. Darian-Smith et al. (1965) have identified four fiber groups in the cat trigeminal nerve with mean conduction velocities of 67, 35, 23, and 12 meters/sec. in the peripheral axon segment. In the post-ganglionic segment, velocities were markedly less (between 6 and 34 meters/sec) than in the periphery. Within the central segments conduction speed (between the ganglion and

brainstem) decreases further caudally, probably due to tapering of the individual fibers (Wall and Taub, 1962).

Although some controversy has existed over the level of termination of the first order neurons in the trigeminal nuclear complex, antidromic stimulation of the spinal tract in cat, at successively more caudal positions, has shown that 86% of the large fibers project at least as far caudally as the obex, 48% at least as far as the first cervical segment and 16% as far as the second cervical segment (Darian-Smith et al., 1965). Similar results were obtained from degeneration studies performed on cat and rat (Kerr, 1963; Clarke and Bowsher, 1962). The level of termination in the medulla is not correlated with the peripheral division to which a fiber belongs as has been previously thought (Torvik, 1956; Wall and Taub, 1962; Darian-Smith et al., 1965), although there is a somatotopic arrangement of fibers at any transverse plane from ophthalmic, maxillary and mandibular branches in ventrodorsal succession (Torvik, 1956; Kerr, 1963).

b. Neurophysiology

There have been relatively few reported neurophysiological investigations of the semilunar ganglion in cat and monkey and none in rat. In the two most extensive investigations carried out (Kerr and Kysak, 1964 on cat and monkey; Darian-Smith et al., 1965 in cat), single unit recording was used to establish some of the receptive field and coding charac-

teristics of these neurons. Kerr and Lysak found neurons that were activated by stimulation of hairs, gentle contact with the skin and pressure or movement of the vibrissae. Darian-Smith et al. usually employed an electrical stimulus which presumably activated all of these categories of units.

The two studies report somewhat different somatotopic organizations within the ganglion. Kerr and Lysak found that units located dorsally in the ganglion had receptive fields in the more posterior regions of the face; ventral units innervated the perioral and perinasal regions. Darian-Smith et al. did not observe such a dorsoventral organization. Both studies, however, reported that the three divisions of the ganglion subserve the three segments of the face, ophthalmic being most medial in the ganglion, mandibular most lateral and maxillary in between them. Darian-Smith et al. stress that the ophthalmic division is located rostrally as well as medially in the ganglion and that the mandibular division is situated caudally as well as laterally. The present experiments provide information regarding somatotopic organization within the maxillary component only, because this is the division which receives projections from the vibrissae.

Both Kerr and Lysak and Darian-Smith et al. found neurons with restricted cutaneous receptive fields, with average receptive field diameters between 1 and 2 cm.; they observed the size of the receptive fields to be smallest in the perioral

and perinasal regions and largest around the pinna and eye. This change in the average size of the receptive field as a function of body locus is similar to that found in dorsal roots in many investigations (e.g. Pubols, Welker and Johnson, 1965).

Kerr and Lysak studied neurons innervating teeth and vibrissae, and these results, along with those from several other experiments recording from the primary afferent fibers in response to stimulation of the teeth and vibrissae, will be discussed after the findings of the present experiments have been reviewed.

There have been many reports of antidromic activity recorded within the primary afferent fibers of the trigeminal (Turnbull, Black and Scott, 1961; Alvarez-Carregal, Crue and Todd, 1963; Darian-Smith, 1965; Darian-Smith and Yakota, 1966a, b; Hammer, Tarnecki, Vyklicky and Wiesendanger, 1966; Stewart and King, 1966, Stewart, Scibetta and King, 1967). The terminology used to describe this activity is not standardized as yet. I shall use the terms chosen by Darian-Smith and colleagues, who have made the most extensive of the investigations.

They describe the existence of the "trigeminal tract reflex," a repetitive discharge of 2 to 7 spikes analogous to the dorsal root reflex (cf. Brooks and Koizumi, 1956; Eccles, Kozak and Magni, 1961). It is characterized as follows:

1) Elicited by electrical or mechanical stimulation of the excitatory receptive field of a unit or of the area surrounding that receptive field.
2) Onset latency of about 5 to 12 msec.; duration of about 3 to 15 msec.
3) Abolished by section of the trigeminal root.
4) Abolished by stimulation rates of about 2/sec. or more.
5) Enhanced by a subnormal body temperature.

The studies by Darian-Smith (1965) and Stewart et al. (1967) also report the existence of a change in excitability in the central terminals of the afferent fibers, termed primary afferent depolarization (PAD, described by dorsal root fibers by Wall, 1958). PAD has many characteristics identical to those of the tract reflex, and it is presumed that the trigeminal tract reflex occurs when PAD reaches threshold for spike discharge. PAD can be elicited by stimulation of the same peripheral areas that produce the tract reflex or by electrical stimulation of the face area of contralateral somatic sensory cortex. Several other cortical loci also produce lesser amounts of PAD, It has a latency of 10 msec., a peak at 20 to 50 msec. and a duration of 150 to 300 msec. The effect is maximal in the primary

afferent terminals in the rostral part of the trigeminal brainstem complex.

Stewart et al. reported an enhancement of PAD when a tractotomy is performed which separates the rostral and caudal brainstem nuclei, suggesting a tonic hyperpolarizing influence exerted by the caudal nuclei. Darian-Smith and Yakota did not find this effect.

Both studies suggest that the tract reflex is an instance of primary afferent depolarization which is responsible for surround inhibition observed in the second order neurons. This will be discussed further in the subsequent section on the brainstem nuclei.

Stewart et al. observed a depression of the trigeminal tract reflex elicited by a test stimulus following the electrical cortical conditioning stimuli effective in producing PAD. They propose that the conditioning stimulus partially depolarizes the afferent fibers which, in turn, inhibits the response of the second order neurons. This decreased response presumably activates fewer of the interneurons which synapse back on the primary fibers, and thus fewer spikes are elicited in the tract reflex.

2. Trigeminal Nuclear Complex of the Brainstem.

a. Neuroanatomy

The trigeminal nuclear complex consists of two main

divisions, an ascending component of the trigeminal spinal tract called the main or principal sensory nucleus and the descending component of the tract called the spinal nucleus of the trigeminal tract (Ramon y Cajal, 1909; Gerard, 1923). The latter structure is composed of at least three divisions, nucleus oralis, interpolaris and caudalis (Olszewski, 1950; Torvik, 1956).

Many of the neurons from these nuclei project to the contralateral posterior (ventrobasal) thalamus (Rose and Mountcastle, 1959). Recent experiments using antidromic stimulation suggest that the rostral nuclei project to the arcuate nucleus of the ventrobasal complex; the neurons from n. caudalis project largely to the posterior nuclear group (the chief receiving area for the spinothalamic tract) of the thalamus (Darian-Smith, Row and Sessle, 1966b). On this basis Darian-Smith (1966) proposed that the former be considered lemniscal neurons and the latter as the homolog of the spinothalamic system, but this seems somewhat premature until additional properties, such as size and location of receptive fields and modality specificity, are seen to agree with this dichotomous classification.

Although a subject of much controversy (see Rose and Mountcastle, 1959), results of recent studies using degeneration methods and antidromic stimulation suggest that there is a projection to ipsilateral thalamus (Torvik, 1957;

Stewart and King, 1963; Eisenman, Fromm, Landgren and Novin, 1964). There is also a projection to the midbrain reticular formation (Nauta and Kuypers, 1958; Stewart and King, 1963) from the caudal brainstem nucleus.

b. Neurophysiology

Although there has been quite a number of electrophysiological studies of these nuclei (Darian-Smith and Mayday, 1960; Gordon, Landgren and Seed, 1961; Kruger, Siminoff and Witkovsky, 1961; Wall and Taub, 1962; Kruger and Michel, 1962 a, b; Darian-Smith, Phillips and Ryan, 1963a; Darian-Smith, Proctor and Ryan, 1963b; Eisenman, Landgren and Novin, 1963), there is little agreement on the size of the cutaneous receptive fields or somatotopic organization. All the investigations agree that the receptive fields are restricted in some subnuclei and large in others, and that the restricted fields are organized somatotopically in the form of an ipsilateral inverted head. However the various experiments disagree as to which of the nuclei and subnuclei possess somatotopic projections and which have receptive fields too large and overlapping to reveal such organization. Some experiments report precisely the reverse of others. Darian-Smith (1966) considers that shrinkage of tissue upon histological preparation, spread of field potentials in macroelectrode studies and biased sampling procedures in micro-electrode studies all contribute

to the thus far confused results.

Units in the brainstem complex with cutaneous receptive fields located in the vibrissae will be discussed following the results of the present experiments.

There has been a number of reports of afferent surround inhibition in the trigeminal brainstem nuclei (Erickson, King and Pfaffmann, 1961; Darian-Smith, 1965; Darian-Smith and Yakota, 1966 a, b; Stewart and King, 1966; Stewart et al., 1967). The inhibition has the same temporal and spatial characteristics as the primary afferent depolarization (PAD) described in the preceding section. Inhibition of response to a test stimulus occurs following a conditioning stimulus to the excitatory receptive field of a unit, to the peripheral region surrounding that receptive field or to the face area of the contralateral somatic sensory cortex. The inhibition also has a latency and time course similar to those of PAD, and it too is maximal in the rostral nuclei. Thus the inhibitory effect has all the characteristics of presynaptic inhibition as characterized by Eccles and his colleagues (see Eccles, 1964) in the spinal cord and dorsal column nuclei. One study of the brainstem nuclei failed to find such surround inhibition (Kruger and Michel, 1962). They examined neurons in the cat responding to stimulation of the vibrissae especially carefully for this phenomenon but did not see it.

3. Thalamic Receiving Areas

Mountcastle and Hennemam (1952) and Rose and Mountcastle (1952) described the somatic sensory projections to the thalamus in monkey, cat and rabbit. They defined the ventrobasal complex as the primary receiving area. Within this region, trigeminal input from the face and mouth is localized to the arcuate nucleus in cat and monkey. In the rabbit, almost the entire ventrobasal region receives facial input, with only a small zone reserved for spinal afferents. Emmers (1965) likewise found a relatively large representation of the face in the ventrobasal complex of the rat, with many evoked potentials elicited by stimulation of just the vibrissae. A somatotopic organization was found in all species. The contralateral face was represented more extensively than the limited ipsilateral projection from perioral zones.

Darian-Smith et al. (1966 b) substantiated these findings for facial input to the arcuate nucleus of the cat. They reported receptive fields of between 2 and 25 mm. for units which, in general, exhibited the highly specific properties found throughout the primary somatic system. Most units adapted rapidly to either light touch or hair stimulation. About 50% of the neurons were inhibited by electrical stimulation. in the areas surrounding the receptive field; the surround usually consisted of the entire contralateral face with an ipsilateral perioral extension.

More than 90% of the neurons which responded to tactile stimulation received their input from the main nucleus and nucleus oralis of the trigeminal complex in the brainstem.

The same study reports that input to the posterior group of the thalamus is largely from nucleus caudalis of the brainstem complex. The receptive fields of these neurons are much larger; some neurons even respond to auditory stimuli.

A third thalamic area responding to facial stimulation was the subthalamus (Darian-Smith et al., 1966b). About one-third of the neurons in this area had relatively small discrete receptive fields and two-thirds had more extensive and diffuse fields, similar to those of the posterior nuclear group.

4. Cortical Receiving Areas

Adrian (1940) and Woolsey (1943; 1958) delimited two areas of the cerebral cortex, designated SI and SII, which receive a somatotopically organized projection from the entire body surface and face. In the rat, the amount of cortex representing the surface of the trunk and limbs is roughly proportional to the skin surface area, whereas the face region of cortex is relatively enlarged (Woolsey, 1952).

In a detailed study in the cat of trigeminal input

to the cortex, Darian-Smith, Ibister, Mok and Yakota (1966a) observed that the functional characteristics of facial neurons were similar to those observed for cortical neurons responding to spinal input (e.g. Mountcastle, 1957; Carreras and Anderson, 1963). Darian-Smith et al. (1966a) also defined a third somatic projection region, SIII, which had similar properties. They suggested that SIII in the cat may be homologous to the split-head projection found in primates (e.g. Ullrich and Woolsey, 1954).

All three regions receive an inverted, forward-pointing projection of the head and face. All three face areas exhibit columnar organization of the receptive fields, such that all units within a column situated at a right angle to the cortical surface receive input from a similar peripheral locus and of similar modality. All three have large contralateral and small ipsilateral facial projections (Darian-Smith et al., 1966a).

In conclusion, the neural organization of touch sensation from the face has many similarities to the more thoroughly studied somatic sensory input from the trunk and limbs (the dorsal column system). As do lemniscal neurons of the dorsal column system, many of the trigeminal neurons have precisely localized somatic sensory receptive fields arranged in a somatotopic pattern. The two systems project side by side to adjacent areas of the medulla, thalamus and cortex. Homologous

distinctions between the dorsal column pathway and the spinothalamic tract are as yet less clear in the trigeminal system, although indications are that such a dichotomy exists there too (Rose and Mountcastle, 1959; Darian-Smith, 1966). Both systems exhibit afferent surround inhibition, with a well-documented presynaptic component of the inhibition in the medulla. One distinct difference is the inclusion of an ipsilateral projection within the trigeminal pathways, whereas the body limb projection appears to be exclusively contralateral.

D. Quantitative Relationships of Stimulus Input, Neural Output

Precise relationships between the intensity of a stimulus and the frequency or amplitude of the evoked neural activity have been established in the primary afferent dorsal root fibers by a number of investigators (Adrian and Zotterman, 1926; Matthews, 1933; Katz, 1950; Lindblom, 1962; Tapper, 1964; Werner and Mountcastle, 1964; Mountcastle, Talbot and Kornhuber, 1966b). In addition, reports have been made of intensity-frequency relationships studying facial input to the medulla (Takata and Yojiro, 1963; Darian-Smith, 1964), and spinal input to the thalamus (Mountcastle, Poggio and Werner, 1962, 1963). All of the above studies report a linear, logarithmic or power function between stimulus input and neural response.

By far the most elegant of these experiments were those

conducted by Mountcastle and colleagues. They have explored the S-R relationships at three locations in the somatic sensory system:

a) in primary afferent fibers of the saphenous nerve in response to mechanical stimulation of Iggo corpuscles (touch spots). The subjects were cats and monkeys under barbiturate anesthesia.

b) in thalamic neurons in response to gentle rotation of the joints of unanesthetized monkeys and

c) in slowly-adapting primary afferent fibers in response to mechanical stimulation of the dermal ridges in the glabrous skin of the hand of macaque monkeys under barbiturate anesthesia.

These experiments revealed that the degree of skin indentation or joint movement was precisely coded by frequency of neural firing. In the first two experiments (a and b above) the relationship of stimulus intensity and impulse frequency was in the form of a power function. When plotted as a double logarithmic transformation, the data showed extremely close fits to a straight line function (e.g. mean correlation coefficient = .96 for 10 primary afferent fibers).

In the third experiment (c above) stimulation of the dermal ridges resulted in a linear relationship between stimulus intensity and frequency of spike discharge. The

correlation coefficient describing the goodness-of-fit of the data to straight line functions was .99 or more in all cases. This relationship can, of course, be considered as a power function with an exponent of 1.

These results are extremely interesting in the light of human psychophysical experiments performed by Stevens and colleagues (e.g. Stevens, 1959, 1961 b, c; 1966), which show a similar power function relationship between stimulus intensity and "subjective sensation" for an impressively wide range of stimulus modalities (e.g. electric shock, loudness, brightness, cold, length of lines, and many others). Stevens uses primarily the methods of "magnitude estimation," whereby subjects assign a numerical value to a stimulus in comparison with an arbitrary numerical value assigned to a standard stimulus and "cross-modality matching," whereby the observers equate the sensations produced by stimuli of different modalities. His results show that the former method produces straight line functions when the data are transformed onto double log coordinates, with a characteristic slope (i.e. the exponent of the power function) representing each stimulus modality. The cross-modality matching procedure produces similar straight line functions with slopes equal to the ratios of the exponents of each modality involved. If instead of the magnitude scaling methods, discriminability scales are constructed, using the just-noticeable-difference

method of Fechner, a logarithmic rather than a power function emerges.

The straight line functions of Stevens are obtained by averaging the results from a large number of trials per subject and a large number of subjects. Data collected from individual subjects, even though a large number of trials may be used (up to 100 at each stimulus intensity), show systematic deviations from a straight line, with slopes of the best-fitting straight line varying widely from subject to subject (Luce and Mo, 1965).

Stevens strongly argues that the power function should replace the classical semi-log relationship of Fechner as the psychophysical law. Other investigators, while not doubting the empirical validity of the power function obtained by magnitude scaling, have reservations about its meaning (see, e.g., Ekman and Sjoberg, 1965).

The implications for one another of the human psychophysical data and the single unit animal data are not entirely clear. One difference in the results of the two kinds of studies is that in the first two experiments described, Mountcastle reports a different exponent for each nerve fiber. This might be somewhat inconsistent with the existence of an exponent uniquely characteristic of each modality as purported by Stevens, since the range of exponents for mechanoreceptive afferent fibers was almost as great as

the range found for all stimulus modalities by Stevens.

Despite such discrepancies, Werner and Mountcastle (1965) assert that the identity of the formal relation between stimulus and response in the two kinds of experiments implies

> "that the neural transforms intervening between input and the final verbal descriptions of an introspective magnitude estimation must be linear for the intensive continuum. This does not imply, of course, that the intervening neural transforms must all be linear, but that the sum of their serial superposition must be so." (p. 391)

This statement is not necessarily true; if successive transformations were power functions rather than linear functions, the sum of the transformations would nonetheless be a power function.

Mountcastle, Talbot, Darian-Smith, and Kornhuber (1966a) performed an experiment designed to compare directly human flutter-vibration thresholds and response properties of first-order mechanoreceptive afferents from the hand of anesthetized monkeys. Using the same stimulator and stimulus program for both humans and monkeys, they found two sets of afferent fibers whose response properties accounted extremely well for the two limbs found in the human threshold curves. This experiment adds weight to the assumption that neurophysiological studies of peripheral fibers can shed light on mechanisms of sensory perception.

E. Purpose of the Present Experiments

The experiments reviewed in the preceding sections describe some of the behavioral, anatomical and neurophysiological data relating to the perception of tactile stimuli. The data indicate, in part, the role tactile stimuli to the vibrissae play in the rat's behavior, how the vibrissae and associated structures are specialized to receive the stimuli and which neural circuits have been discovered that process tactile stimulation of the face.

The present experiments were designed with the goal of relating neural coding characteristics to peripheral mechanical stimuli, in order to understand what input might normally be perceived from the extensive use the rat makes of its vibrissae. The methods of stimulation were chosen so as to mimic some of the stimuli that the rat normally encounters during use of its vibrissae in exploring the environment.

The first order neurons of the trigeminal system were selected for analysis. This is not to imply that these peripheral afferents are the locus of 'perception', but rather that these neurons are an early filtering point of the neural circuit which ultimately underlies the perception of a tactile stimulus. Stimuli which are transmitted by these first neurons, i.e. which are encoded by them, have

the possibility of affecting higher order cells. Conversely, stimulus characteristics which are eliminated by this filter cannot influence later firing in the circuit.

The following general questions were asked in the present study: a) What are the characteristics of adequate stimuli for activation of the first order neurons? b) What characteristics of such stimuli are coded? c) What is the nature of such codes?

Specifically, the experiments were designed to define the receptive field characteristics and topographical organization of units responding to stimulation of the vibrissae and to determine the response of these neurons to vibrissae movement produced by activation of the normal facial motor pathways. The threshold stimulus sufficient to activate the vibrissae units and their response to a sustained stimulus were also determined. Finally, quantitative relationships between the amplitude and velocity of the stimulus and the frequency of impulse discharge were examined.

CHAPTER II. MATERIALS AND METHODS

A. EXPERIMENT 1

Experiment 1 defined receptive field characteristics and adequate stimuli for activation of single units in the semilunar ganglion using the following experimental subjects and techniques.

1. Experimental Preparation

Twenty-four male Sprague-Dawley rats weighing between 190-320 gm were used as subjects. Anesthesia was induced by intraperitoneal injection of 45 mg/kg pentobarbital sodium; subsequent doses were administered as judged necessary by reflex responsiveness. Vibrissae were clipped to about 1 cm. in length and painted black for easier visualization. The trachea was then cannulated and the animal placed in the headholder of a stereotaxic instrument. Body temperature, monitored rectally, was maintained between 32 and 36° C. with the use of a heat lamp.

Under visualization with a binocular dissecting microscope, enough of the left hemisphere was removed by aspiration to expose most of the semilunar (Gasserian) ganglion (See Fig. 7). Hemostasis was achieved with the use of gelfoam. The dura was then teased away from the exposed surface of the ganglion with fine forceps. Continuous accumulation

of cerebrospinal fluid preventing drying of the ganglion. In some animals, the trigeminal root was sectioned to prevent the recording of any possible antidromic activity (trigeminal tract reflex) in the ganglion (See Introduction).

The temperature of the tissues adjacent to the ganglion was measured in a few cases and was typically 35-39°C, i.e., a few degrees higher than rectal temperature. This difference was probably due to the illumination of the ganglion by surgical lamps.

In some animals, a 5 mm. length of the buccal branch of the facial motor nerve was dissected clear of surrounding tissues to permit electrical stimulation producing protraction of the vibrissae. Occasionally a small rostral branch of the facial nerve, stimulation of which produces retraction of the vibrissae, was similarly prepared. Each exposed nerve was covered with a small cotton ball soaked in mineral oil to prevent drying.

2. Recording Methods

Tungsten microelectrodes, prepared according to the method of Hubel (1957) were used to record electrical activity from units in the ganglion. These electrodes had a tip diameter of approximately 1μ and were insulated with epoxylite varnish to within 15 to 50μ from the tip. Figure 8A shows the size and shape of one electrode which successfully recorded from units in a majority of the experiments. The microelectrode was carried in a shielded holder and was itself shielded to within 3 cm. of its tip by hypodermic tubing attached to the holder. The common shield was grounded to the stereotaxic headholder and the indifferent electrode was attached to exposed scalp.

Microelectrodes were lowered onto the ganglion by means of a micromanipulator attached to the stereotaxic instrument. Movement of the electrode onto and through the surface of the ganglion was observed through a binocular dissecting microscope. In each puncture, the electrode was lowered dorsoventrally until the bottom of the ganglion was reached. This point was easily identified by an abrupt cessation of unit 'hash' activity when the face and snout were being stroked. The location of each puncture was marked on a sketch or photograph of the ganglion (See Fig. 8B). The punctures did not sample the ganglion systematically but rather were designed to maximize the recording of units which responded to vibrissae stimulation.

The electrical signs of neural activity were amplified by an Argonaut differential preamplifier (low cutoff filter set at 320 cps and the high cutoff filter at 1600 cps) whose output was led into the amplifier of a Tektronix 502 oscilloscope. The electrical activity, thus amplified, was monitored on the face of the oscilloscope and, with additional amplification, over an 8 in. loudspeaker. Unit activity was recorded on one channel of a two channel magnetic tape (Magnecord tape recorder #728-4), while the second channel recorded verbal descriptions of associated experimental procedures and unit characteristics. For illustrative purposes, selected units were photographed from the oscillographic playback of the recorded data, using a Grass camera (model C4G). The recorded activity was also used in data analysis procedures (see below).

Records were taken only of the electrical signs of single unit activity. Uniformity of spike amplitude and wave form were the major criteria used to distinguish a single unit. Although several units might be recorded from any one electrode position, they were distinguishable by distinct differences in spike amplitude and waveform. Data were recorded only in those cases where the spikes were of uniform amplitude and also sharply differentiated from baseline and background activity. The amplitude of spikes meeting these criteria ranged from about 70 μV to about 400 μV.

Polarity of the spikes varied; 48% were initially positive and 52% were initially negative (Fig. 8C). Some electrodes tended to record more units of one polarity type than the other, but no electrode recorded one polarity type exclusively. In general, initially negative units could be held for longer periods of time than those that were initially positive. Single units were held for as long as two hours, but five to ten minutes were usually sufficient to obtain the relevant data for each unit.

3. Electrical Stimulation of the Facial Nerve

The facial nerve was stimulated electrically to produce movements of the vibrissae which simulated natural motor movements. The buccal branch of the nerve, which yielded protraction when stimulated, was usually chosen, but occasionally a small branch yielding retraction was stimulated as well. The latter was stimulated less often because of the relative difficulty in dissecting it free. Monopolar stimulating electrodes were constructed of .005" diameter Formvar-coated stainless steel wires. A loop was made at the end of each wire and the insulation on its inner surface removed. The stimulating wire loops were then hooked onto the two exposed branches of the facial nerve. The indifferent electrode was inserted subcutaneously over

the dorsal aspect of the neck. The wires were connected to the output of a variable voltage isolation transformer (General Radio Corp.) via a switch box, which allowed selective stimulation of either the protraction or retraction nerve. A potentiometer on the output of the transformer permitted adjustment of stimulus intensity to produce an amplitude of vibrissae whisking movements which would approximate that of the behaving animal. The stimulus to the isolation transformer consisted of a 1 msec. duration pulse, delivered by a Tektronix 161 pulse generator at a rate of 2-8 per second.

4. Methods of Tactile Stimulation

Mechanical stimulation was employed to explore the surface of the animals face. As the microelectrode was advanced slowly into the ganglion, the mystacial vibrissae pad and surrounding facial areas were repeatedly stroked with a polyethylene tube stylus to ascertain if the microelectrode tip was in position to record from a driveable unit. When driveable isolated single units were encountered, the electrode advance was halted, and a more detailed identification of the unit's receptive field was carried out.

First the extent of the receptive field was identified as being either a vibrissa, small sinus hair, or patch of

common fur. In the case of each vibrissa or small sinus hair, the following stimulation procedures were systematically employed:

1) Successive movements in each of four major directions (rostral, caudal, dorsal and ventral) were produced by contacting the hair or vibrissa near its tip (all vibrissae had been cut to 1 cm in length, see above) with a small probe and deflecting it as far as required to activate the unit consistently. Although the planes of deflection were approximately these four, some variation in the precise direction was inevitable. Small deviations from the four 90° positions did not appear to affect the unit response parameters which were studied.

2) The probe was then quickly removed, allowing the vibrissa or hair to return rapidly from its deflected positions (here called "snap release").

3) Next, the tip of the vibrissa or hair was grasped with a fine forceps and alternately pulled and pushed perpendicular to the surface of the skin.

4) The mystacial vibrissae were then activated to protract, and in some cases retract, by electrical stimulation of the facial nerve which innervates the striated muscles that activate the vibrissae. This determined whether or not repetitive movement of the vibrissae in the rostral-caudal direction would activate the unit. Such activation simulated vibrissae whisking in a behaving

animal.

5) While a vibrissa was thus freely moving, a "barrier" was placed in contact with it, simulating what might occur when the animal encountered an object while exploring the environment. The barrier was held, in turn, in each of the four main directions, rostral, caudal, dorsal and ventral.

When the receptive field was associated with common fur rather than with vibrissa or small sinus hairs, the extent of the receptive field was determined by gentle mechanical stimulation, consisting of hair stroking and bending with a fine-tipped probe.

Since some stimulating procedures were not used in the early experiments, and some units were lost before the complete battery of procedures could be applied, not every method of stimulation was employed for every unit studied. Consequently, in the results reported below, the number of units included in each of the several analyses is not equal.

B. EXPERIMENTS 2 and 3

Experiments 2 and 3 extended the findings of the first experiment by using an electronically-controlled mechanical stimulator which precisely regulated the velocity, amplitude and duration of the stimulus to the vibrissae. In addition, a small number of units in Experiment 2 was studied in unanesthetized decerebrate animals to evaluate the effects

of barbiturate anesthesia in these experiments. The changes in technique from the first experiment are described below.

1. Experimental Preparation

Male Sprague-Dawley rats weighing between 200 and 300 grams served as experimental subjects. In Experiment 2, 26 animals were used and in Experiment 3, 6 animals were used. All but two of the animals were anesthetized and subjected to the same surgical procedures as those described for subjects of Experiment 1. The trigeminal root was sectioned in 7 rats used in Experiment 2. None of the animals used in Experiment 1 were used in Experiments 2 or 3. The only rats which were used in both the latter experiments were the two decerebrate animals.

These two rats underwent decerebration prior to the normal surgical procedures. For these animals, ether anesthesia was administered, and 2 stainless steel electrodes were stereotaxically positioned in the midbrain (coordinates, A-P 1; lateral 2 mm on either side of the midline; depth 1 mm above horizontal 0). A 60 ma radio frequency current was passed through the 3 mm. bared tips of the electrodes for 20 sec., using a radio frequency lesion maker. This produced a large bilateral midbrain lesion. The semilunar ganglion was then exposed, as described in Experiment 1, and the animals permitted to recover from the ether anesthesia. Upon recovery they showed brisk reflexes when stimulated, but did not struggle in the headholder. They

were then paralyzed with gallemine triethiodide (Flaxedil) and artificially respirated for the duration of the experiment.

The vibrissae were cut to 1 cm. in length in all animals; in a few animals, they were clipped to successively shorter and shorter lengths during the course of the experiments. This was done to determine the influence on unit responses of position of the stimulator probe in relation to the length of the vibrissa (see "position" effect below).

2. Recording Methods

Recording techniques for Experiment 2 and 3 were identical to those described in Experiment 1, except for the following modifications: a Tektronix 2A61 differential preamplifier and 565 oscilloscope replaced the Argonaut preamplifier and Tektronix 502 oscilloscope.

Isolated single units were held for as long as five hours, but 30 minutes to 2 hours were the typical range of time for which these units were studied.

3. The Vibrissae Stimulator

An electronically-controlled mechanical stimulator, shown in Fig. 9, was used to manipulate single vibrissae in any of four directions: rostral, caudal, dorsal and ventral. The stimulating probe consisted of a hollow, cylindrical wand, into which the vibrissa could be slipped (Fig. 10). The probe was usually positioned 5 mm. from the base of the vibrissa. In some cases, the distance from the base was varied to determine the influence of several positions of the probe on unit firing (see the "position" effect below).

The stimulator produced an angular motion of the wand

proportional to the input at the RAMP terminal. (See block diagram, Fig. 11). The signal fed to the RAMP terminal was a sawtooth waveform initiated by manual triggering of the first of two Tektronix 162 waveform generators. Prior to stimulus initiation, the START STOP FLIP-FLOP held storage capacitor C_1 discharged and the wand in its rest position. Coincident with the start of the sawtooth, the first waveform generator also produced a start pulse, which permitted the voltage on C_1 to follow the sawtooth. At the end of the sawtooth, C_1 held the highest value of voltage that the sawtooth had achieved. This voltage was held for the time of the HOLD TIME GATE, which was produced by the second 162 generator and triggered by the end of the sawtooth. The termination of this gate caused the reset of the FLIP-FLOP, which in turn discharged C_1 at a rate dependent on the time constant selected by the OFFSET switch.

A range of 10 msec. to 10 sec. was available for both the sawtooth and the gate times, which were independently adjustable on the two 162 generators. The onset velocity of the wand was approximately linear, although there was an initial mechanical lag which varied with the length of the sawtooth. The mechanical latency usually constituted about 10% of the total sawtooth rise time. There were three OFFSET time constants available, 15 msec. ("slow"), 6.8 msec. ("medium"), and 2.2 msec. ("fast"). The offset

velocity followed the exponential time course of its RC circuit.

The voltage on the capacitor C_1 was read out by the FOLLOWER AMPLIFIER and applied to the GAIN control. The position of this control determined the percentage of full scale traversed by the wand. The greatest deflection at the tip of the wand was 1 cm. In practice, 5 mm. was the maximum tip excursion used, since deflections greater than this caused excessive deformation of the mystacial pad underlying the vibrissa. The minimum reliably reproducible amplitude of excursion was 0.8 mm. Since sawtooth rise time varied from 10 sec. to 10 msec. (see above), the range of velocities for the useful amplitudes, 0.8 to 5 mm, was .08 mm/sec. to 500 mm/sec. The amplitude of excursion refers to the distance traversed by the tip of the stimulating probe, which was positioned 5 mm. from the base of the vibrissa (see above). The sensory receptor endings are located intradermally at the vibrissa base. Therefore the "stimulus amplitude" does not express the actual deformation at the receptor but rather a deformation which is an unknown but presumably constant multiple of the stimulus which is exerted on the receptor endings.

The pPOSITION control detemined the rest position of the wand, which was variable from about 1 cm. on one side of zero to 1 mm. on the other side. This adjustment permitted

the wand to be positioned exactly coincident with the axis of rotation of the galvonometer. To allow the wand to pivot through the galvonometer axis, a mechanical linkage called a squash plate was used. This changed the axis of rotation by 90° while maintaining a fixed relationship between the angle swept by the galvonometer and that swept by the wand. The squash plate consisted of a disk mounted on the galvonometer shaft with one face at an angle of 108° from the axis of rotation. A rocker arm rested on this face in such a way that when the disk was rotated, the rocker arm was tilted. The wand, mounted on the rocker arm, tilted with it. The entire galvonometer assembly was mounted on gimbals to permit complete freedom of position. The apparatus was then mounted on the stereotaxic apparatus which held the experimental animal.

A stimulus artifact marker pulse was produced, by the first 162 waveform generator, coincidentally with the onset of the sawtooth. This pulse was tape recorded, along with the unit discharges, to facilitate data analysis. The latency from the marker pulse to the first spike includes the mechanical lag of the stimulator as well as the receptor-axon latencies.

4. Stimulating Procedures

Vibrissae units were isolated using the procedures described in Experiment 1. When a unit was encountered

that could be activated by stimulation of a vibrissa, the surrounding fur and vibrissae were stimulated to insure that these did not also activate the unit. In a few cases, the vibrissa was stimulated repetitively at 2 cycles/sec. for a few seconds. Then the following stimulating procedures were executed.

a. Experiment 2.

1) Velocity threshold determination. A modified method of limits procedure (the staircase method, Guilford, 1954) was used in Experiment 2 to determine the threshold stimulus velocity required to activate a unit (Table 1).

Table 1. Procedures used to determine velocity threshold in Experiment 2.

A. Staircase method: used if no variability of the velocity threshold occurred in 4 determinations. An example.

Number of spikes elicited by successive presentations of stimuli which vary only in deflection velocity. Amplitude and direction of deflection are constant.

↘: descending series
↗: ascending series

stimulus velocity	stimulus presentation number					
	1	2	3	4	5	6
200mm/sec.	4					
160		1		1		1
125			0		0	

Computed threshold: 142.5 mm/sec.

B. Modified staircase method: used if any variability of the velocity threshold occurred in 4 or less determinations. An example.

Number of spikes elicited by successive presentations of stimuli which vary only in deflection velocity. Amplitude and direction of deflection are constant.

stimulus velocity	stimulus presentation number 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
160 mm/sec 125 100 80 62	1 3 0 0 1 2 1 0 0 0 0 1 4 1 0 0 2 3 1 0 0 0 1

Computed threshold: $(112.5 + 90 + 90 + 112.5 + 112.5 + 90 + 90 + 90)$

$= 787.5$

$\frac{787.5}{8} = 98.6$ mm/sec.

Such a threshold was determined for all units which were not activated by the minimum stimulus velocity available with the stimulator. If a unit responded to the minimum velocity, no threshold determination was possible. The criterion for unit activation throughout the threshold determinations was the discharge of one or more spikes in response to the stimulus. If the minimum velocity did not activate the unit, the velocity was increased by successive factors of 10, to determine the general region in which the threshold lay. Then the stimulus was decreased in steps until the unit ceased to fire. Alternating ascending and descending series were run twice, If the four threshold values thus obtained were identical, the determination was halted. If any variability occurred, a more extended series was employed. In the more extended run, after the unit was activated for the first time, the velocity was increased one step further before the descending series was begun. The descending series continued one step below the point at which the unit ceased to respond, and then the ascending run began. Eight such alternating series were used to permit statistical determination of the threshold.

Whenever possible, the entire velocity threshold determination was repeated in each direction for each unit at three different deflection amplitudes, 0.8, 2 and 4 mm. Since this required a large number of trials, it was accom-

plished only when recordings could be made from a unit for a relatively long period of time. In less ideal cases, only two deflection distances were used.

2) Determination of adaptation rate. To study adaptation rate, a vibrissa was maintained in a deflected position for 10 sec. Several stimulus amplitudes were used successively in a random order for each unit. Velocity was not varied on these trials; a speed of 50 mm/sec. was always used to reach the final deflected position.

3) Determination of response to stimulus release. This parameter was not as precisely investigated as deflection velocity since only three stimulus return times were available with the stimulator (see above). Thus velocity could not be held constant over the range of stimulus amplitudes. For example, using a fixed offset time, the release velocity from a 4 mm. deflection is twice as rapid as the release from 2 mm. and five times more rapid than the return velocity from 0.8 mm. The three available offset times were used with one or more deflection distance to determine the effects of rate and amplitude of stimulus return.

b. Experiment 3.

The program of stimulus presentation in this experiment was designed to investigate the psychophysical relationship tween spike frequency and deflection amplitude or velocity. Sequences, chosen from a random numbers table, of nine

stimulus velocities were presented: 100, 50, 25, 10, 5, 2.5, 1, 0.5, and 0.25 mm/sec., all at 2 mm deflection amplitude. Randomly chosen sequences of eight available stimulus amplitudes were used: 5, 4, 3, 2.5, 2, 1.5, 1, and 0.8 mm., all at a stimulus velocity of 50 mm/sec. Three or more seconds elapsed between each stimulus presentation to prevent interaction of successive unit responses. Due to time limitation, only one velocity and one amplitude sequence was tested once for most units. In one unit, the same sequence was presented 5 times to determine the reliability of the response measure.

5. Data Analysis

Where measures of unit discharge frequency were required, it was necessary to count the number of spikes produced by each experimental manipulation. This was accomplished by playing the magnetic tape recordings into a Schmitt trigger which in turn activated an electronic counter (Hewlitt-Packard #5212A, modified for gate control). The stimulus artifact pulse served to start the counting interval; the length of the interval could be varied and was determined by the gate setting of a Tektronix 162 waveform generator. This counting procedure was highly reliable. For example, for two randomly selected units, successive counts of the same data showed the following distributions of counts in

spikes per second: 1. 118, 117, 118, 119, 118;
2. 34, 34, 34, 35, 34.

Data were analyzed using either non-parametric statistical methods (Siegel, 1956) or parametric methods (Ferguson, 1959).

CHAPTER III. RESULTS

A. EXPERIMENT 1

1. Locus of Cutaneous Receptive Fields

The receptive fields of a total of 485 isolated single units were studied from the maxillary division of the semilunar ganglion in 24 rats. The peripheral receptive field for every unit examined could be placed in one of three categories: a single vibrissa, a single small sinus hair, or a patch of common fur. Fig. 12 shows the distribution of these fields on the face and snout of the rat. Of the 485 units, 370 (76%) were activated by stimulation of one and only one vibrissa, 37 responded to stimulation of a single small sinus hair, 75 responded to underfur stimulation, and 3 units (not shown in the figure) were activated by stimulation of deeper receptors. As Fig. 12 and Table 2 indicate, the longer, more caudal vibrissae were more frequently represented in this sample than the shorter, finer rostral ones. These figures cannot be assumed to represent the entire population of units in the maxillary division since both the location of electrode punctures and methods of stimulation were designed to maximize detection of vibrissae units.

Table 2. Location on the mystacial pad of single vibrissa receptive fields.

Each square in the table designates the location of one vibrissa. The numbers within each square refer to the number of single units activated by stimulation of that vibrissa in all animals in Experiment 1. (Cf. Fig. 12). Total n = 370 units.

VIBRISSAE COLUMNS

Rostral ⟷ Caudal

VIBRISSAE ROWS: Dorsal ↕ Ventral

	8	7	6	5	4	3	2	1
V				3	13	7	11	4
W				4	12	13	22	11
X		1	6	9	11	20	26	18
Y	1	3	12	9	18	21	22	15
Z	3	2	3	8	16	15	13	18

The receptive field was always a restricted region at the periphery; never did stimulation of an extended area surrounding this region activate a unit. This was true in all animals regardless of whether or not the trigeminal root was sectioned. These results differ from those found in the cat by Darian-Smith et al. (1965) and others, who report that electrical stimulation of the area surrounding the receptive field of a unit usually activated the "trigeminal tract reflex" if the trigeminal root is intact (see Introduction).

2. Organization of Receptive Field Projections in the Ganglion

Within the maxillary division of the semilunar ganglion, the receptive fields are organized somatotopically (i.e. in a spatially systematic projection of the peripheral fields) in two planes.

Table 3. Somatotopic organization of single vibrissa projections within the semilunar ganglion.

The position of any vibrissa on the mystacial pad is specified in the table by a lettered row and a numbered column.

A. Medio-lateral organization in the ganglion as a function of vibrissae location on the mystacial pad.

Each "m" or "l" in the table refers to a medial or lateral ganglion unit, respectively, which is activated by the specified vibrissa. Number of medial units = 52; number of lateral units = 25.

VIBRISSAE COLUMNS

VIBRISSAE ROWS	7	6	5	4	3	2	1
V			mmmm	mmmmm	mm	mm	mm
W			mmm	mmmm mmm	mmm	mmmm	m
X	m	mm	mll	ml	mm	mmll	mml
Y		mm		mmmml	ml	lll	ll
Z		ml	l	l	ll	llll	lll

B. Dorso-ventral organization in the ganglion as a function of vibrissae location on the mystacial pad.

Each "d" or "v" in the table refers to a dorsal or ventral ganglion unit, respectively, which is activated by the specified vibrissa. Number of dorsal units = 30; number of ventral units = 28.

VIBRISSAE COLUMNS

VIBRISSAE ROWS	7	6	5	4	3	2	1
V					v	dd	d
W		v	d	d		dddd vv	
X		dv	vv	dv	dd	dd	ddd
Y	v	dd vv	vvv	ddd vv	dd	v	dd
Z	v	v	vv	dvvv	v	dv	dv

Table 3A compares the distribution of the peripheral receptive fields of vibrissae units in the most lateral and most medial punctures in the ganglion. Vibrissae rows V and W project more frequently to medial units in the ganglion ($\chi^2 = 36.17$, $p < .001$, $df = 1$). Similarly, the distribution of peripheral fields differs between dorsal and ventral units (Table 3B). Vibrissae columns 1, 2, and 3 project more frequently to dorsal units in the ganglion; columns 5, 6 and 7 project more frequently to ventral units

($\chi^2 = 14.46$, $p < .001$, $df = 1$). Insufficient numbers of units were recorded from caudal electrode punctures to evaluate the possibility of somatotopic organization in the rostral-caudal plane.

The medial-lateral somatotopic organization confirms the data reported by Darian-Smith et al. (1965) in cat; the dorso-ventral somatotopic projection supports the findings of Kerr and Lysak (1964) in cat and monkey.

3. Adequate Stimuli

After the peripheral field of a neuron was localized to a vibrissa, small sinus hair, or patch of common fur, more delicate forms of stimulation (see Methods) were applied.

a. Vibrissae Units

1) Response to angular deflection. Four major categories of receptive fields were defined by their responsiveness to vibrissae deflection (see Table 4). Units responded to a) deflection and release in complementary directions (see below), b) deflection and release in all four directions, c) snap release only in all four directions, or d) deflection only in one to four directions. One-half of all the vibrissae units were in the complementary class; that is, they responded to deflection of the vibrissa in one, two or three directions and to its release from deflection

in the remaining directions. Of these units, 70% responded to the deflection in two directions and to the release from the remaining two. The two directions which responded alike were always adjacent directions (e.g. rostral and dorsal or rostral and ventral, but never rostral and caudal.)

A miscellaneous category consisted of units which responded to stimulus deflection and/or release in various combinations of directions. Only two vibrissae units failed to respond to the deflection and release stimuli in any way: these responded only to pull (see below).

Table 4. Classification of 485 semilunar ganglion units in terms of type of effective peripheral stimulus.

Experiment 1, all animals combined. Number of units = "n"

	n
A. Single vibrissae units.	370
1. Angular deflection	370
a. Deflection and release in complementary directions (deflection in 1 direction, release in 3: n=30. deflection in 2 directions, release in 2: n=129. deflection in 3 directions release in 1: n = 25)	184
b. Deflection and release in all 4 directions	62
c. Snap release in all 4 directions: no deflections	38
d. Deflection only in 1 to 4 directions; no release	37
e. Deflection and release in misc. combinations of directions	47
f. No response to deflection or release	2
2. Push-pull at right angles to the skin surface	210
a. Respond to push	82
b. Respond to pull	31
c. Respond to both	17
d. Respond to neither	80
B. Single small sinus hair units	37
C. Common fur units	75
D. Deep receptor units	3

Fitzgerald (1940) has suggested that vibrissae units in cats fire optimally when a vibrissae is deflected toward the center of the mystacial pad, e.g. when dorsal vibrissae are pushed ventrally, rostral vibrissae are pushed caudally etc. Neither this nor any other relationship between location of a vibrissa on the peripheral mystacial pad and the preferred deflection direction of its unit was found in the present study of the rat. Nor was there any organization within the ganglion according to the category of response to deflection. In any quadrant of the ganglion examined, the probability of finding vibrissae units in each of the 4 major categories was similar to the probability of occurrence of that category in the entire sample of units studied.

2) Response to push-pull. Despite the large deformations of the skin resulting from push-pull stimulation as compared with the deflection stimuli, only slightly more than half the vibrissae units tested responded to push or pull and only 8% responded to both.

There was some correlation between the way a unit responded to angular deflection of its vibrissa and the way it responded to push-pull. Pushing or pulling activated a majority of the units which also responded to complementary deflection (77 responded to push-pull, 18 did not); it activated slightly less than half the units which also responded to deflection and release in all directions

(18 out of 39); twenty units that responded to snap release in 4 directions never fired to push or pull.

b. Small Sinus Hair Units

The distinction made here between the large vibrissae and the small sinus hairs at the rostral and lateral edges of the mystacial vibrissae pad was somewhat arbitrary. Sinus hairs that were so short and fine that it was more difficult to apply a controlled stimulus were placed in the small sinus hair category. However, the classification of such hair units with respect to type of adequate stimulus was similar to that of the large vibrissae units. As was found for the large vibrissae units, the category of response most frequently observed was the complementary on and off response.

c. Common Fur Units

Seventy-five units were activated by very gentle stroking of a patch of fur between and around the vibrissae. The size of the receptive field of fur units was always small, rarely over 1 mm in diameter.

d. Deep Receptor Units

Three units were activated only by relatively stronger pressure over a somewhat wider peripheral region. On this basis they were classified as having deep rather than cutaneous surface receptors. It should be noted that initial stimulating methods were such that the surface receptors

were much more likely to be activated than deep receptors, (see Methods), and therefore the sample is not representative in this respect.

e. Spontaneously Firing Units

Only 9 units were observed to discharge in the absence of a deliberately applied mechanical stimulus. The rate of this discharge was increased by vibrissae deflection in one or more directions. Upon return of the vibrissae from such a deflection, the units typically showed a brief 'silent period," followed by a gradual resumption of their spontaneous rate (Fig. 13). In 5 of the units, spontaneous firing was halted by deflection in another direction. Similar results were reported for vibrissae units of the cat by Fitzgerald (1940) and Kerr and Lysak (1964).

4. Electrical Stimulation of the Facial Nerve

The musculature which produces the normal whisking movements of the rat's vibrissae (See Introduction) is innervated by the buccal branch of the facial nerve. This nerve was stimulated to produce vibrissae movements of about the same rate and amplitude as those seen in the behaving animal. A total of 233 vibrissae units were tested for response to protraction of the mystacial vibrissae produced by electrical stimulation of this normal motor pathway. Almost half the vibrissae units responded to such active movement; in these cases, the units fired on each occurrence

of the repetitive movement. Whether or not a unit responded to active vibrissae protraction was not correlated with the nature of its response to passive vibrissa deflection. Thus units in each of the four major deflection categories were equally likely to be activated by vibrissae protraction.

For 184 of these units, a barrier was inserted successively in each of the four directions while the vibrissae were being thus repetitively protracted. Whereas about half of the units had responded to protraction without a barrier, almost 90% fired synchronously with the movement if the vibrissa struck a barrier while protracting (Table 5A). Comparable data are shown in the same table for 16 units during retraction of the vibrissae.

The barriers exerted force against an actively moving vibrissa in the same four directions in which the vibrissa had been passively deflected (see above). In about half of the units, the effective barrier directions were identical to the directions of passive deflection which produced a unit response. An additional 30% of the units responded to barriers placed in any of the four positions against the protracting or retracting vibrissae (Table 5B). The latter units did not respond to passive deflection in all directions. However, the barriers elicited more spikes in the directions which corresponded to the effective passive deflections.

Table 5. Unit activation by vibrissae movement produced by electrical stimulation of the facial nerve. Number of units = "n".

A. Number of units which responded to whisking vibrissae movements, alone and against barriers.

	Units fire to movement against 1 or more barriers		Units do not fire to movement against barrier	
	Protraction n	Retraction n	Protraction n	Retraction n
Units fire to movement, no barriers	82	3	3	3
Units do not fire to movement withour barriers	81	10	18	0
TOTALS	163	13	21	3

B. Number of units showing various relations of effective barrier directions during vibrissae protraction and retraction to the effective passive deflection directions

	n	%
Effective barrier and deflections identical	86	49
All barriers effective; not all passive deflections effective	52	30
Other relationships	38	21
TOTALS	176	100

B. EXPERIMENT 2

In this experiment, by means of the electronically-controlled tactile stimulator, the adequate stimulus for activation of vibrissae units was more precisely defined. Response parameters such as velocity threshold at different excursion amplitudes, adaptation rate and response to several rates of stimulus release were determined.

1. Classification of Units According to Adequate Stimulus

Recordings were made from 117 single neurons in 24 anesthetized rats. An additional 10 units were studied in 2 paralyzed, decerebrate animals. All of these units were activated by stimulation of one and only one vibrissa; units with other tactile receptive fields (described in Experiment 1) were encountered during this experiment but were not explored beyond the determination that they were not vibrissae units.

The response of vibrissae neurons to manual angular deflection (the same stimulus as used in Experiment 1) permitted similar categorization into four major groups plus a miscellaneous category (Table 6). The percentage of units in each of the categories was similar in the two experiments. The category types and their relative sizes were similar among units recorded from decerebrate animals as well (Table 6).

Table 6. Categories of unit response to manual deflection of vibrissae.

Number of units = "n"

	Experiment 1		Experiment 2 anesthetized		Experiment 2 decerebrate	
	n	%	n	%	n	%
Complementary directions of deflection and release	184	50	66	56	6	60
Deflection and release in all directions	62	17	27	23	3	30
Snap release only	38	10	9	8	1	10
Deflection only	37	10	6	5	0	0
Misc.: includes various direction specific responses to deflection and release	49	13	9	8	0	0
TOTALS (n)	370		117		10	

Thirty-four of the 117 units were recorded from animals with the trigeminal root sectioned. No differences in localization of receptive field or in categories of response to angular deflection were seen in these units, compared with those recorded with the root intact. Therefore the data are combined in the following results.

As in Experiment 1, stimulation in the region surrounding a vibrissa was never an adequate stimulus for activation of the units responding to that vibrissa. This remained true in the anesthetized animals with the root intact or sectioned as well as in decerebrate animals with the root intact.

A somewhat revised classification of unit responses to deflection was required because the mechanical stimulator permitted much more rapid vibrissae deflection speeds than had been possible manually. With a manual stimulus, many units did not respond at all to deflection in a given direction but fired only to release from the deflected position. Use of rapid stimulator velocities revealed that most such units would indeed fire to deflection in these directions <u>if</u> the velocity were great enough. Thus the difference between "on" directions and "off" directions was not an absolute difference, but rather depended on <u>velocity threshold</u> differences. The new classification did not alter which units were categorized together, but rather required that the names of the categories be changed. The revised nomenclature is based on the minimal vibrissae deflection velocity which was sufficient to activate the units in each category. The succeeding sections, which present the velocity threshold results, will explain the reasons for remaining each category. The revisions of the terminology are shown in Table 7.

Table 7. Reclassification of units "in Experiment 2", according to differences in velocity threshold.

Classification with manual vibrissae stimulus. (Experiment 1)	Classification with electronically-controlled vibrissae stimulus. (Experiment 2)
Complementary units, "on" direction	Low velocity threshold complementary units (LVT-comp)
Complementary units, "off" direction	High velocity threshold complementary units (HVT-comp)
Deflection and release, in all directions	Moderate velocity threshold units (MVT)
Snap release only, in all directions	High velocity threshold units (HVT)
Deflection only, in all directions	Low velocity threshold units (LVT)

In subsequent analyses, the number of observations reported is usually based on the number of deflection directions rather than the number of units studied. This was necessary because thresholds and other parameters of response were determined separately for more than one direction of deflection for most units; the responses to each direction are considered separately. The letter "N" will refer to the number of unit-directions under consideration on a given topic; "n" will denote the number of units.

2. Response to Vibrissae Deflection: Absolute Velocity Threshold in Anesthetized Animals

a. Preliminary Considerations

Before presenting the threshold values that were obtained in each category, it is necessary to consider further certain limiting capacities of the mechanical stimulator. Because the minimum stimulus rise time was a fixed quantity (10 msec.), the maximum possible velocity varied at each deflection amplitude. At 4 mm. deflection, the maximum was 400 mm/sec.; at 2 mm., it was 200mm/sec.; and at 0.8 mm., it was 80 mm/sec. (Fig. 14). When a unit was not activated by the maximum velocity available at a given amplitude, the threshold was designated simply "greater than maximum." Clearly this designation was assigned more frequently at the lower amplitudes, since the maximum was lower. In order to determine whether an interaction between stimulus amplitude and velocity occurred, it was necessary to select for comparison just those unit-directions at the larger amplitude such that a less than maximal velocity threshold would be expected at the smaller excursion amplitude. For example, the units which have a threshold less than 200 mm/sec. with a 4 mm. deflection may be compared with any observation at 2 mm. deflection. If the threshold at 4 mm. is over 200 mm/sec., only the qualitative threshold designation "greater than maximum" would be expected for

the corresponding unit-direction at 2 mm. Likewise, the units with thresholds less than 80 mm/sec. at 2 mm. may legimately be compared with any unit at 0.8 mm. deflection. (Fig. 14). These comparisons will then permit evaluation of possible interactions between velocity threshold and excursion amplitude (see below).

Since the maximum rise time was also a fixed quantity (10 sec.), the slowest velocities should also vary as a function of stimulus amplitude. However, when very slow velocities were used at small amplitudes, the mechanical stimulator was somewhat unreliable. Therefore it was decided to use a minimum stimulus velocity of 5. mm/sec. for all stimulus amplitudes, from 0.8 to 5 mm.

b. Stimulus Presentation Procedures

The velocity thresholds were determined about equally often by the staircase method of limits (see Methods), signifying no variation in threshold occurred (N, number of unit-directions, = 125) and the modified staircase method (that is, in which threshold variation did occur, N = 116). When velocity threshold variation did occur, it was seldom very great. Thresholds on all ascending and descending runs for a given direction of a unit were usually within two velocity steps of one another and almost always within three steps.

No variation occurred in about half the threshold determinations; this implies that the order of stimulus presentation was not an important variable, since for these units

ascending and descending runs produced the same results. For units in which variation did occur, a sign test was used to compare the means of the ascending and descending thresholds for each unit. No significant difference was seen as a function of the order of stimulus presentation ($p < .05$, 2-tailed test).

c. Low Velocity Threshold (LVT-comp) and High Velocity Threshold (HVT-comp)Complementary Units.

It was usually impossible to establish precise thresholds for the LVT-comp units (see example in Fig. 15A), since they were almost always activated by the minimal stimulus velocity employed, 0.5 mm/sec. (Table 8).

A sign test performed on HVT-comp units (see example in Fig. 15B) indicated that there was no significant difference between the velocity thresholds at 0.8 and 2 mm., but a trend was revealed indicating a somewhat higher velocity threshold at 0.8 mm. deflection ($p = .144$, 2-tailed test). This comparison was made as described above in section a. Although 79 unit-directions were tested for threshold responses at both 0.8 and 2 mm., only 19 of these had a threshold $\leq$ 80 mm/sec. with the 2 mm. excursion. The sign test just described compared these 19 thresholds at 2 mm. with paired observations at 0.8 mm.

Similarly, a sign test performed on paired observations at 2 and 4 mm. showed that there was no significant difference

between the velocity thresholds at these two amplitudes ($p = .718$, 2-tailed test). This result was based on 35 unit-directions for which the threshold at 4 mm. was 200 mm/sec., and thus for which a threshold of less than maximal velocity at 2 mm. (200 mm/sec.) would be expected.

Since the 2 and 4 mm. thresholds did not differ, these values were combined in the calculation of a median velocity threshold. Because of the tendency for the 0.8 mm. velocity threshold to be higher than that at the other amplitudes (and thus suggesting a velocity - amplitude interaction), the 0.8 thresholds were not included in the computation of the median. The overall median for 79 unit-directions was calculated by including the 4 mm. velocity threshold whenever it was available; when no determination had been made at 4 mm., the 2 mm. threshold value was used. Such an interdigitation of the 2 and 4 mm. velocity thresholds provided a more precise estimate than the 2 mm. values alone, since at 2 mm., quantitative velocity thresholds above 200mm/sec. were not obtainable. It was also more precise than the 4 mm. velocity threshold alone, since the number of unit-directions tested at this amplitude was smaller.

The median value for the 79 interdigitated velocity thresholds was 158 mm/sec (Table 8). Thus the nomenclature used at the beginning of this section for complementary units is elucidated. In the low threshold directions, these units are almost invariably activated at the minimal velocity available of .5 mm/sec. In the high threshold directions,

Table 8. Absolute velocity thresholds in response to vibrissae deflection
Number of units = "n"; Number of unit-directions = "N".

Category of unit	Stimulus Amplitude (mm.)	THRESHOLD VALUES ANESTHETIZED ANIMALS Total n	Total N	Median Threshold	% N less than min. (.5 mm/sec)	THRESHOLD VALUES UNANESTHETIZED, DECEREBRATES Total n	Total N	Median Threshold	% N less than min. (.5 mm/sec)
LVT-comp	0.8	64	121	< min	95%	6	12	< min	100%
	2	66	126	< min	99	6	12	< min	100
	4	52	90	< min	100	5	10	< min	100
LVT	0.8	5	19	< min	100	0			
	2	5	19	< min	100	0			
	4	4	19	< min	100	0			
MVT	0.8	30	107	< min	63	3	12	< min	75
	2	30	107	< min	84	3	12	< min	83
	4	23	82	< min	94	3	12	< min	100

Category of unit	Stimulus Amplitude (mm.)	THRESHOLD VALUES ANESTHETIZED ANIMALS Total n	Total N	Median Threshold	N greater than max. (400mm/sec)	THRESHOLD VALUES UNANESTHETIZED, DECEREBRATES Total n	Total N	Median Threshold	N greater than max. (400mm/sec)
HVT-comp	2 or 4	43	79	158mm/sec	11	6	10	148mm/sec	1
HVT	2 or 4	10	35	130mm/sec	1	1	4	119mm/sec	0

the median velocity threshold is 158 mm/sec., a value which includes 11 unit-directions which failed to respond even at 400mm/sec.

d. Moderate Velocity Threshold (MVT) Units

Units in this category responded in a similar way to deflection stimulation in all directions. Whereas a majority of units had velocity thresholds below the minimal stimulus velocity (0.5 mm/sec.), a substantial number responded only to a supraminimal stimulus (Table 8). Thus this category is designated MVT units (see example in Fig. 15C). The median threshold value at each amplitude lies below the minimum available velocity. A significant interaction between velocity threshold and amplitude of excursion was found. Comparison of the numbers of less than minimal and greater than minimal velocity thresholds at 0.8 and 2 mm. showed that a higher proportion of the 2.0 mm. thresholds were less than minimum ($\chi^2 = 12.65$, $p < .001$, $df = 1$). Similarly a higher proportion of velocity thresholds were less than minimum at 4 mm. as compared with those at 2 mm. ($\chi^2 = 4.33$, $p < .05$, $df = 1$). Thus, unlike the complementary units, velocity-amplitude interactions exist for MVT units at higher as well as lower stimulus amplitudes.

e. High Velocity Threshold (HVT) Units

Like the MVT units, and unlike the HVT - comp ones,

the units in this category responded to deflection in all directions. In other respects, however, they closely resembled the HVT-comp units, particularly in that they did not respond to deflection unless the velocity was high (see example in Fig. 15D).

A sign test revealed that although no significant difference existed between the velocity thresholds at 0.8 and 2 mm. in 12 pairs of unit-directions, a trend existed for the 0.8 velocity threshold to be higher ($p = .146$, 2-tailed test). Eight pairs of unit directions at 2 and 4 mm. showed no significant difference in threshold ($p = .726$, 2-tailed test). These results closely parallel those obtained in HVT-comp units.

The median of 35 interdigitated threshold values at 2 and 4 mm. show that the median velocity threshold for these unit-directions was 130 mm/sec. (Table 8).

f. Low Velocity Threshold (LVT) Units. The five units in this category were activated by vibrissae deflection at the minimal velocity (0.5 mm/sec.) at all stimulus amplitudes and in all deflection directions (Table 8).

g. Summary of Velocity Threshold Results

The results presented in the preceeding sections suggest that LVT and HVT units closely resemble LVT-comp and HVT-comp units respectively, except that the latter are direction-

sensitive while the former do not respond differentially to vibrissae deflection in different directions. MVT units are similar to LVT and HVT units in that they respond to all directions of vibrissae deflection but with velocity thresholds intermediate between the other categories. The categories defined with the manual stimulus in Experiment 1 reflected the directional properties, but did not reveal the important differences in velocity thresholds among the categories. Succeeding sections of Experiment 2 present additional response properties in the five categories of units which define and describe each category more completely.

3. Velocity Thresholds in Unanesthetized, Decerebrate Animals

The velocity thresholds in unanesthetized, decerebrate animals (Table 8) are categorized similarly to those obtained in anesthetized subjects. LVT-comp units respond to the available velocity and thus no determination of the threshold can be made. HVT-comp and HVT units have high median thresholds, quite similar to those in the larger sample of units recorded from anesthetized animals. In the MVT category, most units have a threshold which lies below the minimal .5mm/sec., but a few have thresholds above this velocity. This result also resembles that seen in the animals under barbiturate anesthetic.

4. Correlation Among Velocity Thresholds in Several Directions for Individual Units

Velocity thresholds were usually obtained for more than one direction of deflection for a given unit. Are the several velocity thresholds compared among the different deflection directions in an individual unit more similar than thresholds compared across units of the same category?

It is not possible to answer this question for the LVT-comp and LVT categories, since virtually all these unit-directions were activated by the minimal velocity available with the stimulating apparatus, and thus no threshold could be delimited. Similarly for MVT units, at 2 and 4 mm. deflection, a large majority of units had thresholds below the minimal velocity. At 0.8 mm., however, over one-third of the units had thresholds which lay above the minimum velocity. A binomial probability expansion was used to test whether or not the distribution was the same, of less than minimal and supraminimal thresholds, in each of 26 units in which threshold values had been determined in four directions at 0.8 mm. The results indicated that the less than, and greater than, minimal thresholds were not distributed randomly among the units ($\chi^2 = 56.54$ $p < .001$ $df = 1$). This would suggest that the thresholds obtained for an individual unit are correlated with one another. Such correlation was further substantiated by 4 of the 26 units

which had quantitative threshold values in all four deflection directions. A Kendall coefficient of concordance of ranks for these units indicated that the velocity threshold values in the four directions for an individual unit were related to each other ($W = .925$, $\chi^2 = 11.1$, $p < .02$, $df = 3$).

A similar analysis was carried out for HVT units. Five units at 2 mm. deflection had quantitative thresholds in all four directions. The Kendall coefficient showed that the velocity thresholds in the four directions of an individual unit were positive correlated ($W = .8375$, $\chi^2 = 13.4$, $p < .01$, $df = 4$).

Among the HVT-comp units, data was usually obtained for two directions of a unit (the other two directions being, of course, LVT-comp). Many of the thresholds lay above the maximum velocity available (see Fig. 14); thus quantitative correlations of the two directions could not be carried out. To obtain a description of within-unit variance as compared to the variance of all the units as a group, the thresholds were divided into 5 arbitrary intervals. (Thresholds greater than the maximum velocity were included in the fifth interval.) The interval variance was computed for each pair of unit-directions as well as for all unit-directions together. For 35 units at 2mm. deflection amplitude, the within-unit variance was 2.4 intervals and the between-unit variance was 2.2. For 22 units at 4 mm., the within-unit variance and the

between-unit variance were both 2.3. Although such a categorization into five intervals permits only a rough description of the data, it is apparent that no strict correlation occurs among the two directions of HVT-comp units.

Thus, for MVT and HVT units, in which thresholds can be compared in an individual unit in response to four directions of deflection, the thresholds are positively correlated within each unit. For HVT-comp units, in which only two directions are comparable, there does not appear to be such a relationship.

5. Unit Responsiveness to Suprathreshold Stimuli

The number of spikes elicited by a suprathreshold deflection of the vibrissae varied markedly among the categories of units. (see Fig. 15 A-D.) The numbers of spikes obtained for units in each category are not strictly comparable since the velocities of the test stimuli were not the same amount above the threshold for each unit. They were of necessity closer to the velocity thresholds in some categories than in others. However, large differences between the categories are apparent.

Table 9. Number of spike discharges in three categories of units at three deflection amplitudes. Number of unit-directions = "N".

	Stimulus Amplitude (mm.)	Average number of spikes in first sec.
LVT and LVT-comp units. test velocity=50 mm/sec. N= 40 at each amplitude	0.8	42
	2	79
	4	97
MVT units. test velocity=50 mm/sec. N=14 at each amplitude	0.8	6
	2	11
	4	21

LVT and LVT-comp units fired many more spikes than units in any other category (Table 9). The number of spikes increased monotonically as a function of deflection amplitude for 33 of the 39 unit-directions included in the table (see Experiment 3 for further discussion of this point).

The number of spikes recorded from units in the MVT category was considerably less than in the low velocity threshold categories. However, number of spikes was again a monotonic function of stimulus amplitude, for 11 of the 14 units contributing to the means shown in Table 9.

At maximal stimulator velocities, the MVT and MVT-comp units typically produced only a few spikes. Most of these units were not activated at all by the 50 mm/sec. test stimulus used above for LVT, LVT-comp and MVT units. At velocities near threshold, which was often near the

maximal capacities of the stimulating apparatus, these units usually fired about three to six spikes.

6. Adaptation Rate

Adaptation rate to a sustained stimulus also varied among the categories of unit response type and, within some categories, according to deflection amplitude (Table 10).

The HVT and HVT-comp units were all very fast adapting; that is, the impulse discharge did not outlast the stimulus onset time even though the vibrissa remained in the deflected position. (Stimulus onset time refers to the period of time from the initiation of the stimulus to the attainment of the final deflected position. Stimulus duration denotes both the onset time and the length of time the probe remains in the deflected position.)

The MVT units adapted to the stimulus somewhat more slowly but were still rapidly-adapting units. At all spike amplitudes, impulse discharge slightly outlasted stimulus onset time. (With a deflection velocity of 50 mm/sec., at amplitudes from 0.8 to 4 mm., onset time varied from 16 to 80 msec.) However, almost all the units had ceased firing within 60 msec. after the stimulator reached its steady-state deflected position.

Table 10. Adaptation rate as a function of time and stimulus amplitude in LVT-comp units.

Number of unit-directions = 39 at each deflection amplitude.

A. Average number of spikes per second in successive time periods at three stimulus amplitudes.

Stimulus Amplitude (mm)	Spikes/sec. during: sec. 1	sec. 2-5	sec. 6-10
0.8	40	12	6
2	78	34	29
4	95	44	34

B. Average spikes per second in later time intervals expressed as percentages of the average number in sec. 1. Such transformation of the data permits comparisons of adaptation rates at all stimulus amplitudes, independently of the absolute number of spikes at each amplitude.

Stimulus Amplitude (mm)	Average spikes/sec. expressed as % of the average during the first second. sec. 1	sec. 2-5	sec. 6-10
0.8	100	30	15
2	100	44	37
4	100	46	38

The adaptation rate for LVT and LVT-comp units varied as a function of stimulus amplitude. However, even at the smallest amplitude, these units usually responded for a longer period of time than the MVT units. In order to

evaluate adaptation rate independently of the absolute number of spikes at each amplitude (since number of spikes was also a function of amplitude, see above), it was necessary to express the data for each time interval as a percentage of the maximum response at that amplitude. Tables 10A and B show the data before and after conversion to percentage scores. It is evident that the rate of impulse discharge decreases as a function of time at all stimulus amplitudes; however, the rate declines more rapidly with 0.8 mm. deflection amplitude than with 2 or 4 mm. deflection.

The average percentage data were ranked, with the most-rapidly adapting amplitude (lowest percentage) within each unit direction assigned rank 1 and the most slowly-adapting unit assigned rank 3. Comparison of the ranks revealed that unit discharge adapted significantly more slowly at 2 mm. than at 0.8 mm. deflection (^{2} = 84.8, p .001, df = 2). In addition, adaptation occurred significantly more slowly at 4 mm. than at 2 mm. (^{2} = 6.96, p .05, df = 2).

7. Responses to Release of the Deflection Stimulus

Among the five categories of units which have been defined, responses to release of the deflection stimulus occurred in units of the MVT, HVT, and HVT-comp categories but rarely in the LVT or LVT-comp categories. This result is similar to the classification developed in Experiment 1 using a manual vibrissae stimulus. Thus, the threshold for the

release discharge varied among the three categories in which release responses occurred.

In evaluating the release threshold, it was often impossible to differentiate between thresholds that were dependent on release rate or on release distance. Since only three offset times were available, a constant velocity could not be maintained when amplitude was varied (see Methods). Thus the two parameters varied dependently and their effects cannot be distinguished. However, a qualitative evaluation of the release threshold can be achieved by rating the responses as follows:

a) Low release response thresholds: units respond to release at all distances and velocities available with the present stimulator.

b) Medium release response thresholds: units respond at all velocities to some but not all stimulus amplitudes and

c) High release response thresholds: units do not respond to all three release velocities at any stimulus amplitude.

These ratings can be considered to form an ordinal scale of thresholds, with the first having the lowest, and the third the highest, threshold in response to release of the deflection stimuli.

Table 11. Relationship between release and deflection threshold responsiveness.

The numbers in the table represent the number of unit-directions, "N", which manifested the combination of deflection and release characteristics specified by the row and column subheadings.

	Category of response to release		
Category of response to deflection	Response occurs at all deflection amplitudes and velocities (low)	Response occurs at all velocities for some but not all amplitudes (medium)	Response does not occur at all velocities for any amplitude (high)
HVT-comp units N = 52	18	26	8
MVT units, N = 45	25	18	3
HVT units N = 27	1	4	22

The data in Table 11 indicate that the nature of the response to release of the stimulus is not independent of a unit's response to defelction of the vibrissa. Thus, HVT units had a significantly higher threshold to stimulus release than did HVT-comp units ($\chi^2 = 34.5$, $p < .001$, $df = 2$). Thus the term "snap release" used to describe these units in Experiment 1 is borne out with the stimulator; the reslease

response must be rapid to activate these units. MVT-comp units tended to have a higher release threshold than the MVT units ($\chi^2 = 5.61$, $p < .1$, df = 2; for significance at .05 level. $\chi^2 = 5.99$ is required).

In addition to the threshold for occurrence of the response to stimulus release, the number of spikes in the release discharge was also often a function of amplitude and rate of stimulus release. This relationship was not studied systematically; however an example of a unit which discharged increasing numbers of spikes as release rate was increased (at a given amplitude) is shown in Fig. 15E.

8. Summary of Response Characteristics in Each Category of Unit

The data in the preceding sections indicates that every category of unit responses has a number of characteristic features which, taken as a group, distinguish each category from all others. The salient features of each category are as follows (see also Table 12):

1) Low velocity threshold, high frequency, slowly-adapting discharge; unresponsive to stimulus release.
   a. Direction-sensitive units: showed the above response in one, two or three directions and a high threshold response in the complementary directions (LVT-comp units)
   b. Non-direction sensitive: showed this response in all directions (LVT unit).

2) High velocity threshold, low frequency, very rapidly-adapting discharge; responds to rapid stimulus release.

   a. Direction-sensitive units: showed the above response in complementary directions to the low threshold response (HVT-comp units).

   b. Non-direction sensitive: showed this response in all directions (HVT units).

3) Moderate velocity threshold, moderate frequency, rapidly-adapting discharge; responds to stimulus release; no direction sensitivity (MVT units).

Table 12. Summary of major characteristics of each category of unit response type. For detailed descriptions of these response characteristics see preceding sections 1, 2, 5, 6 and 7.

Category of unit	% of total	Direction specificity	Velocity threshold	Adaptation rate	Relative # of Spikes	Release response
LVT-comp	56	yes	low	relatively slow	many	seldom
LVT	5	no				
MVT	23	no	moderate	relatively rapid	moderate	moderate threshold
HVT-comp	56	yes	high	very rapid	few	higher threshold
HVT	8	no				highest threshold

9. Spontaneously Firing Units

Each of 23 units which fired in the absence of an externally-applied mechanical stimulus was also activated by stimulation of one vibrissa. The categories of response to such external activation were similar to the deflection categories established for units which did not fire spontaneously (Table 13).

Table 13. Spontaneously firing units: number of occurrences and categorization of response patterns.

Number of units = "n".

A. Number of occurrences of spontaneously firing units in two subject groups.

Subject groups	Spontaneously firing units n	Spontaneously firing units % of total n
Anesthetized animals	23	20% of 117
Unanesthetized, decerebrate animals	0	0% of 10

B. Number of occurrences of unit response pattern categories in spontaneously firing units

Response pattern category	n
Complementary units	16
MVT units	3
HVT units	0
LVT units	1
Misc. units	3
TOTAL	23

In the 16 comp. units, spike frequency was increased by deflection in the LVT directions; firing temporarily ceased after stimulus release (the "silent" period), and then gradually resumed its spontaneous rate (Fig. 13) In addition to systematic increases above the spontaneous rate of firing, the spontaneous activity could be decreased or eliminated in 13 of the 16 comp. units, by deflection in the opposite or HVT directions. Upon release from deflection in this direction, the units fired a release response and then resumed the spontaneous rate of discharge.

In a few units, although the rate of discharge could be increased by deflection in some directions, no systematic decreases in the spontaneous activity were seen. In these units, the spontaneous rate was sporadic rather than regular. It is possible that such sporadic firing could be attributed to occasional muscle twitches producing slight movements of the vibrissae that were imperceptible to the observer. If this were the case, no systematic response decreases would be expected. None of the units in the decerebrate animals exhibited spontaneous activity (Table 13). The impression was also gained that the small, spontaneous background activity, of units never sufficiently isolated to be included in the sample, was less in the decerebrate animals than in the anesthetized ones. Since these animals were paralyzed, no muscle twitches could occur in this preparation.

The percentage of spontaneously firing units in animals with the trigeminal root sectioned (18%) did not differ from that in animals with the root intact (20%). Thus the spontaneous activity cannot be attributed to antidromic activation of the units.

10. The Trigeminal Tract Reflex

No evidence for the relatively long latency, repetitive trigeminal tract reflex, described in the cat by Darian-Smith (1965) and others (see Introduction), was found in these experiments. As discussed previously, no unit was activated by stimulation of the area surrounding the main receptive field of a unit. Although response latencies were not measured, the following evidence is not consistent with the existence of early orthodromic and later antidromic impulses, as described for the tract reflex.

a) The pattern of the spike discharge sometimes varied within the same unit in response to the same stimulus (Fig. 16A). If the later spikes are not consistently temporally-separated from the earlier ones, it seems less likely that they have an antidromic origin.

b) Occasionally a short latency spike followed by a longer latency burst was seen in units where any antidromic impulses had been prevented by section of the trigeminal root (Fig. 16B). Thus, longer latency is not a certain indicator of antidromic origin of a discharge.

c) The pattern of short latency, long latency spikes could be maintained during repetitive stimulation of the vibrissae at 2/sec (Fig. 16 C), although the antidromic spikes of the tract reflex are much less probable at repetition rates of 2/sec. or more (Darian-Smith, 1965). Thus these long latency spikes may not be of antidromic origin.
d) In most units, two temporally-separated bursts of spikes did not occur (examples in Fig. 16 D). The events described in a, b and c above were seen less commonly than a continuous discharge of unit impulses.

11. The "Position" Effect

Because simple deflection of the vibrissae very consistently activated vibrissae units, it was the stimulus used throughout these experiments. For some units, however, a slight difference in the position of the stimulating probe used to deflect the vibrissa altered the unit's response pattern. For example, with the probe situated 6 mm. from the base of a vibrissa, a unit might exhibit a slowly-adapting response to deflection and release; with the probe positioned 3 mm. from the base, a more rapidly-adapting deflection response and a release response would occur. It was never possible to reproduce a rapid "on" and "off" pattern for these units with a manual stimulus. A total of 20 complementary units showed this "position" effect (out of n= 66).

Figure 17 illustrated the behavior of such a unit,

whose response pattern changed according to the position of the stimulating probe. Responses to stimulation are shown with the tip of the probe located successively at 5 mm. (A), 4 mm. (B) and 3 mm. (C) from the base of the vibrissa. The unit fired fewer and fewer spikes although the only variable aspect of the stimulus was the position of the probe on the vibrissa. The vibrissa was then cut from its former length of 10 mm. to 7 mm. in length. The tip of the stimulator probe was then positioned 3 mm. from the base (the same stimulus position as in C, above). The unit now exhibited a slowly-adapting response (D). When the probe was moved to 2 mm. from the base, the rapidly-adapting response again occurred (Fig. 17E). The vibrissa was cut again, this time to a total length of 4 mm. Now with the probe positioned 2 mm. from the base (as in E, above), the unit produced a slowly-adapting, rather than a rapidly-adapting, response. Whenever the unit adapted rapidly, it responded to stimulus release (not shown) as well as deflection. The successive vibrissae cutting procedure produced similar results on three units for which it was tried.

Thus, for these units, distance of the probe from the base of the vibrissa was not a crucial determinant of firing pattern, but rather relative distance of the probe from the cut tip of the vibrissa was critical, with all other stimulus

parmeters held constant. Since the receptor is located intradermally at the base of the vibrissa, it is difficult to explain this finding if deflection alone is the adequate stimulus. It seems probable that a slight bending of the hair within the follicle is required in addition to linear deflection for these units. When the probe is positioned far from the tip of a vibrissa, a large part of the hair is enclosed within the probe, and the vibrissa is held rigidly as it moves. With the probe nearer the vibrissa tip, only a small part of the vibrissa is encased within it, and a slight bending of the hair can occur. This permits optimum activation of some units. It is assumed that the manual stimulus always permitted a slight bending, since the hand-held probe never maintained the vibrissa completely rigid. The vibrissae are deflected and bent when they contact an object as the rat explores its environment. The position effect found here may indicate that this deflection and bending may produce the most effective stimulus for some vibrissae units.

C. EXPERIMENT 3

To study psychophysical relationships in primary vibrissae afferents (cf. Introduction), the relationship of stimulus input (deflection amplitude or velocity) to

neural discharge frequency was determined for 18 units. Fourteen of the units were studied in animals under barbiturate anesthesia and 4 in paralyzed, decerebrate animals. No differences between the two groups were observed in these small samples (see below), and the data are combined in the following results.

1. Stimulus Amplitude

Figures 18-22 show the influence of different stimulus amplitudes in determining neural response frequency, expressed in spike discharges per second. Part A of each figure describes the untransformed arithmetic function. Part B is the semi-log transformation; a straight line function is predicted on these coordinates by the Fechner psychophysical equation ($R = \log S + a$). Part C, the double logarithmic transformation, is predicted to be a straight line function by Stevens' power law ($R = kS^n$ or $\log R = n \log S + \log k$).

It would appear from the data shown in these graphs, and the correlation coefficients of the data to the best-fitting straight lines, that the S-R relationship is described equally well by all three functions. The similarity of the correlation coefficients for each of the arithmetic, semi-log or log-log transformations implies that the range of stimulus values was too small to permit adequate differentiation among the functions. It is evident that response frequency is a monotonically-increasing function of stimulus

amplitude, but a more precise statement of the relationship is impossible without employing a wider range of stimuli. Responses of a unit to a series of deflection amplitudes are shown in Fig. 23.

As stated above, this measure of neural responsiveness did not differ in the decerebrate and anesthetized animals. For LVT-comp units at 1 sec. observation time (Fig. 19), there were 9 unit-directions in anesthetized animals and 6 in decerebrate animals. No significant difference was found when the Mann-Whitney U test was used to compare the correlation coefficient of the best-fitting-straight line for each group (in log-log coordinates) ($U = 29$; critical U for $p = .1$ is 12).

The slopes of the functions for LVT-comp units (Fig. 18-21) become steeper as successively longer time intervals are counted. This is attributable to the fact that adaptation rate, which plays an increasingly important role as time is increased, is also a monotonic function of stimulus amplitude (see Experiment 2). Presumably if only steady state firing were observed, the slopes would be more similar for the different counting intervals. The shorter observation times have slopes less than 1, which is in accord with the values obtained in other experiments on first order and thalamic lemniscal afferents (Mountcastle et al., 1963; Werner and Mountcastle, 1965).

2. Stimulus Velocity

In determining the influence of deflection velocity on the frequency of spike discharge (Fig. 24 and 25), the stimulus range employed was considerably wider (2.6 log units as compared to .8 log units for the stimulus amplitude range). The relationship between velocity and impulse frequency is much better described by a power function (log-log transformation, Graph C) than by straight lines in either the arithmetic or semi-log coordinates.

The data on stimulus velocity pertain to discharge frequency during the transient period of stimulus onset only. Mountcastle et al. (1963) observed that although the transient frequency might be correlated with stimulus velocity, the steady state frequency in their study was not. Steady state data would have to be obtained to determine whether the power [illegible] relationship between velocity and neural discharge seen in the present experiment was limited to the period of stimulus onset.

3. Limiting Considerations

The data presented in Figures 18-22 and 24-25, for both deflection amplitude and velocity, are based on the arithmetic averages of the responses of a number of units. Correlation coefficients for the best-fitting straight lines of data based on single units are somewhat variable, with some units describing functions very similar to the averaged curves and others showing less orderly relationships. There are several probable explanations for this variability

of goodness-of-fit among unit responses as compared with the extremely good fits of individual unit responses described by Mountcastle and his associates. One major factor is that, due to limitations of time and the lack of automatic programming equipment, each stimulus amplitude or velocity was used only once in the present study. Twenty to fifty random presentations of each stimulus were averaged in the Mountcastle studies. The plot for individual units the latter experiments was an average of the values at each stimulus magnitude. Five repetitive trials, in the same random sequence, were run for one unit in the present experiments; the correlation coefficient of the averages of the 5 trials with the best-fitting regression line in log-log coordinates was .985 for stimulus amplitude and .991 for stimulus velocity.

A second factor likely to have increased deviations from the best-fitting line was the failure to record exclusively the steady state condition. Rapid transient firing during stimulus onset affects the frequencies recorded in the shorter counting intervals. In addition, the confounding variable of adaptation rate (see above) influenced frequency differentially at different stimulus amplitudes; the consistently low frequency at the minimum stimulus amplitude is probably attributable to the relatively rapid adaptation which occurs at this amplitude.

CHAPTER IV. DISCUSSION

A. Coding in First Order Vibrissae Afferents

The results of these experiments indicate that first order neurons of the trigeminal system, taken as a group, encode many parameters of the mechanical stimuli delivered to the vibrissae and face of the rat. Specificity of locus of peripheral stimulation is achieved by differential activation of some neurons and not others. That is, each neuron responds to stimulation of a single vibrissa, a small sinus hair, or a small patch of common fur. Such a topographical coding system appears to be typical for metathetic (or extensive) continua, both in other parts of primary somatic sensory system and in other primary sensory systems. In neurons which responded to stimulation of a single vibrissa, the spike discharge pattern coded many aspects of the stimulus in addition to peripheral locus. Thus variations of at least six other parameters of vibrissae deflection (onset, direction, velocity, amplitude, duration and offset) were capable of activating different response patterns. Because of the strict correlation among the features of each stimulus-response pattern, observing the response of a neuron to one or two of these parameters permitted an almost certain prediction as to its responses to the other variables.

These consistent constellations of stimulus-response

relationships in different vibrissae unit categories were striking features of all the experimental results. This categorization suggests that multiple receptor ending locations and/or types may account for these features in the response of the first order neurons. It is known that a single vibrissa is supplied with numerous receptor endings; Vincent (1913) found as many as 150 neurons per vibrissa follicle. However, anatomical investigations reveal such a tangled mass of arborizations about the hair follicle that it is difficult to ascertain whether the peripheral axon of a single ganglion cell actually terminates in some restricted or specific way within the sinus hair capsule as the present data suggest. The present results do show that a particular type of stimulus to a single vibrissa is capable of activating a number of units each of which exhibits a different response pattern category, thus permitting many aspects of a stimulus to a given vibrissa to be transmitted centrally. For example, if a stimulus to one vibrissa in one direction activated both HVT rapidly-adapting receptors and LVT slowly-adapting endings, the stimulus will be coded in the first order units for both onset and steady state conditions. Although relatively few neurons were studied in each animal in the present experiments, it was not uncommon to find several units, each responding to a different type of stimulation to one vibrissa in a single animal. Such units would have different response pattern characteristics. It is possible

that some of the fibers entering a vibrissa follicle are collaterals of a single semilunar ganglion cell.

Two previous studies have examined smaller samples of first order neurons supplying the vibrissae in cat and monkey. (Fitzgerald, 1940; Kerr and Lysak, 1964). Although neither of these species possesses the whisking vibrissae seen in the rat, many of the findings in the present experiments on the rat are in agreement with these earlier studies. For example, most units showed directional sensitivity. Kerr and Lysak reported that unit discharge often occurred in response to stimulation in two adjacent directions and not in the other two. This is a similar result as that obtained in the present study when comparable procedures were used to explore complementary units. Fitzgerald claimed that the optimum direction of stimulation was toward the center of the mystacial pad, but neither the results of Kerr and Lysak nor the present data are in agreement with this observation.

Neither previous study appears to have employed stimuli sufficiently rapid to activate the high velocity threshold units, although Kerr and Lysak noticed one unit which responded only to rapid release of the vibrissa stimulus. Both earlier studies found that the majority of units were slowly-adapting and a few fast adapting. Kerr and Lysak stated that slowly adapting units in the cat were more likely to be direction-sensitive; the present data on the rat are similar in that

respect. The finding that many vibrissae units are slowly adapting is in marked contrast to the results of other studies of first order spinal and trigeminal afferents which respond to common hair stimulation almost exclusively by a rapidly-adapting discharge (Hunt and McIntyre, 1960; Kerr and Lysak, 1964). However, both slowly-adapting and rapidly-adapting common hair units have been found in trigeminal primary afferents in the coatimundi and raccoon. (W. I. Welker, personal communication).

B. Coding in Higher Order Vibrissae Afferents

A number of studies have investigated the characteristics of second order vibrissae neurons in the trigeminal brainstem complex of the cat (Gordon et al., 1961; Kruger and Michel, 1962, a, b; Eisenman et al., 1963, 1964). Kruger and Michel (1962 b) observed that the vibrissae are by far the most extensively represented structures in the trigeminal complex. They found that most units responded to stimulation of a single vibrissa; however, other authors observed a smaller percentage of neurons with such restricted fields. For example, Eisenman et al. (1963) found that the extent of the peripheral receptive field varied with the location of the neuron in the nuclei. About half the neurons in the main sensory nucleus responded to one vibrissa, but only 1 out of 13 in nucleus oralis was similarly restricted. Gordon et al. (1961) reported that in the fibers lateral

to the spinal nucleus, 14 out of 20 units were activated by one vibrissa only, but two-thirds of the vibrissae cells within the nucleus responded to more than one vibrissae. Obviously a large number of the primary afferents have converged on the second order neurons to produce these results. However, specificity seems to be maintained in the brainstem trigeminal complex in that these neurons respond only to vibrissae and not to skin or common hair stimulation. Furthermore, a rostral-caudal columnar segregation of the various types of vibrissae appears to occur, with mystacial, genal and ophthalmic vibrissae represented in adjacent columns but not in the same column (Eisenman, et al., 1963). The latter authors also found a few units which responded either to all of the mystacial vibrissae or to all of the ophthalmic ones. Eisenman et al. (1963) found units in the brainstem complex similar to first order neurons in that the more sensitive units (in the present experiments, low velocity threshold units) were slowly adapting and less sensitive units (high velocity threshold) were rapidly adapting.

To summarize, although many of the second order neurons appear to maintain the highly specific receptive field-response properties found in the primary afferents, a number of the brainstem units lose this specialization in favor of a converging organization. Neurons in at least three of the four nuclei (main sensory nucleus, nucleus

oralis and spinal nucleus) appear to respond to vibrissae input. Variations in anatomical localization and sampling procedures make comparisons among the experiments on the second-order neurons tenuous. Since none of the studies has provided a complete mapping of all the nuclei, conclusions concerning differences in representation in the various nuclei must await more thorough investigations.

In work currently in progress, single units have been found in rat somatic sensory cortex which respond to single vibrissa deflection (C. Welker, personal communication).

C. Comparisons with Primary Tooth Afferents

A number of experiments investigating the responses of primary trigeminal afferents to stimulation of the teeth reveal that some characteristics of these units are similar to those of vibrissae units (Pfaffmann, 1939; Ness, 1954; Kerr and Lysak, 1964; Kawamura and Nishiyama, 1966). These studies reported that many units respond to stimulation of just one tooth; many are direction-specific, with an increased adaptation time and frequency, and a decreased threshold and latency, in the optimum direction. The majority were slowly adapting. Pfaffmann (1939) and Ness (1954) found that about 10% of the tooth units were spontaneously active; the spontaneous firing rate could be modified by comparable procedures and with similar results to those described for vibrissae units (see below). Both rate of application

of pressure and absolute level of pressure were found by Pfaffmann to determine the spike frequency of a unit. He found thresholds to be much lower in kittens than in adult cats. Teeth units differ from vibrissae units in that most of them require a rather substantial force to activate them, as compared with the exquisite sensitivity of many vibrissae neurons. All of the other response characteristics appear very similar to those reported here for vibrissae units.

D. Anatomical Mechanisms of Adaptation

The marked variation in adaptation rate among the different response pattern categories of first order neurons can probably be attributed to properties of the receptor apparatus. In addition to variation between the categories, adaptation rate varied as a function of stimulus amplitude within the low velocity threshold categories. Loewenstein and colleagues (Loewenstein, 1956); Loewenstein and Mendelson, 1965; Loewenstein and Skalak, 1966) have proposed an explanation in terms of the mechanical features of receptors which may account for at least some of the observed differences in adaptation rate.

Using cat Pacinian corpuscle receptors, Loewenstein and Mendelson (1965) demonstrated that if the lamellar layers were stripped from the corpuscle, the remaining decapsulated receptor adapted more slowly than did the intact

corpuscle. If an artificial capsule was constructed around the decapsulated receptor, the endings again became very rapidly adapting. They also found that although the intact capsule responded to stimulus "on" and stimulus "off", the decapsulated receptor responded only to stimulus onset. They argued that release of energy stored in the elastic elements of the receptor structure accounts for the "off" response in the normal capsule. They concluded that mechanical features of the Pacinian corpuscle provide the rate-limiting factor in adaptation and the mechanism for response to stimulus offset. That the receptor is the limiting factor in adaptation rate was suggested in a previous study by the fact that adaptation of the Pacinian corpuscle receptor structure occurred more rapidly than the accomodation of its own axon (Gray and Matthews, 1951).

In the vibrissae neurons of the present study, units which were activated by stimulus onset and offset were more rapidly adapting than units which responded only to stimulus onset. A difference in the mechanical features of the receptor sites might account for such response differences in the peripheral neurons.

Loewenstein (1956), in experiments on somatic sensory receptors of frog skin, found fibers which responded to some stimuli with a rapidly-adapting "on" and "off" response, which changed to a slowly-adapting discharge with no "off" component when stimulus intensity was increased. This

phenomenon is similar to the "position effect" described above for vibrissae units, in which the response is rapidly-adapting "on" and "off" or slowly-adapting "on" according to the position of the stimulating probe. Loewenstein used a mechanical hypothesis to explain his results. He suggested that with a less intense steady state stimulus, in-series, non-elastic components of the receptor fold back on one another, whereas with increased intensity, a receptor ending becomes fully expanded and provides a steady depolarizing current. It is interesting to note that, as in his data on Pacinian corpuscles, the occurrence of rapid adaptation is correlated with response to stimulus offset and the occurrence of slow adaptation is correlated with lack of an off response. The present experiments, rather than showing either a rapid or a slow response, demonstrated a gradation of the position effect according to the precise position of the probe on the vibrissa and a gradation of adaptation rate in LVT-comp units as stimulus amplitude was increased. A differential activation of mechanical elements in the receptors, as proposed by Loewenstein, is consistent with different adaptation rates among the categories of units, with gradation of adaptation with stimulus amplitude, with gradation of adaptation with the position of the probe, and with occurrence of an "off" response in rapidly-adapting units.

E. Spontaneous Discharge

In the present experiments, as well as in the earlier studies of vibrissae first order units (Fitzgerald, 1940; Kerr and Lysak, 1946), small proportions of spontaneously discharging units were observed. In all the experiments, it was found that firing could be eliminated by deflection of the vibrissa in one or more directions, whereas deflection in the other directions resulted in an increase in the rate of discharge. Such an increase was followed, upon release of deflection, by a silent period and gradual resumption of the spontaneous rate.

Substantial differences in the number of spontaneous units were found between Experiment 1 (less than 5%) and Experiment 2 (almost 20%) of the present series. Fitzgerald found an intermediate number (10%). One possible explanation for the discrepancy in the two present experiments was the failure to rigidly control body temperature. Spontaneous discharge can be affected by small changes in temperature in lemniscal afferents (Hunt and McIntyre, 1960). Another variable often seen to influence the occurrence of spontaneous firing is anesthetic level . Mountcastle (1957) found that spontaneous discharge decreased rapidly in cortical somatic sensory neurons when the level of barbiturate anesthesia was increased. In the present experiments, in the small sample of units obtained in the paralyzed decerebrate animal, no spontaneous firing was observed. It is possible that

in animals under relatively light barbiturate anesthesia, muscle twitches produce slight movements, imperceptible to the observer, which account for at least some of the "spontaneous" discharge. The present experiments were occasionally interrupted because slight twitches in the vibrissae were observed; these were seen prior to any of the other usual reflex signs of light anesthesia and were eliminated by an additional injection of anesthetic.

In second order trigeminal units in cats, Kruger and Michel (1962b) observed that spontaneous firing was rare, whereas Eisenman et al. (1963) found that about half of their units discharged spontaneously. This difference is especially interesting in that the latter experiment studied cats under barbiturate anesthesia, while the former used paralyzed, decerebrate cats. These results are consistent with the idea suggested above that some of the "spontaneous" activity may be attributable to muscular activity which is not present in the paralyzed animal.

Elimination of the anesthetic agent in the decerebrate animals had little effect on any of the parameters of response which were recorded. This is in accord with many of the characteristics of higher order lemniscal neurons (Poggio and Mountcastle, 1963). It is only when more complex response features are examined, such as recovery cycle or following rate, that barbiturate interference seemed to become evident in the lemniscal units in their study. It is probable that

anesthesia has even less influence on primary afferent fibers in the present experiment than on the higher order fibers studied in the latter experiments.

F. Unit Responses to Actively Protracting Vibrissae

The responses to movement of the vibrissae produced by stimulation of the normal motor pathways suggest that when a rat is aroused to active exploration, the successive waves of vibrissae protraction and retraction are coded by many but not all primary vibrissae neurons. Furthermore, information regarding a physical stimulus contacted by such whisking movements is transmitted in a series of bursts corresponding to the rate at which the vibrissae whisk back and forth. The data from interposition of a barrier against the vibrissae also indicate that most of the units maintain the directional sensitivity during movement that was found when the vibrissae were stimulated when stationary. In Experiment 1, the directional sensitivity to barriers placed against the whisking vibrissae was identical to that in stationary vibrissae for about half the units. Another 30% responded to the barriers in all directions, although with a longer, higher frequency discharge in the directions found to be effective for the stationary vibrissae. The response of these latter units corresponds to the distinction between LVT and HVT directions established in Experiment 2, but which was not seen with the manual stimulus in the first

experiment. Thus for these 30%, the vibrissa whisking against a barrier was a sufficiently intense stimulus to activate the HVT as well as the LVT directions of a unit.

G. The Trigeminal Tract Reflex

One somewhat puzzling feature of the present experiments was the failure to find the antidromically-conducted trigeminal tract reflex when the trigeminal root was intact, as described by Darian-Smith et al. (1965) and others (see Introduction). No such activity was observed in response to mechanical stimulation of the region surrounding the receptive field of a unit, and although latency analyses were not carried out, there did not appear to be a response to stimulation of the receptive field with the latency characteristics described by Darian-Smith et al. (1965). Although the other studies of primary vibrissae afferents (Fitzgerald, 1940; Kerr and Lysak, 1964) did not specifically look for the tract reflex, activity resulting from stimulation outside the restricted receptive fields would probably have been observed had it existed. In one study on the brainstem nuclei which specifically sought surround inhibition of vibrissae neurons, no such effect was found (Kruger and Michel, 1962 b). Yet the existence of this tract reflex in the primary afferent sensory fibers and the resulting surround inhibition in the second order neurons are well-documented in several studies (see Introduction).

Two possible explanations may account for these discrepancies. One is the differences in the type of stimuli used to elicit the responses in the several experiments. The present study, and the others which have yielded similar results, employed the most delicate possible methods of tactile stimulation, in the interests of defining the adequate stimulus, i.e. the stimulus which activates the unit with the lowest mechanical stimulus threshold. On the other hand, the experiments which observed the tract reflex used much stronger stimuli. Thus, Stewart and King (1966) and Stewart et al. (1967) employed electric shock to the afferent nerves. Darian-Smith (1965) usually used electric shock to the skin of the face; although when he occasionally employed mechanical stimuli (of an unspecified nature), these produced the antidromic phenomenon to a lesser extent. Although the stimuli which were adequate for eliciting the orthodromic response in the present experiments failed to activate a clear antidromic response, it is possible that stronger stimuli might have been effective. This idea is supported by the results of Erickson et al. (1961), who found the trigeminal tract reflex in rats only when electrical stimuli were employed. If only very intense or electrical stimulation effectively elicit this activity, its physiological significance may be limited to environmental situations involving extremely intense or noxious stimulation.

Another possibility is that these phenomena do not exist in the neurons responding to vibrissae input. The purpose of surround inhibition appears to be to sharpen the boundaries of the receptive field, and thus to increase the discriminatory capacities of a system (Hartline, Wagner and Ratliff, 1956; Rose and Mountcastle, 1959). Whereas this is clearly an important function when stimuli can impinge on spatially contiguous areas (e.g. the skin surface), it would appear to be much less useful when the peripheral field consists of spatially discrete elements. The latter is, of course, the case for vibrissae. The locus of stimulation is already perfectly defined by each neuron: it responds to one and only one vibrissa, with no overlapping receptive fields. An additional mechanism for sharpening the discrimination of the peripheral locus of a stimulus would seem less useful in such a system.

H. Psychophysical Thresholds

With few exceptions, determinations of the absolute threshold for neural discharge have not been obtained. Only for the first order neurons terminating in Pacinian corpuscles have thresholds been defined. Gray and Malcom (1950) found that a minimum movement of 0.5 μ in 100 μsec. was required to activate most of such receptor neurons.

The present threshold data have some bearing on von Bekesy and Stevens' theory of neural quanta as the basis

for sensory difference limens (von Bekesy, 1930; Stevens, Morgan and Volkmann, 1941; Stevens, 1961a). Although their theory pertains to difference thresholds, it is also applicable to the absolute threshold. They suggest that the psychometric function is rectilinear in form, with the transition from no detection to 100% detection occuring as a consequence of the activation of a given number of "neural units" or "quanta." Von Bekesy (1930) proposed that the neural unit of a single quantum was the peripheral nerve fiber; Stevens et al. (1941) argued that the quantal unit was a centrally-located functional unit rather than a peripheral structural entity.

One basis for their rejection of the peripheral fiber as the unit was that the critical increment or quantum, while a relatively stable quantity, displayed some variability in size. The present experiments show that about half the single units studied had invariant thresholds and half showed some variation in threshold. Thus the existence of variation in quantal size is not an adequate basis for rejection of the peripheral fiber as the unit of the neural quantum.

A second argument of Stevens et al. (1941) against the identity of the peripheral unit and the neural quantum is that there are more fibers, for example in the auditory nerve, than there are quanta in either pitch or loudness modalities. In the present study, many of the vibrissae units had identical threshold values, and thus a given

stimulus increment would activate all these units. Therefore several peripheral fibers could conceivably constitute one quantum. There is no necessity of this occurring more centrally. The present data are not sufficient to evaluate several other points of their argument.

Human psychophysical threshold data show that thresholds for one parameter of a stimulus are altered by the value used for another parameter. For example, auditory intensity thresholds depend in part on the frequency of a tone (Licklider, 1951); similarly, visual intensity thresholds depend partly on the wavelength of a light (Judd, 1951). Such an interaction occurs to some extent in the primary afferent vibrissae neurons. There was a trend for velocity threshold to be higher at the lowest deflection amplitude in HVT-comp units; in MVT units, significantly higher velocity thresholds existed at the lower stimulus amplitudes.

I. Stimulus-Response Relationships and the Psychophysical Laws

The results of the experiments plotting response rate of vibrissae neurons against stimulus input show systematic changes of discharge frequency as a function of stimulus amplitude and velocity. The precise functional relationship between stimulus amplitude and impulse frequency cannot be thoroughly evaluated without further experiments using a broader stimulus range; it is evident, however, that a monotonically-increasing function exists. Spike discharge

frequency exhibits a power function relationship with stimulus velocity, although whether this relationship may be applicable only to the transient stimulus onset period remains to be determined.

The psychophysical laws of Fechner and Stevens were formulated with reference to the intensive continuum of stimuli; exactly what constitutes "stimulus intensity" in the present study is not clear. It is possible, of course, to define that continuum which obeys a psychophysical law as the intensive continuum, but this is hardly an independent evaluation of the law. Mountcastle et al. (1963) argue that for their data, stimulus amplitude and not velocity is the intensive continuum. In a few cases, in which they were able to convert the stimulus measure into a measure of force, they found that the power law predicted the force psychophysical function even more accurately than the amplitude function, although both were power functions.

The present data caution against hasty conclusions about the formal relationship between stimulus and response. Much of the previous physiological experimentation has concluded that the S-R relation is a linear, logarithmic or power function, without testing the alternative possibilities. The data on stimulus amplitude in the present study would have permitted any of these three conclusions had not the other relationships been tested as well.

It is evident that a synthesis of the results, techniques and theories of human sensory psychophysics and single unit neurophysiological analysis is only at the initial stages of development. Subsequent experiments in both disciplines should further elucidate mechanisms of sensory perception.

CHAPTER V. SUMMARY

The electrical signs of neural impulse discharge in response to mechanical stimulation of the vibrissae were recorded from single units in the trigeminal semilunar ganglion of albino rats. The majority of units was studied in rats under barbiturate anesthesia; a few units were recorded from unanesthetized, decerebrate rats. In some animals, the trigeminal root was sectioned. This procedure did not appear to affect any of the response characteristics that were observed.

To delimit the receptive field of each unit, delicate forms of mechanical stimulation were applied to the mystacial vibrissae and surrounding facial regions. The receptive fields were localized to a single vibrissa, a small sinus hair or a small patch of common fur. Without exception, units which were activated by vibrissa stimulation were activated by movement of one and only one vibrissa. Almost all vibrissae units (over 99%) responded to angular deflection and/or release of a vibrissa. In Experiment 1, the directional specificity of unit responses was defined for deflection ("on") and release ("off") stimuli in rostral, caudal, dorsal and ventral directions. In Experiment 2, additional parameters of the adequate stimulus were studied, by means of an electronically-controlled vibrissae stimulator which permitted

variation of velocity, amplitude, duration and release, as well as direction, of vibrissae deflection. Manipulation of these parameters revealed a number of consistent constellations of unit discharge characteristics. The following unit response patterns occurred in the percentages shown:

1. Units responding to vibrissae deflection with a low velocity threshold exhibited a relatively high frequency, slowly-adapting discharge. Adaptation time increased as stimulus amplitude increased. Such units seldom responded to stimulus release. Low velocity threshold units could be subdivided into two classes:

   a. Direction-sensitive units, which showed the above low threshold pattern in one, two or three deflection directions and responded in the remaining (complementary) directions with a high velocity threshold response pattern (see 2a). (56%)

   b. Non-direction-sensitive units showed the low threshold pattern in all directions. (5%)

2. Units responding to vibrissae deflection with a high velocity threshold exhibited a low frequency, very rapidly-adapting discharge and in addition, responded to stimulus release. Such units could also be subdivided into two classes:

   a. Direction-sensitive units which showed the high velocity threshold pattern in complementary direc-

tions opposite to those in which the low threshold pattern occurred. (56%)

b. Non-direction-sensitive units showed the high threshold characteristics in all directions. (8%)

3. Moderate velocity threshold units responded to vibrissae deflection with a moderate frequency, rapidly-adapting discharge. These units were also activated by stimulus release. They showed no directional sensitivity. (23%)

4. A miscellaneous category of units responded with varied threshold and adaptation characteristics to various combinations of vibrissae deflection and release stimuli. (8%)

In addition to determining response patterns evoked by passive deflection, unit activity was observed during repetitive whisking movements (protraction) of the vibrissae. Such movements, elicited by electrical stimulation of the facial motor nerve, activated about half the vibrissae units. Almost 90% of the units responded if, in addition, a barrier were placed against the vibrissae while they protracted. The directional sensitivity of most units to such barriers inserted successively in four directions was similar to that observed when the vibrissae were stimulated when stationary. The procedure of placing a barrier against the whisking vibrissae was designed to simulate a natural encounter of the vibrissae with an

object as the rat explores its environment.

In Experiment 3, systematic variations of stimulus amplitude and velocity revealed that unit impulse frequency was a monotonically-increasing function of both these parameters. Impulse frequency was observed to increase as a power function, rather than a linear or semi-logarithmic function, of stimulus velocity during the period of stimulus onset. The range of deflection amplitudes was too narrow to permit a specification of its exact functional relationship with response frequency; the data were equally well described by all three functions examined.

In the small number of units studied in decerebrate rats, neither response pattern categories nor response frequency relationships differed from those observed in anesthetized animals.

These three experiments suggest that when a rat encounters objects which deflect either its actively whisking or stationary vibrissae, the first order neurons of the trigeminal circuit precisely code the locus and direction of peripheral mechanical stimulation as well as its onset velocity, amplitude, duration and offset.

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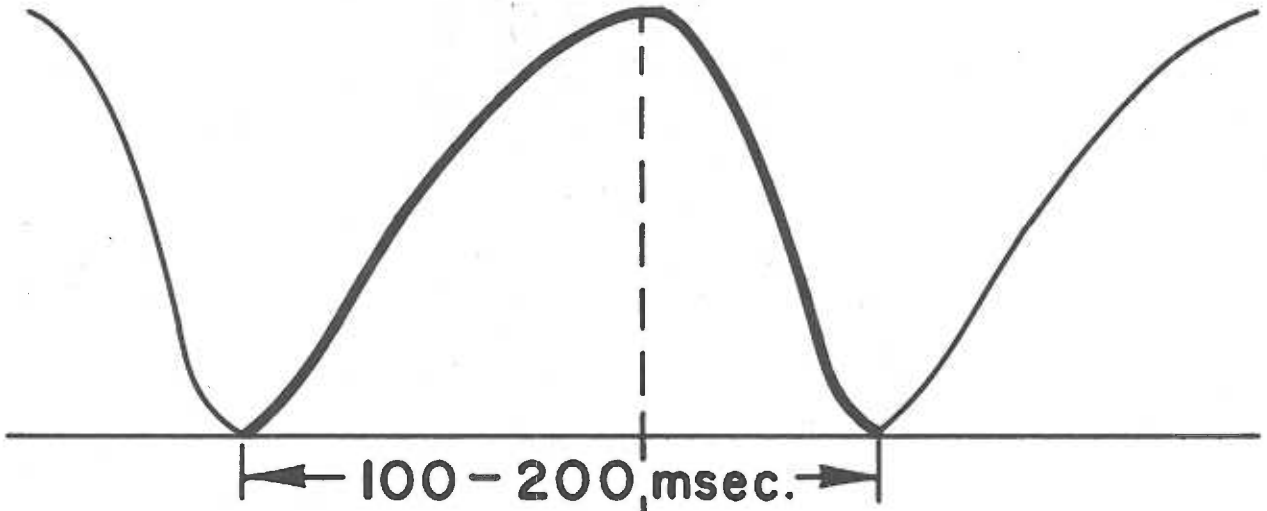
Figure 1. The rat sniffing cycle. Schematic representation of temporal organization of the four major "sniffing" actions during one complete cycle (heavy line). Vertical dashed line indicates that the protraction phase is more prolonged than the retraction phase. Time is on the horizontal axis and amplitude on the vertical one.

THE SNIFFING CYCLE

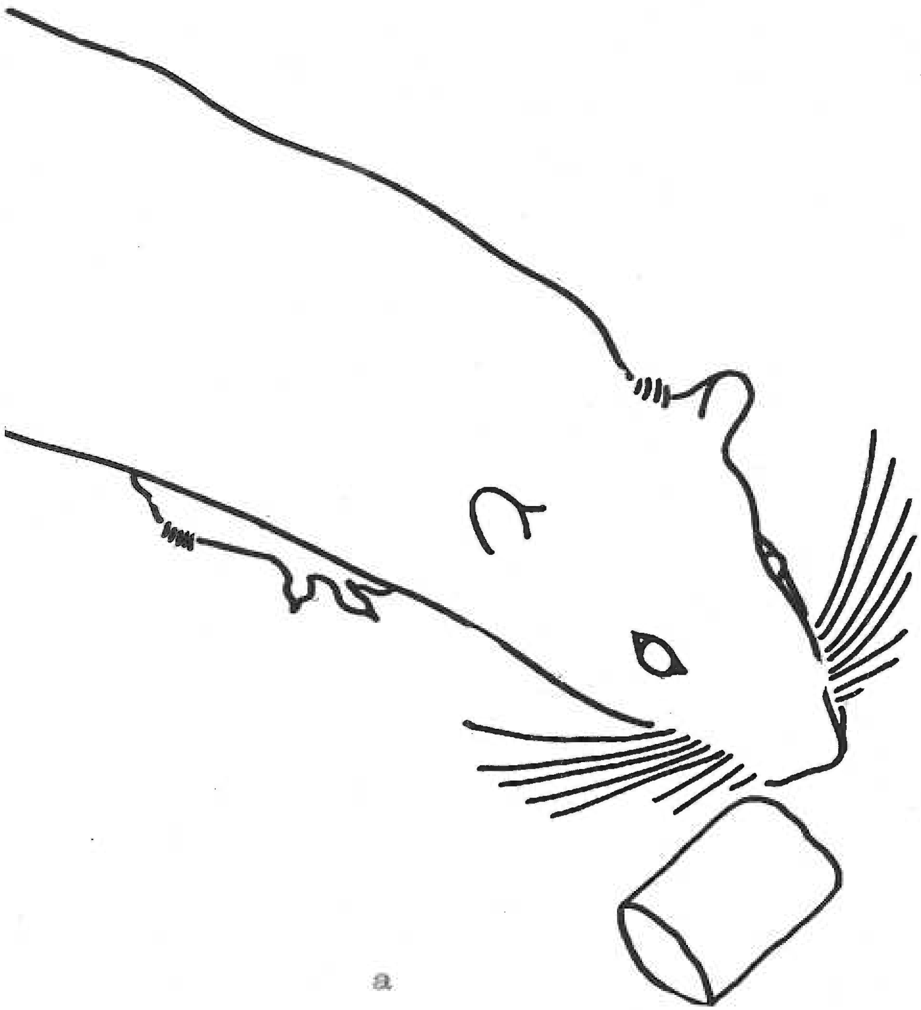


VIBRISSAE:	PROTRACTION	RETRACTION
NOSTRIL:	DILATION	RELAXATION
RESPIRATION:	INSPIRATION	EXPIRATION
HEAD:	APPROACH	WITHDRAWAL

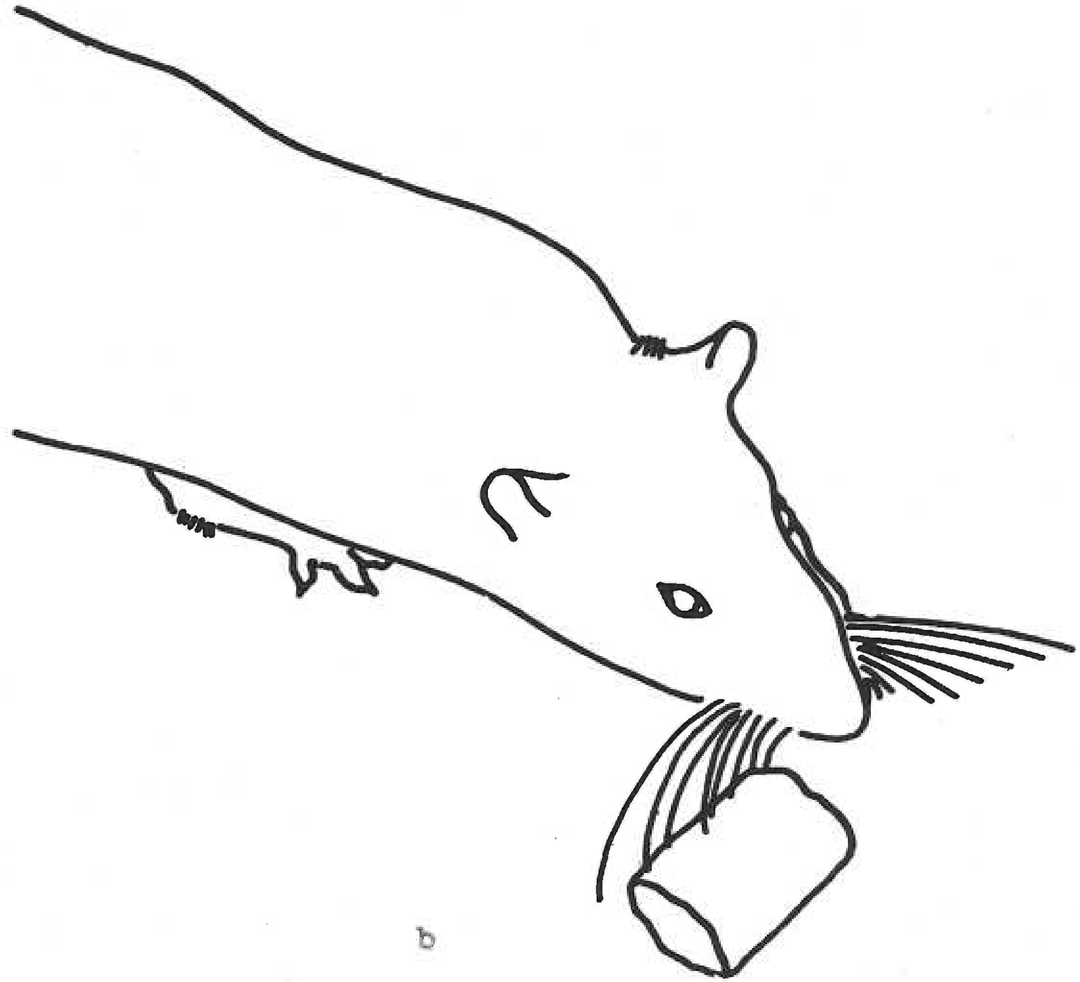
Figure 2.

a. Sketch of rat with vibrissae in relaxed position.

b. Sketch of exploring rat with protracted vibrissae contacting a food pellet.



a



b

Figure 3. Photograph of lateral aspect of face and snout of albino rat. Mystacial vibrissae are cut short and painted black for easier visualization of orderly rows and columns. Caudal vibrissae are large; more rostrally, they are shorter and finer, gradually tapering to the small sinus hairs around the lips and snout. Mm. scale in lower corner.

Figure 4. Longitudinal section through a rat vibrissae follicle, drawn from a Cajal silver preparation, with some features of the nerves and arteries added from other preparations. (Taken from Vincent, 1913)

a. Nerve from dermal plexus running down to form the nerve ring
b. Conical body
c. Sebaceous gland
d. Artery entering the ring sinus
e. Ring sinus
f. Nerve ring
g. Dermal sheath
h. Ringwulst
i. Root sheath
j. Cavernous sinus with trabeculae
k. Main sensory nerve entering from below
l. Large artery entering with the nerve
m. Dermal papilla

TACTILE HAIR OF THE WHITE RAT

S. B. VINCENT

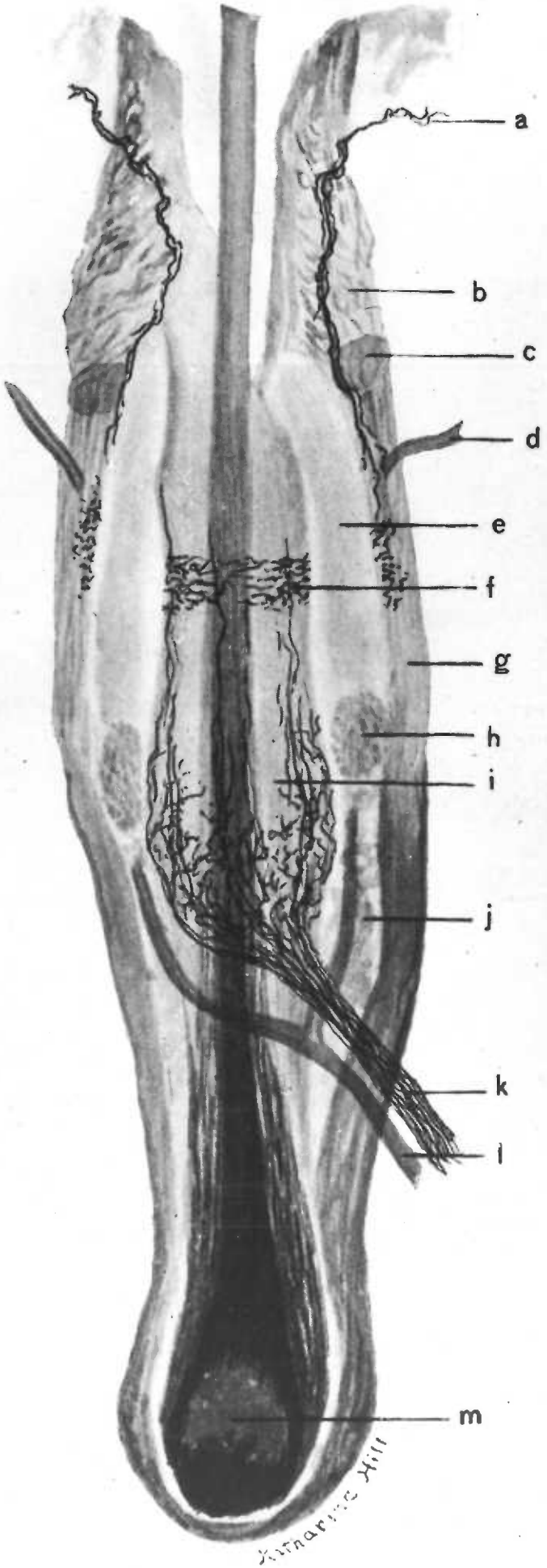


Figure 5. Horizontal section through left semilunar ganglion of an albino rat. Cut at 15μ, stained with thionin and embedded in paraffin. Magnification: 49 X. Some shredding of the tissue occurred. Long medial branch (at left in photograph) consists of the ophthalmo-maxillary division of the ganglion. The shorter lateral branch is the mandibular division. Note the pale fiber bundles irregularly interrupted by dark-stained cell body clusters.

Figure 6. Coronal section through left semilunar ganglion of an albino rat. Cut at 30 μ, stained with thionin and embedded in celloidin. Magnification: 100 X. The medial branch (at top in photograph) consists of the opthalmo-maxillary division of the ganglion. The shorter lateral nerve branch is the mandibular division. Note the pale fiber bundles irregularly interrupted by dark-stained cell body clusters in the opthalmo-maxillary division.

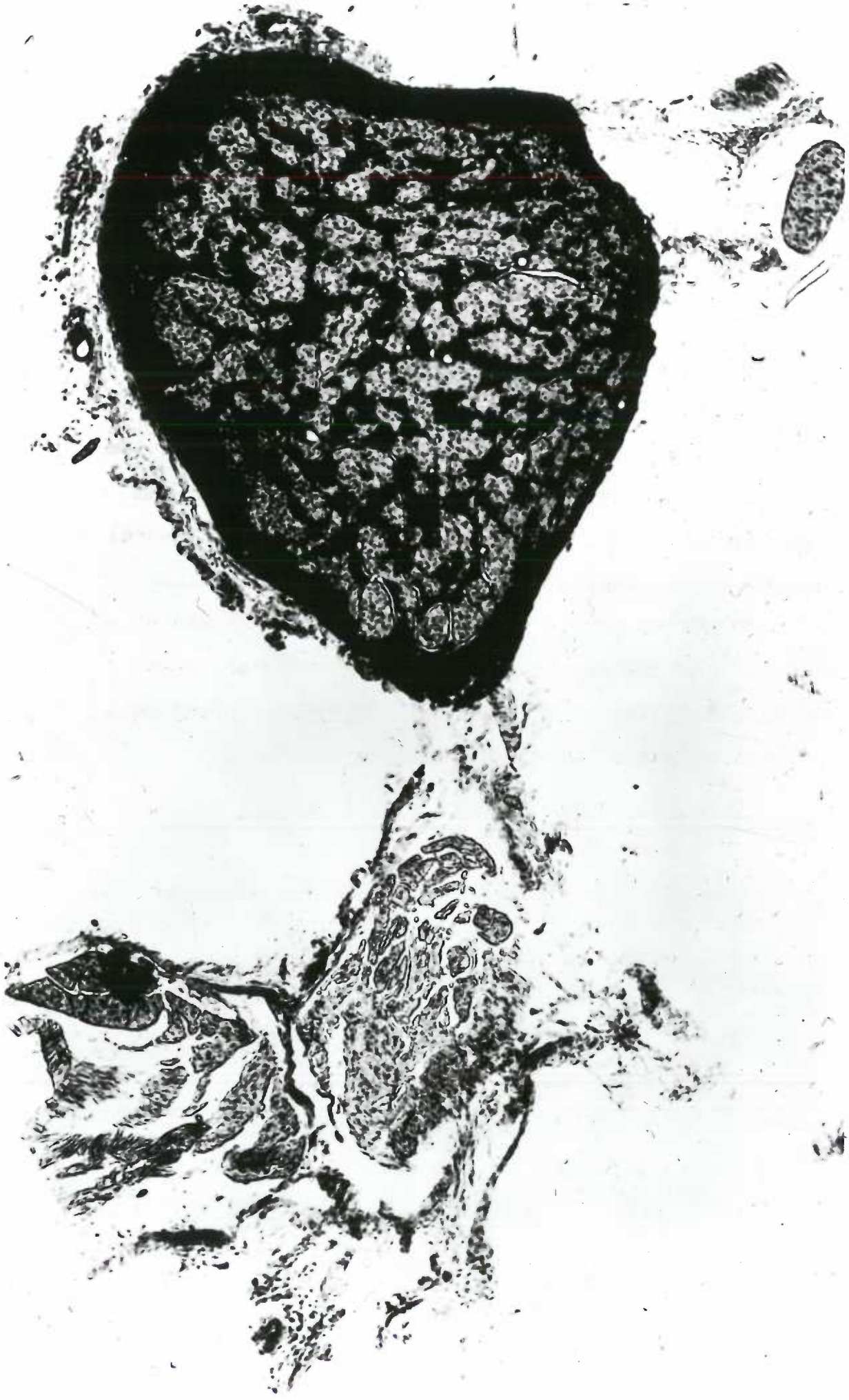


Figure 7. Photograph, taken from above, of the left semilunar ganglion *in situ*. Exposure of the ganglion was accomplished by partial removal of the left cerebral hemisphere. The dural layer is stripped from the ganglion surface. Mm. scale in left-hand corner.

a. Ophthalmo-maxillary division of the ganglion

a'. The general region of the maxillary division in which most electrode punctures were made.

b. Mandibular division of the ganglion.

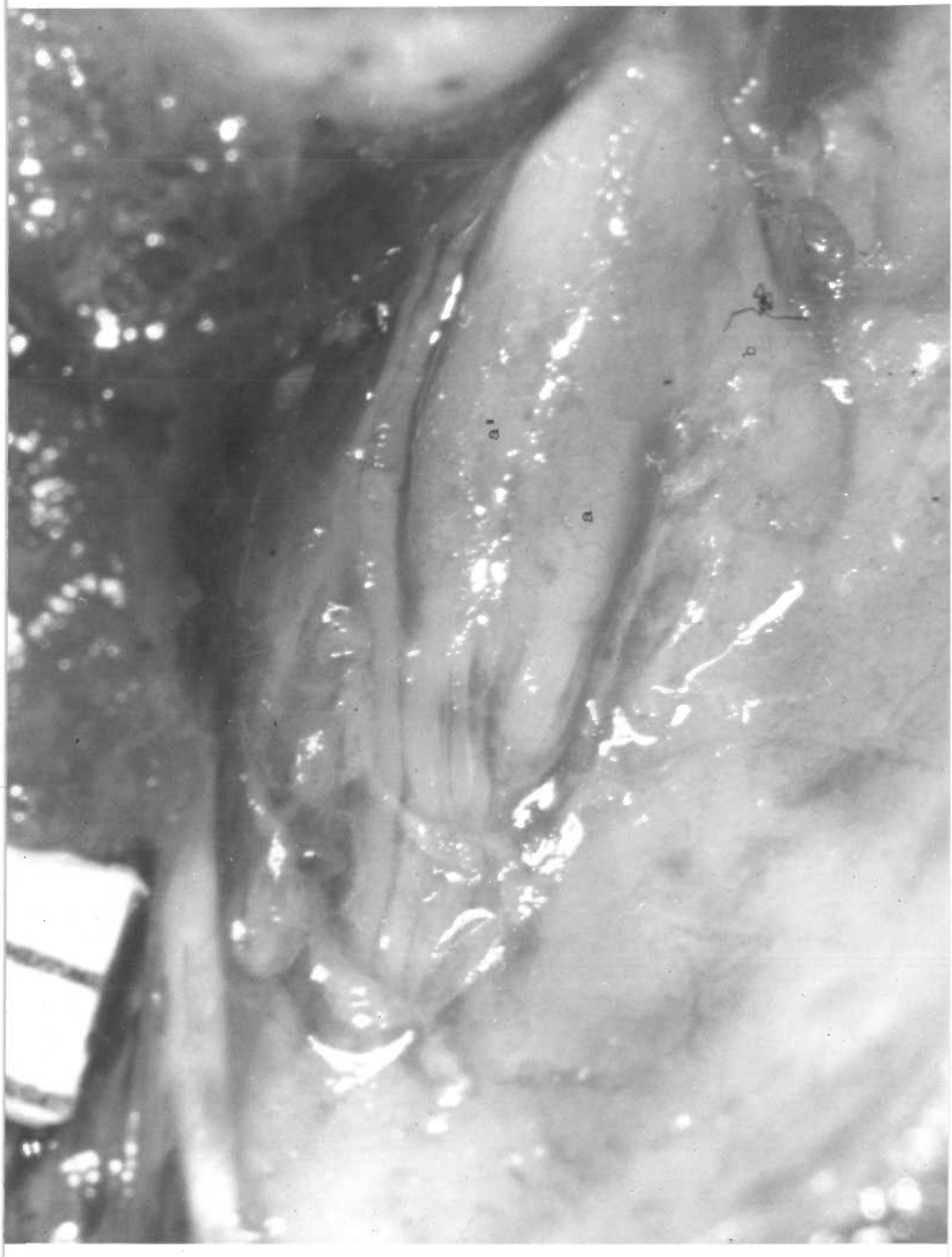


Figure 8.

A. Drawing of shank and tip of a typical tungsten micro-electrode used in these experiments. Also sketched are outlines of two semilunar ganglion cells drawn to show relative dimensions of electrode tip and cell bodies.

B. Sketch of semilunar ganglion as viewed from above. Black dots represent the locations of electrode punctures in Experiment 1. The composite of 160 punctures in 24 rats is shown.

C. Single unit discharges, recorded with the electrode in A, illustrating one initially positive and one initially negative spike discharge. In this and all subsequent photographs of unit discharge, positive polarity is recorded as an upward deflection.

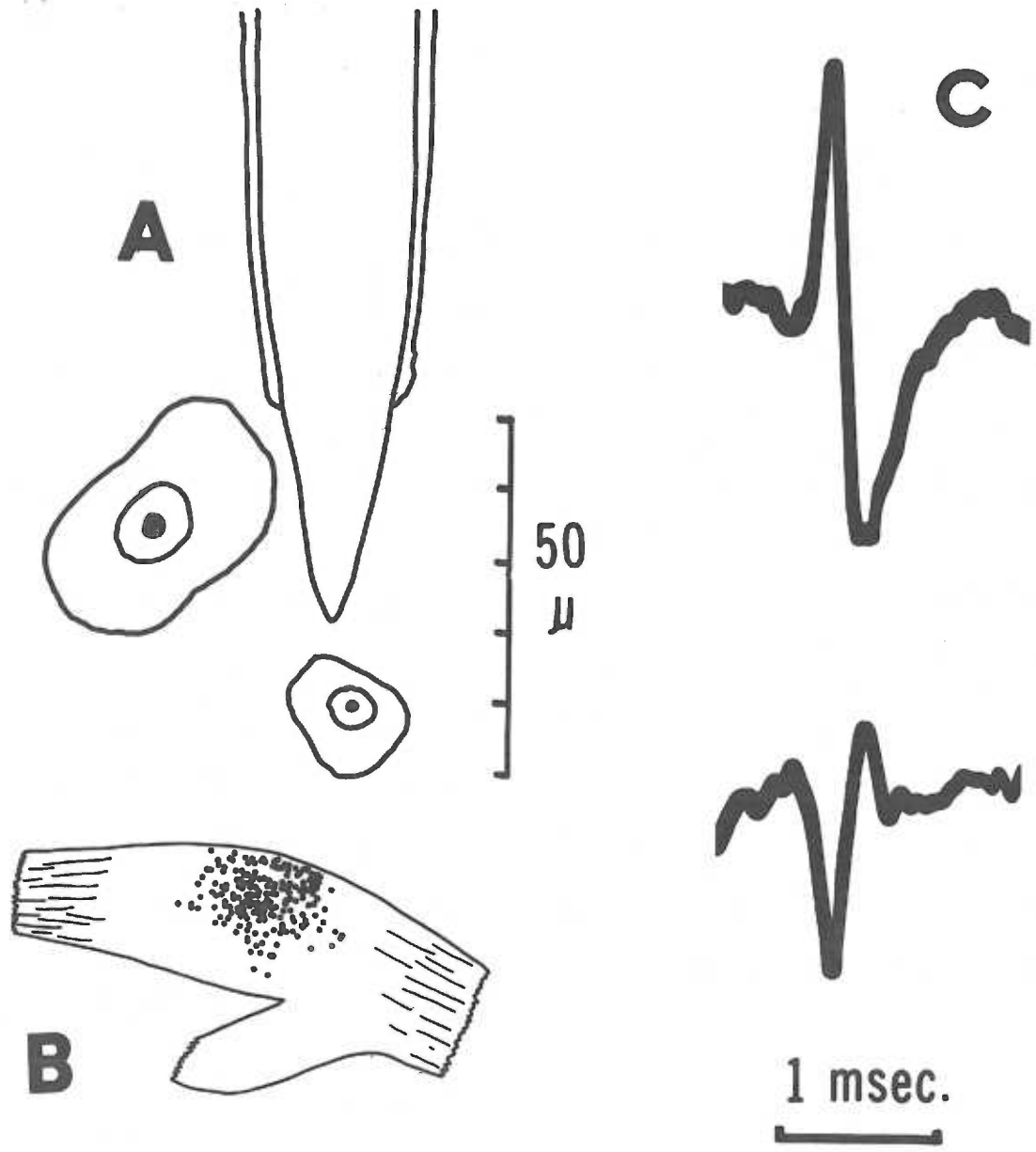

A
50
μ
B
C
1 msec.

Figure 9. Photograph of electronically-controlled vibrissae stimulator, designed to deflect a vibrissa different distances at varying rates. The stimulator is shown mounted in the position for use, as employed in Experiments 2 and 3. Note the gimbal mounting, which permits complete flexibility of position, enabling the probe to be precisely aligned with any vibrissa.

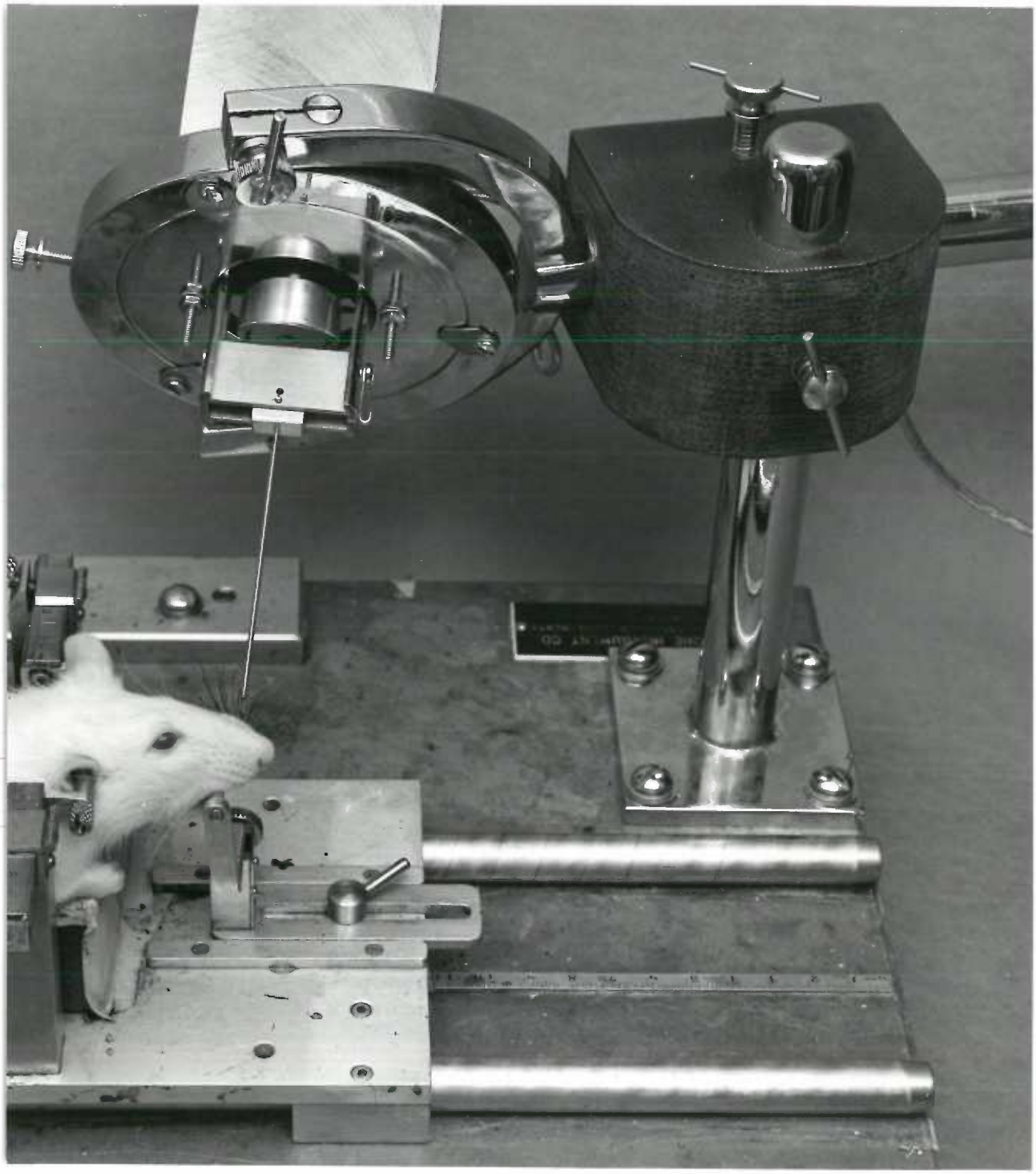
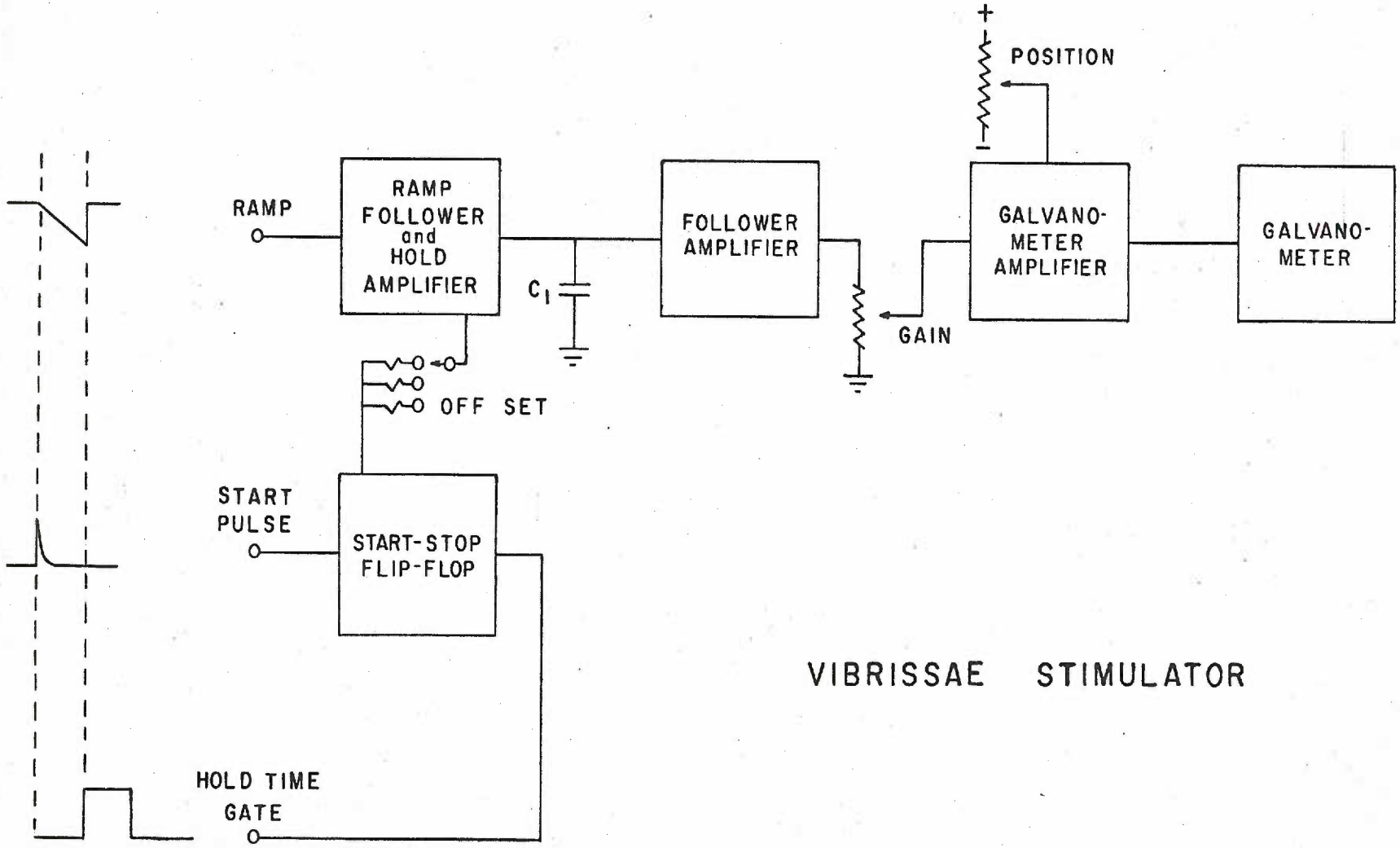


Figure 10. Close-up photograph of the stimulating probe of the electronic vibrissae stimulator. The probe consists of a length of hollow metal tubing, into which a vibrissa can be slipped. The galvonometer assembly can be rotated through 360° , permitting deflection of the probe in any direction.

2
1 ½ mm
½ mm

Figure 11. Block diagram of the electronic circuit of the vibrissae stimulator. See text for details of its operation.



VIBRISSAE STIMULATOR

Figure 12. Photograph of a three-dimensional model of rat's face and snout. The curved lines are wires that represent the vibrissae. Each black bead designates the locus of the receptive field of one unit, which was localized to a single vibrissa, a small sinus hair or a small patch of common fur in Experiment 1. Number of units represented is 482.

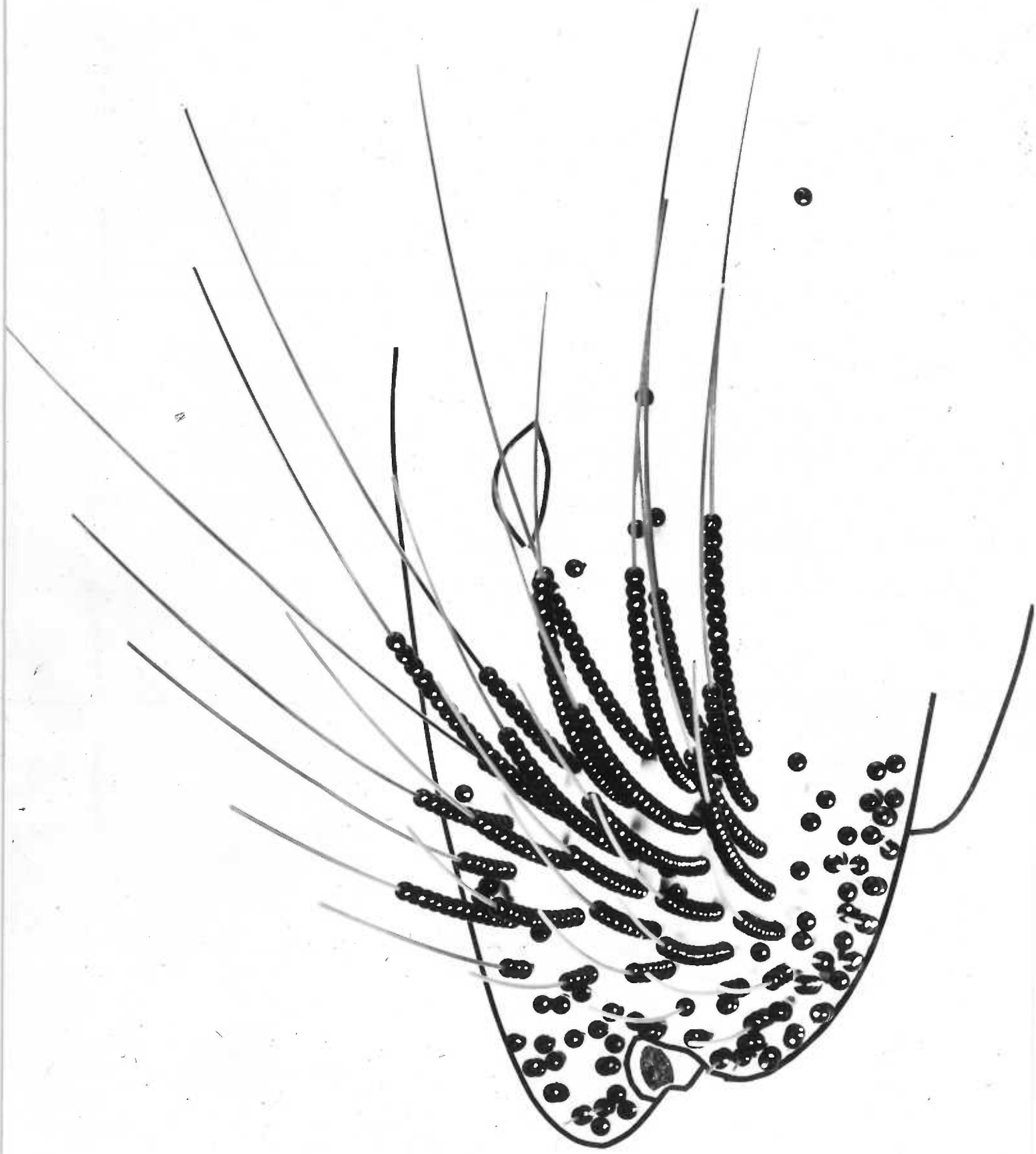


Figure 13. A spontaneously discharging unit. Rapid initial rate was produced by deflection (push) of the vibrissa. Upon release, a silent period occurs, followed by resumption of the spontaneous rate of firing.

Time calibration: ⌊⌋ =10 msec.

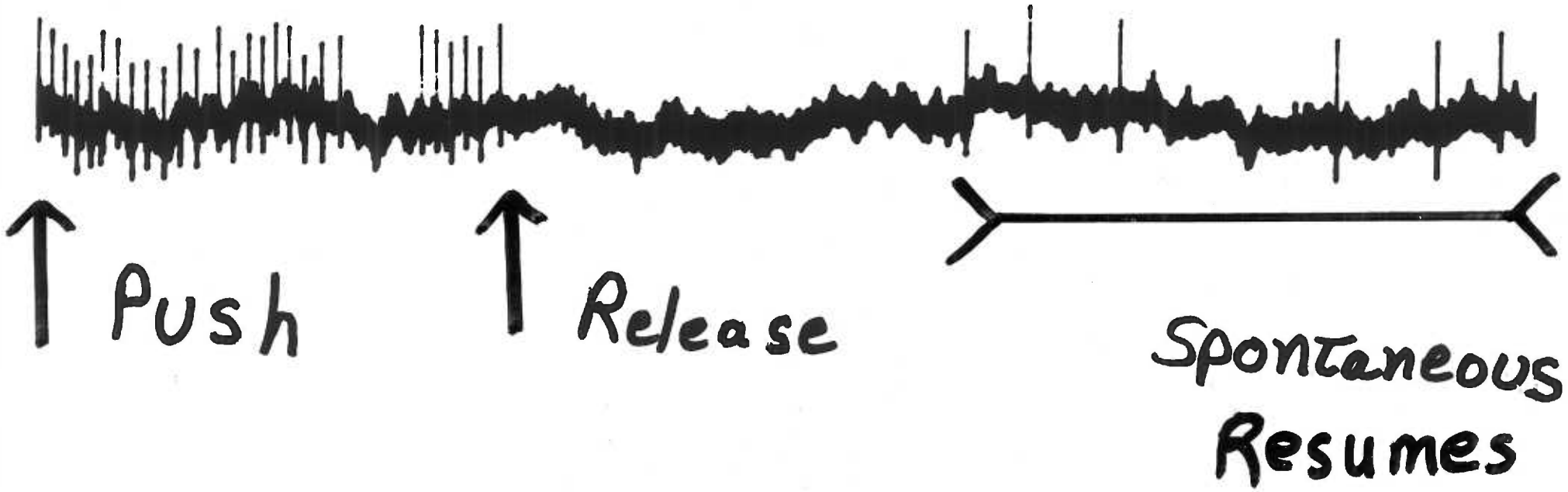
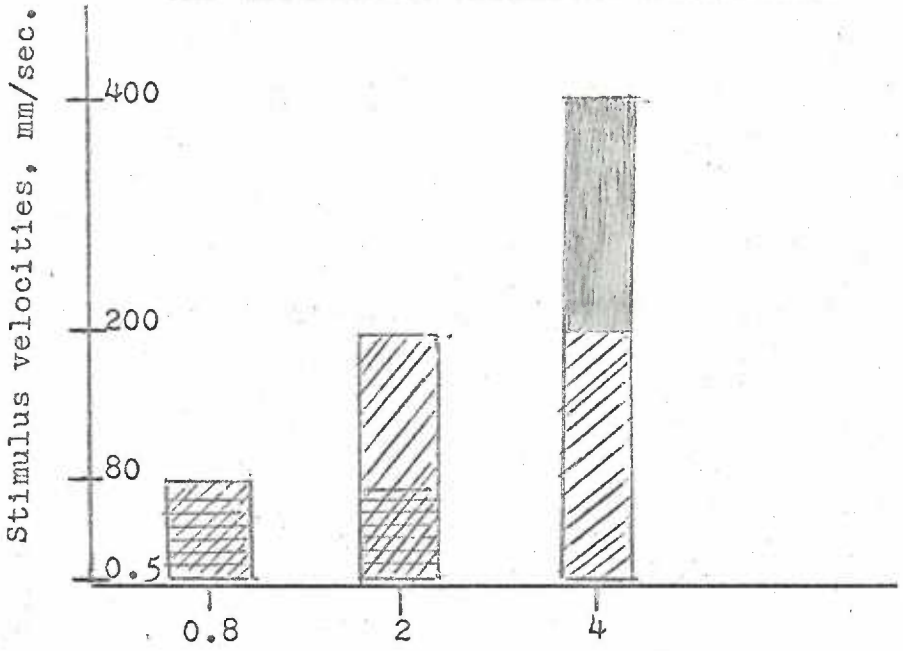

Push
Release
Spontaneous
Resumes

Figure 14. The range of deflection velocities available at three deflection amplitudes with the machanical vibrissae stimulator. The minimum velocity was .5 mm/sec. for all amplitudes. The maximum available velocity varied with amplitude: it was 80 mm/sec. at 0.8 mm., 200 mm/sec. at 2 mm. and 400 mm./sec. at 4 mm. deflection amplitude.

Range of stimulus velocities available at three stimulus amplitudes with the mechanical vibrissae stimulator



---Stimulator velocities available at both 0.8 and 2 mm. deflection amplitude

---Stimulator velocities available at both 2 and 4 mm. deflection amplitude

---Stimulator velocities available only at 4 mm. deflection amplitude

Figure 15. Examples of different categories of unit response patterns found in Experiment 2. All photographs were taken from oscilloscopic playbacks of tape recorded data. Initial positive pulse in the upper left corner of the first trace which occurs in most series is the stimulus onset marker. Each trace = 100 msec.

A. Low velocity threshold, complementary unit (LVT-comp.).

Unit produces a slowly-adapting discharge in response to deflection of a single vibrissa in two adjacent directions. Stimulus: 4 mm. deflection at 50 mm/sec. Three consecutive 100 msec. traces are shown at the following time samples after stimulus initiation:
a. 0 sec. b. 1 sec. c. 4 sec. d. 8 sec.

B. High velocity threshold, complementary unit (HVT-comp.).

Velocity threshold determination is shown, using staircase method presentation of effective and non-effective deflection stimuli. The unit also fired several spikes on release of the stimulus (not shown). Deflection amplitude is 4 mm.
a. 200 mm/sec. stimulus velocity. Unit fires 1 spike.
b. 160 mm/sec. velocity. Unit is not activated.
c. 200 mm/sec. velocity
d. 160 mm/sec. velocity
e. 200 mm/sec. velocity

C. Moderate velocity threshold (MVT) unit.

Response is similar to all directions of deflection.
a. Deflection (on) response. Stimulus: 4 mm. at 500 mm/sec.
b. Release (off) response. Stimulus: 4 mm. at approx. 45mm/sec.

D. High velocity threshold (HVT) unit.
a. Deflection (on) response. Stimulus: 4 mm. at 200 mm/sec.
b. Release (off) response. Stimulus: 4 mm. at approx. 180 mm/sec.

E. Release response in an HVT unit as a function of stimulus release rate.
a. "Fast" release. b. "Medium" velocity release.
c. "Slow" release.

Time calibration: ⌊—⌋ = 25 msec

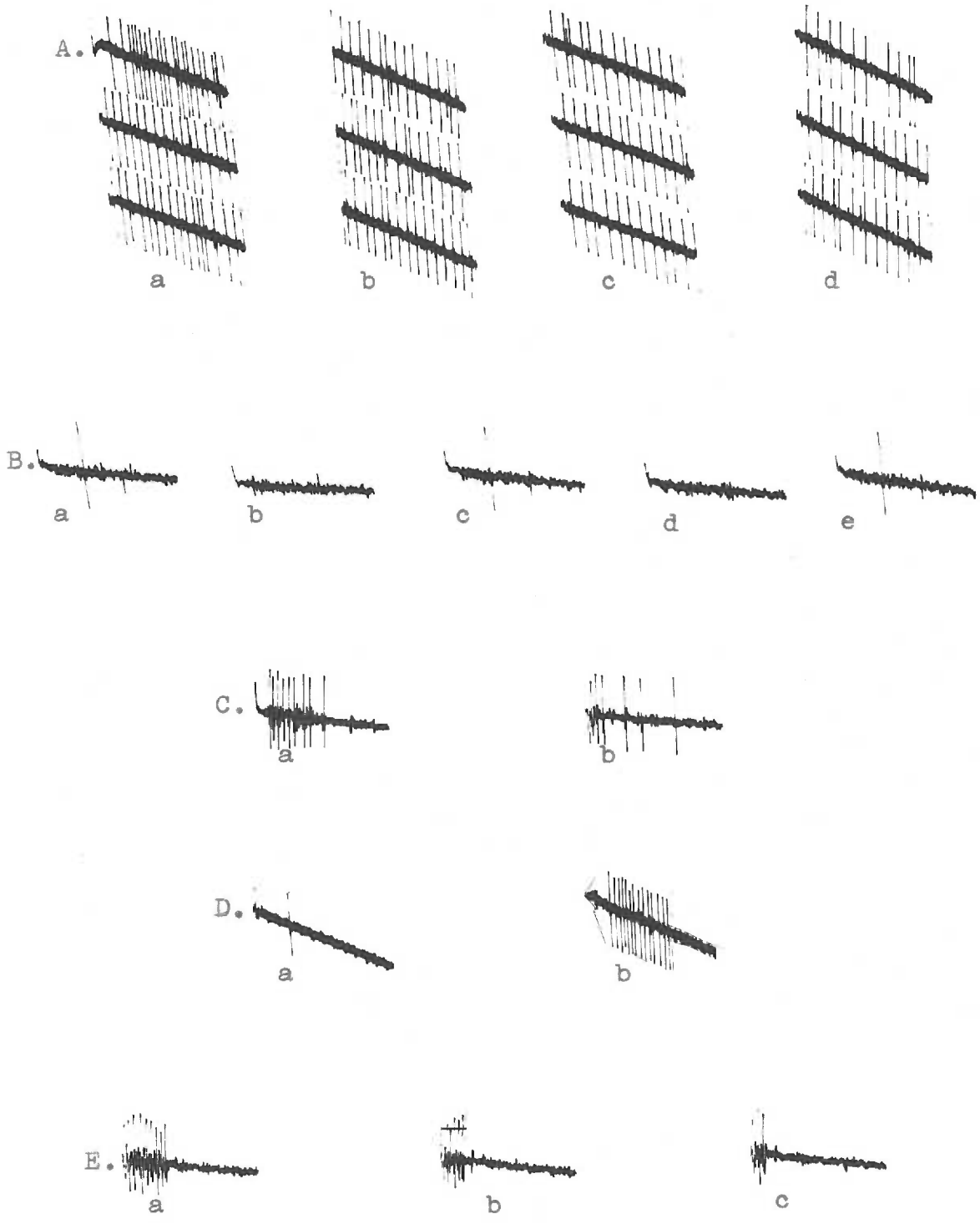

A.
a
b
c
d
B.
a
b
c
d
e
C.
a
b
D.
a
b
E.
a
b
c

Figure 16. Lack of clear evidence for the occurences of the trigeminal tract reflex. Each oscilloscope trace = 100 msec.

A. Latency of unit discharge may be variable in response to repetitions of identical stimuli. Stimulus: 2 mm. deflection at 50 mm/sec. Repetitions are separated by 3-5 sec. The trigeminal root is intact.

a. Two temporally-separated bursts of spikes.

b. and c. Same unit responding without distinct spike groupings.

B. Two temporally-separated discharges in an animal with the trigeminal root sectioned to prevent recording of antidromic activity. Stimulus: 4 mm. deflection at 50 mm/sec.

C. Maintenance of temporal separation of bursts of spikes with repetitive stimulation of the vibrissa at 2/sec. Stimulus: 0.8 mm. deflection at 50 mm/sec. Trigeminal root is intact.

D. Examples of lack of temporally distinct bursts of spikes. Such continuous impulse discharge as these were observed much more commonly than the patterns in A, B and C above.

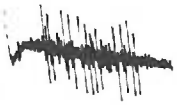
a. A rapidly-adapting unit, no temporal separation into spike bursts. Stimulus: 4 mm. deflection at 50 mm/sec. Trigeminal root is intact.

b. A slowly-adapting unit, no temporal separation into spike bursts. Stimulus: 2 mm. deflection at 50 mm/sec. Trigeminal root is intact.

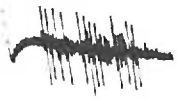
Time calibration: ⌊⌋ = 25 msec.

A. 

a



b



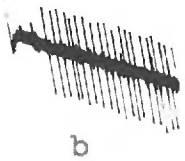
c

B. 

C. 

D. 

a



b

Figure 17. The "position" effect. All oscilloscope tracings in the figure are responses of the same unit to a stimulus of identical amplitude and velocity. The stimulus variables were the position of the stimulating probe and the length of the vibrissa. Stimulus: 4 mm. deflection at 50 mm/sec.

A. The vibrissa is 1 cm. long and the stimulating probe is located 5 mm. from the vibrissa base. A slowly-adapting discharge is activated by vibrissa deflection. Three consecutive 100 msec. traces are shown at the following time samples after stimulus initiation:

a. 0 sec. b. 4 sec. c. 8 sec

B. Vibrissa 1 cm. long, stimulating probe positioned 4 mm. from base. Unit adapts more rapidly; frequency of firing is decreased. Three consecutive 100 msec. traces are shown at the following time samples after stimulus initiation:

a. 0 sec. b. 4 sec. c. 8 sec.

C. Vibrissa 1 cm. long, stimulating probe positioned 3 mm. from base. Unit ceases to discharge in less than 100 msec.

D. Vibrissa is now cut from 1 cm. to 7 mm. in length. With stimulating probe positioned 3 mm. from vibrissa base (as in C), unit discharges a slowly-adapting response. Three consecutive 100 msec. traces are shown at the following time samples after stimulus initiation:

a. 0 sec. b. 4 sec. c. 8 sec.

E. Vibrissa 7 mm. long, stimulating probe positioned 2 mm. from base. Rapidly-adapting response occurs.

Time calibration : ⌊⌋ = 25 msec.

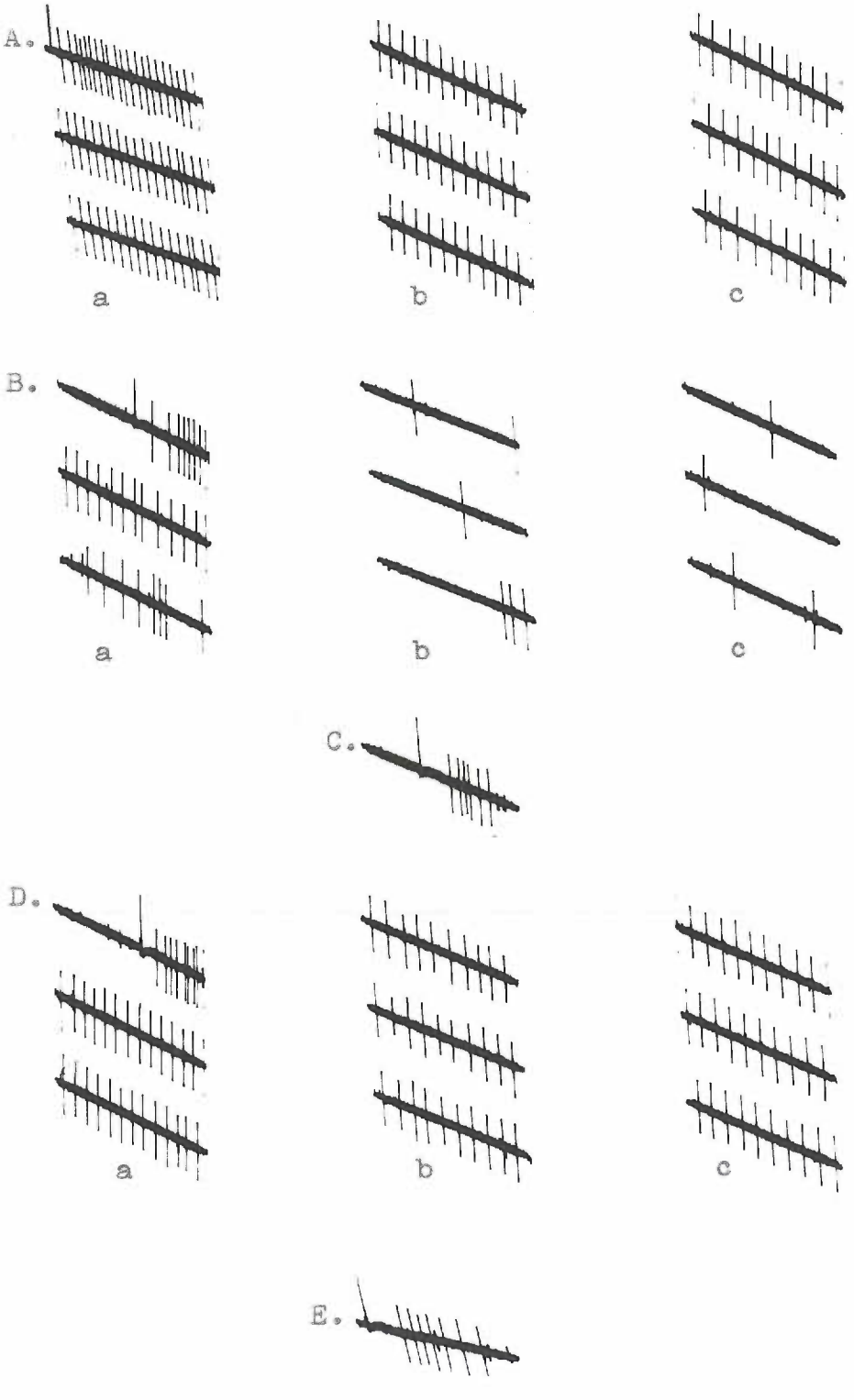

A.
a
b
c
B.
a
b
c
C.
D.
a
b
c
E.

Figure 18. Relationship of stimulus deflection amplitude (S) to response frequency in spikes/sec. (R) in LVT-comp. units. Graphs A, B. and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 11 unit-directions (N) in 10 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. All data have been normalized as follows: Stimulus amplitude values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was 100msec.

LOW THRESHOLD DIRECTION, COMPLEMENTARY UNITS

observation time = 100 msec N = 11, n = 10

S = stimulus amplitude

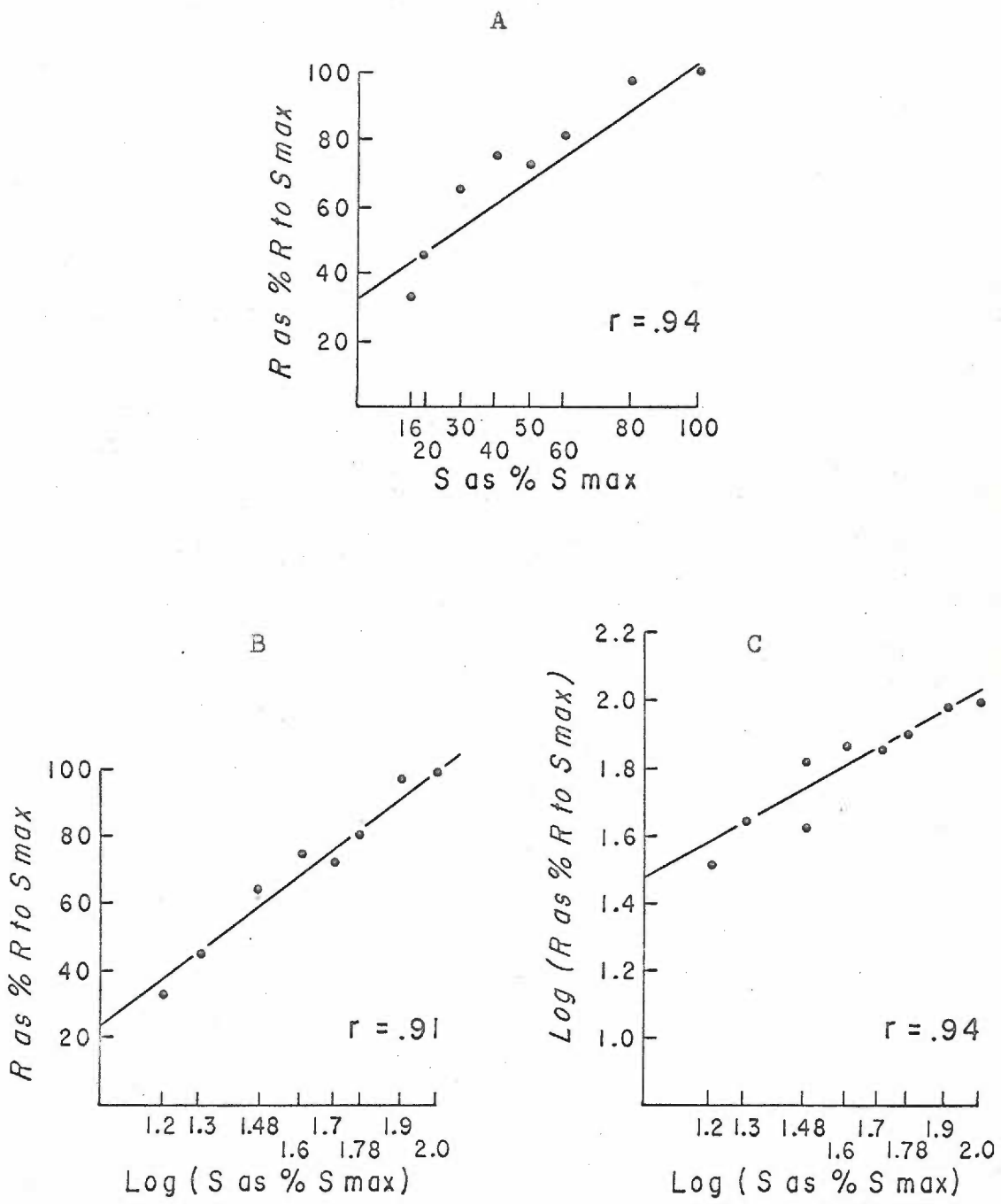


Figure 19. Relationship of stimulus deflection amplitude (S) to response frequency in spikes/sec. (R) in LVT-comp units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 15 unit-directions (N) in 12 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. All data have been normalized as follows: Stimulus amplitude values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was 1 sec. The 1 sec. interval includes the first 100 msec. shown in Fig. 18.

LOW THRESHOLD DIRECTION, COMPLEMENTARY UNITS

observation time = 1 sec N = 15, n = 12

S = stimulus amplitude

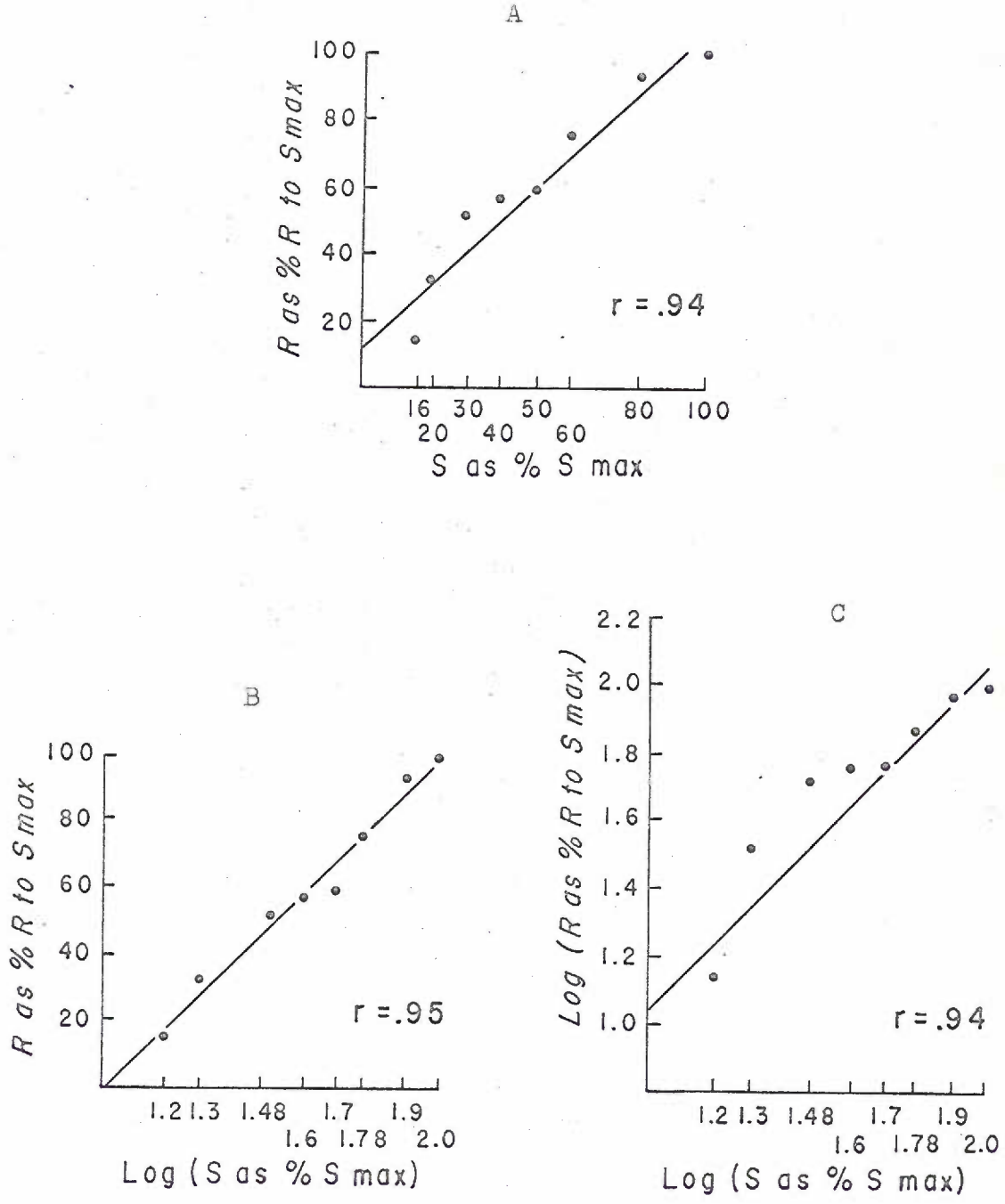
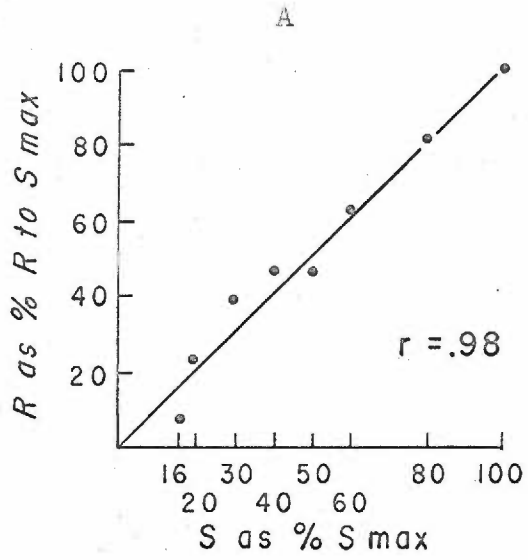


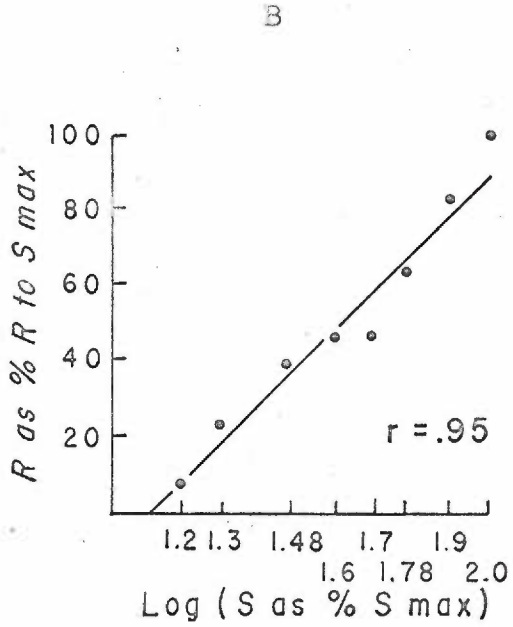
Figure 20. Relationship of stimulus deflection amplitude (S) to response frequency in spikes/sec. (R) in LVT-comp units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 9 unit-directions (N) in 8 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. All data have been normalized as follows: Stimulus amplitude values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was 5 sec. The 5 sec. interval includes the first 1 sec. shown in Fig. 19.

LOW THRESHOLD DIRECTION, COMPLEMENTARY UNITS

observation time =5 sec N=9, n = 8

S = stimulus amplitude





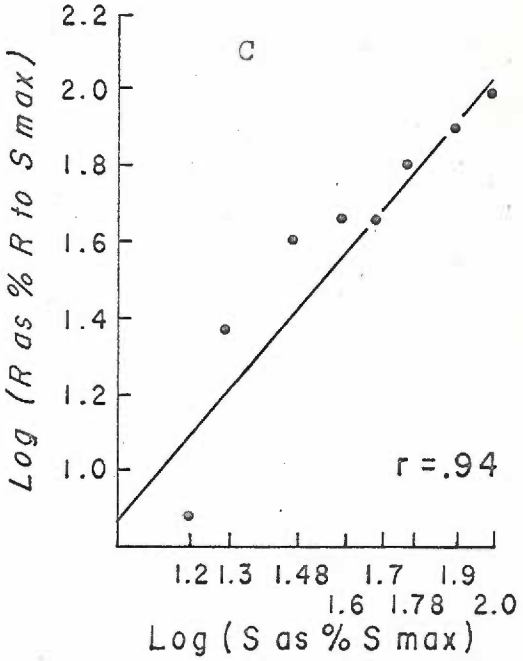


Figure 21. Relationship of stimulus deflection amplitude (S) to response frequency in spikes/sec. (R) in LVT-comp units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 15 unit-directions (N) in 13 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. All data have been normalized as follows: Stimulus amplitude values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was 10 sec. The 10 sec. interval includes the first 5 sec. shown in Figure 20.

LOW THRESHOLD DIRECTION, COMPLEMENTARY UNITS

observation time = 10 sec N = 15, n = 13

S = stimulus amplitude

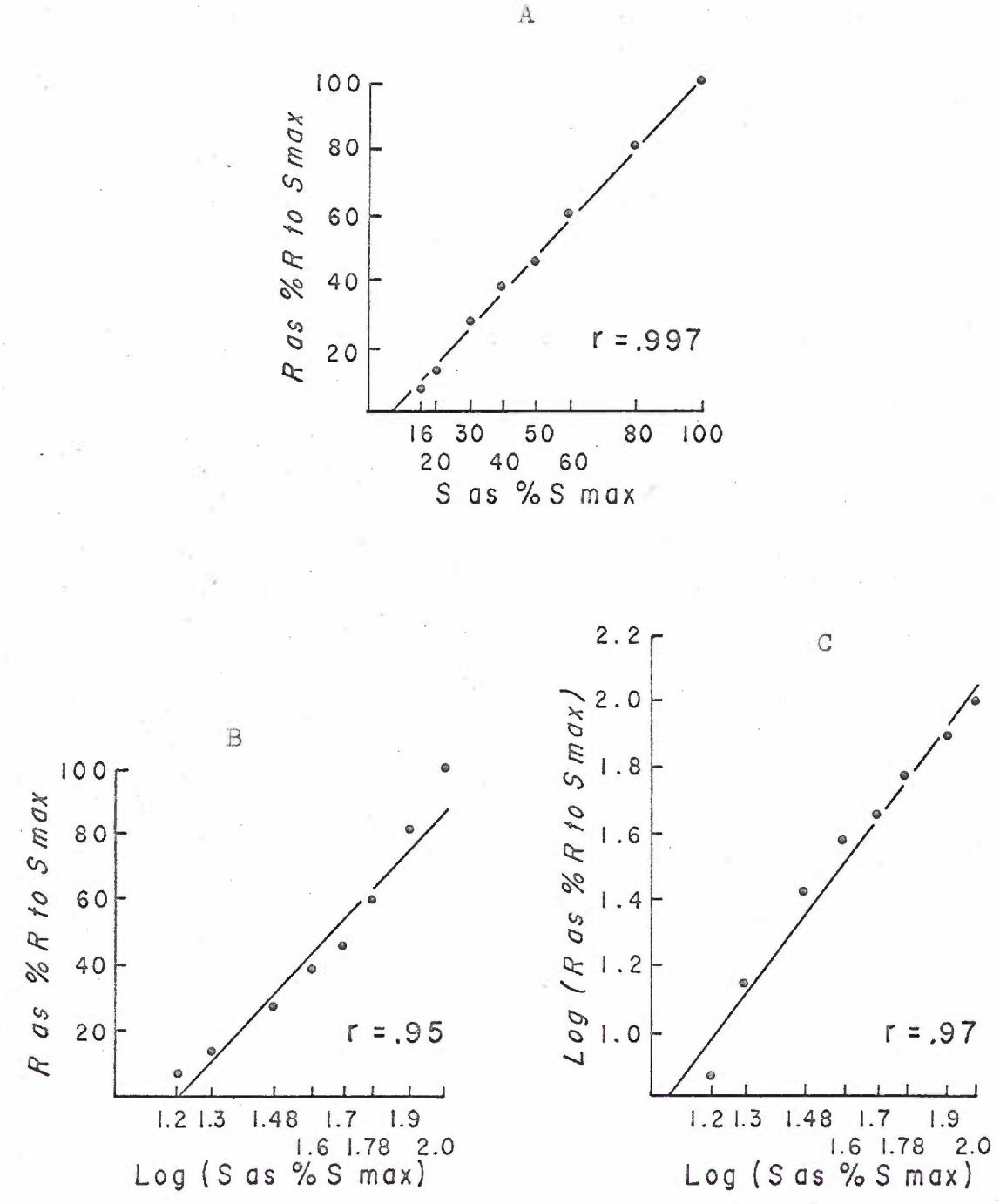
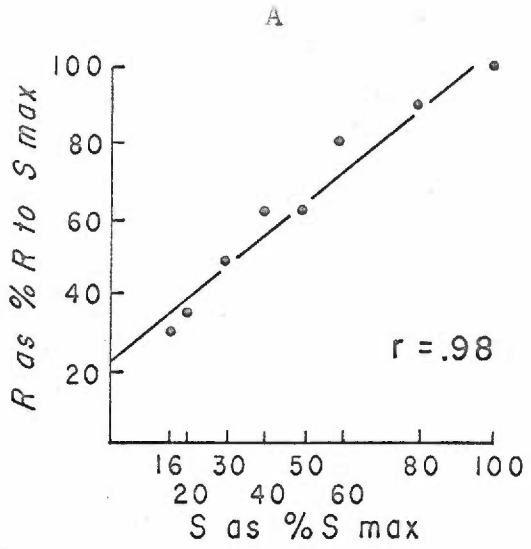


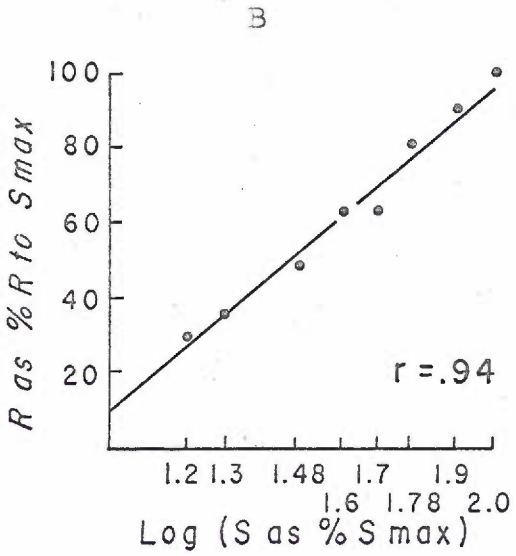
Figure 22. Relationship of stimulus deflection amplitude (S) to response frequency in spikes/sec. (R) in MVT units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 6 unit-directions (N) in 2 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. All data have been normalized as follows: Stimulus amplitude values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was 100 msec.

MODERATE THRESHOLD UNITS

observation time = 100 msec N = 6, n = 2

S = stimulus amplitude





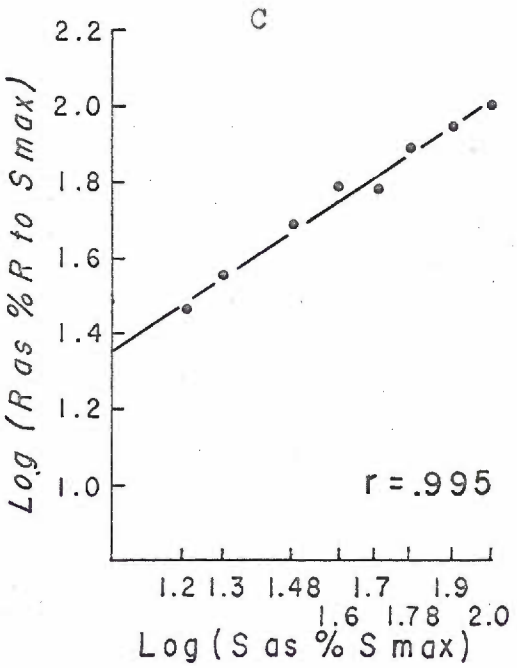


Figure 23. Stimulus amplitude, neural response frequency relationship for one LVT-comp unit. Deflection amplitudes were presented in a random order to the same vibrissa; the results are presented here in order of increasing stimulus amplitude. Velocity was 50 mm/sec. for all stimuli.

A. 0.8 mm. amplitude. Unit does not respond.

B. 1.0 amplitude. Unit does not respond.

C. 1.5 mm. Discharge ceases within 300 msec. after stimulus initiation. Three consecutive 100 msec. traces are shown.

D. 2.0 mm. Three consecutive 100 msec. traces are shown at the following time samples after stimulus initiation:

a. 0 sec. b. 4 sec. c. 8 sec.

E. 2.5 mm. a. 0 sec. b. 4 sec. c. 8 sec.

F. 3.0 mm. a. 0 sec. b. 4 sec. c. 8 sec.

G. 4.0 mm. a. 0 sec. b. 4 sec. c. 8 sec.

Time calibration: ⌊ = 25 msec.

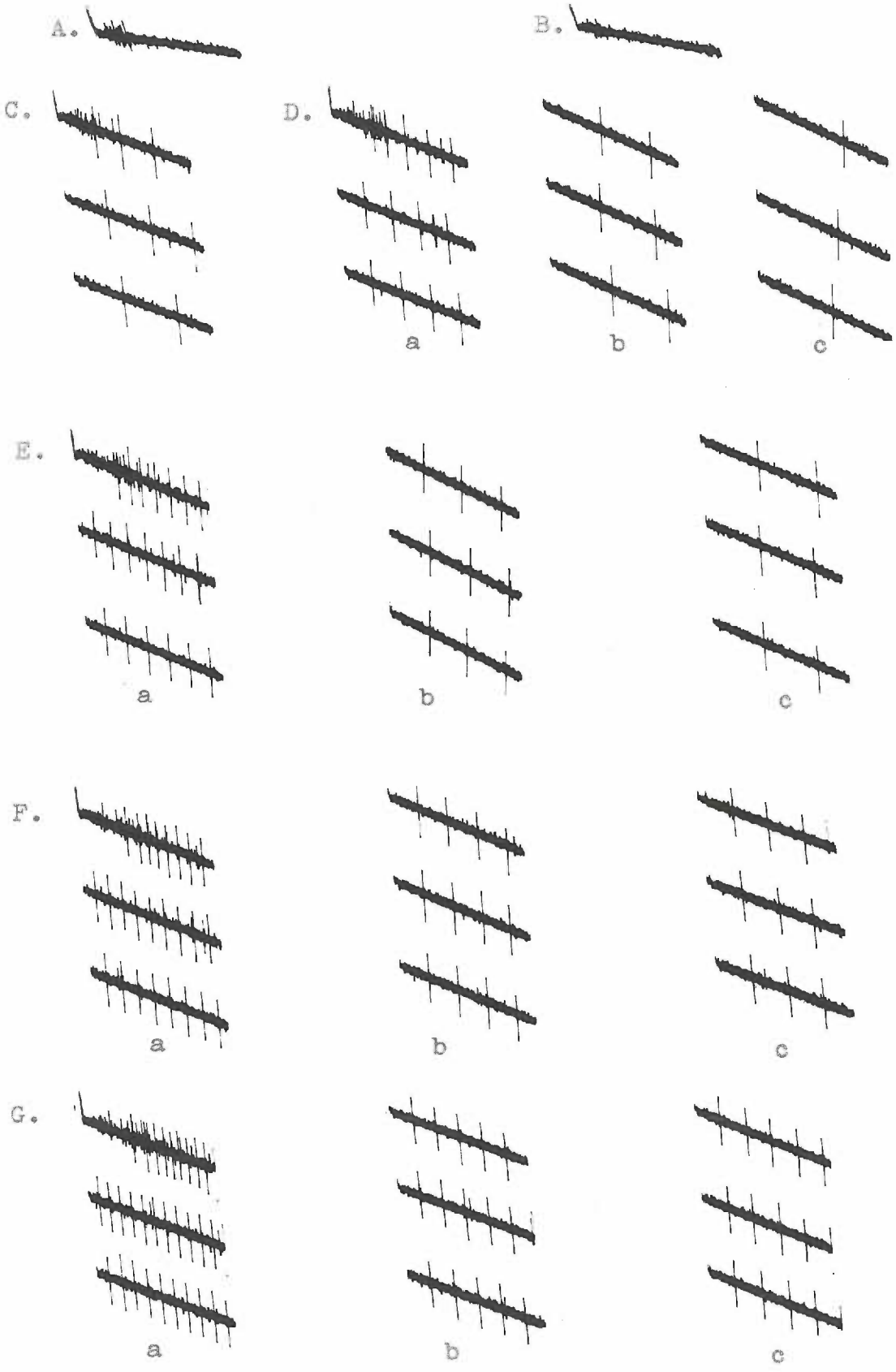
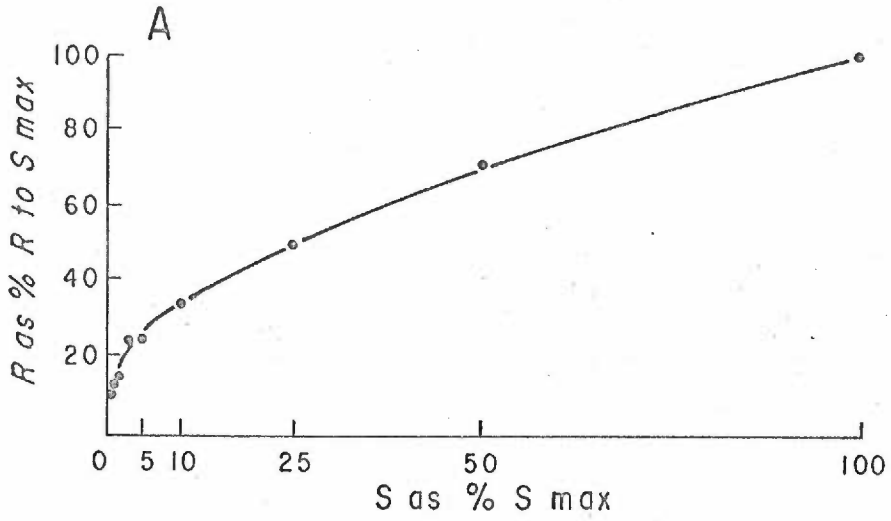

A.
B.
C.
D.
a
b
c
E.
a
b
c
F.
a
b
c
G.
a
b
c

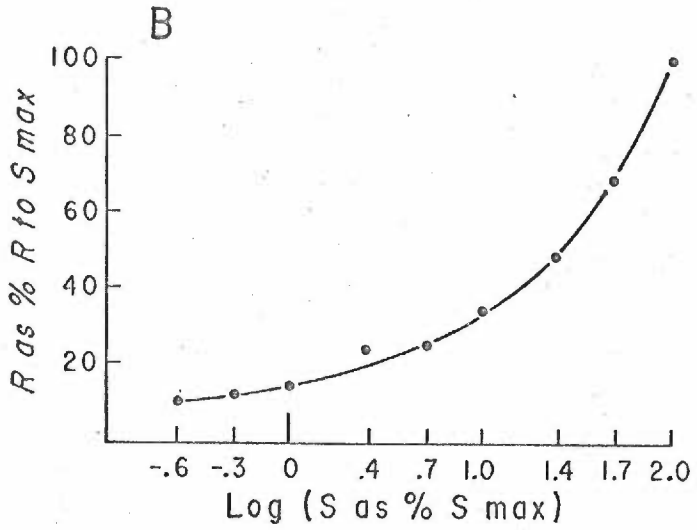
Figure 24. Relationship of stimulus deflection velocity (S) to response frequency in spikes/sec. (R) in LVT-comp units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 11 unit-directions (N) in 9 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. The curved lines drawn in graphs A and B were fitted to the data points by eye. All data have been normalized as follows: Stimulus velocity values are expressed as percent (in A) or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximum stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was stimulus onset time, that is until the final deflection amplitude was reached.

LOW THRESHOLD DIRECTION
COMPLEMENTARY UNITS

observation time = stimulus onset time
N = 11, n = 9

S = stimulus velocity





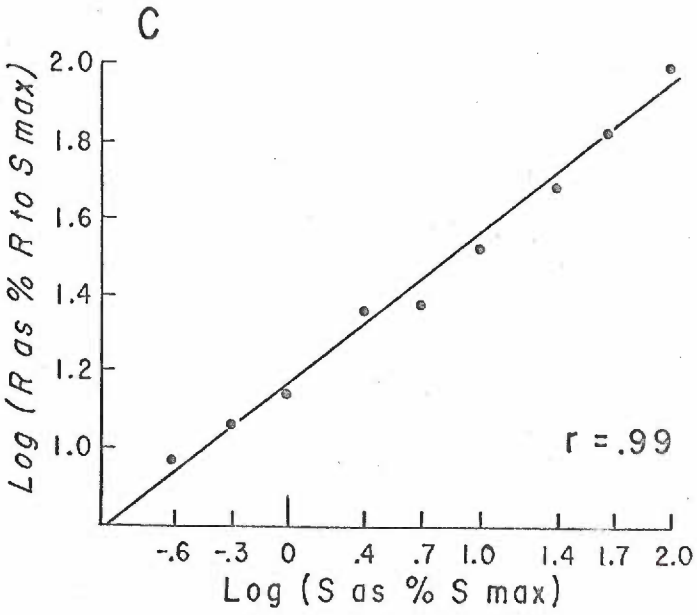
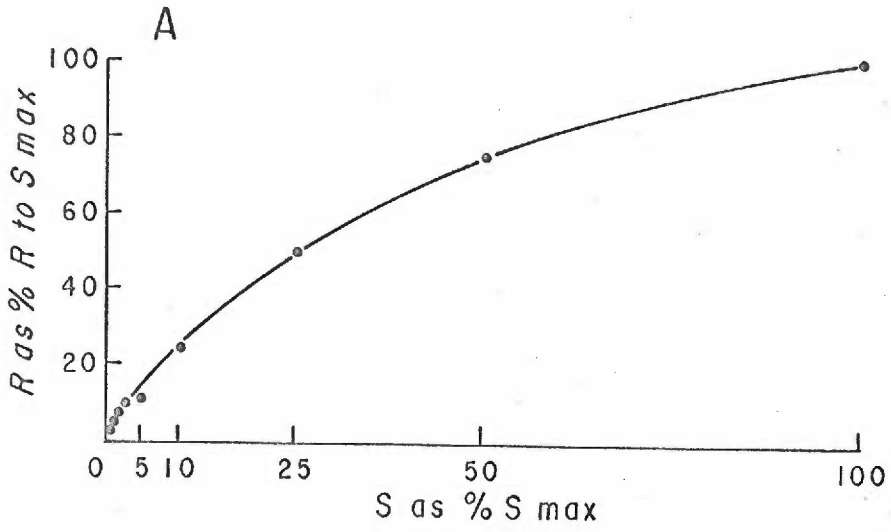
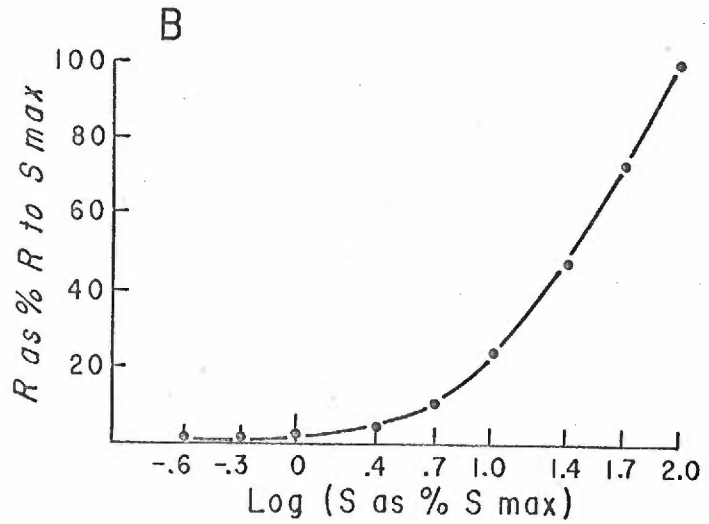


Figure 25. Relationship of stimulus deflection velocity (S) to response frequency in spikes/sec. (R) in MVT units. Graphs A, B, and C show the data plotted arithmetically, semi-logarithmically and double logarithmically respectively. Each point is the mean of 12 unit-directions (N) in 4 units (n). The correlation coefficient, r, expresses the fit of the mean values to the best-fitting regression line drawn through those values. The curved lines drawn in graphs A and B were fitted to the data points by eye. All data have been normalized as follows: Stimulus velocity values are expressed as percent (in A or log percent (in B and C) of the maximum stimulus value; response frequencies are expressed as percent (in A and B) or log percent (in C) of the response to the maximim stimulus. Observation time, the length of the interval after stimulus initiation in which impulses were counted, was stimulus onset time, that is until the final deflection amplitude was reached.





MODERATE THRESHOLD UNITS

observation time = stimulus onset time
N = 12, n = 4

S = stimulus velocity