MONTANA STATE UNIVERSITY

Antidromic and orthodromic responses evoked in cat cerebral cortex following brainstem stimulation : contribution of the pyramidal tract and other fiber systems
by Kent Walter Frette

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Zoology
Montana State University
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Abstract:
The physiological properties of two surface-positive potentials, recorded from the senserimeter area of the cerebral cortex following brainstem stimulation were studied in adult cats. These potentials, designated the a and b potentials, had latencies of 0.3-0.5 msec and 0.9-1.0 msec, respectively, following midbrain stimulation. The a potential is known to result from antidromic activation of corticofugal fibers. The present study was designed to determine if the b potential results from antidromic activation of a more slowly conducting corticofugal fiber group, or whether it results from orthodromic activation of a corticopetal fiber system. Rostral pontine and midbrain stimulating sites were used because the two principle fiber systems under consideration, the pyramidal tract and medial lemniscus, are separated by 4 to 5 millimeters at this level. This separation reduced the problem of volume conduction of the stimulus current and allowed for the more effective study of each fiber system individually.

The a and b potentials of largest amplitude were recorded at separate cortical areas. The largest A potentials were recorded near the lateral tip of the cruciate sulcus, while the b potentials of largest amplitude were recorded near the coronal sulcus. The largest b potentials were evoked when the stimulating electrode was positioned dorsal to the corticospinal tract in the pons and dorsal to the basis pedunculi in the midbrain. The a potential was most readily evoked when the stimulating electrode was in the basis pedunculi. The b potential was suppressed by conditioning stimulation to the contralateral forepaw between conditioning-test intervals of 20 and 200 msec. The a potential was not significantly effected by such conditioning stimulation at any conditioning-test interval. The a potential could follow repetitive stimulus rates in excess of 100/sec, while the b potential was greatly attenuated at comparable frequencies. The a potential showed a greater resistance to asphyxia than the b potential.

The results in this study indicate that the a and b potentials are mediated by different fiber systems. The a potential is most likely antidromically mediated by the pyramidal tract, while the b potential probably results from activation of an afferent fiber system following midbrain stimulation.

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KENT WALTER FRETTE

A thesis submitted in partial fulfillment
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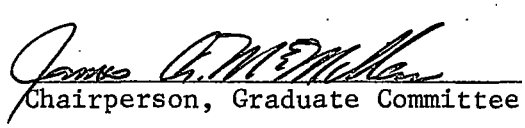
Approved: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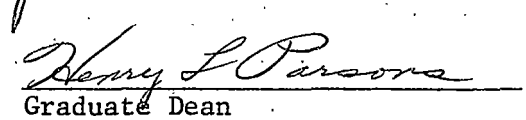
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ABSTRACT

The physiological properties of two surface-positive potentials, recorded from the senserimeter area of the cerebral cortex following brainstem stimulation were studied in adult cats. These potentials, designated the *a* and *b* potentials, had latencies of 0.3-0.5 msec and 0.9-1.0 msec, respectively, following midbrain stimulation. The *a* potential is known to result from antidromic activation of corticofugal fibers. The present study was designed to determine if the *b* potential results from antidromic activation of a more slowly conducting corticofugal fiber group, or whether it results from orthodromic activation of a corticopetal fiber system. Rostral pontine and midbrain stimulating sites were used because the two principle fiber systems under consideration, the pyramidal tract and medial lemniscus, are separated by 4 to 5 millimeters at this level. This separation reduced the problem of volume conduction of the stimulus current and allowed for the more effective study of each fiber system individually.

The *a* and *b* potentials of largest amplitude were recorded at separate cortical areas. The largest *a* potentials were recorded near the lateral tip of the cruciate sulcus, while the *b* potentials of largest amplitude were recorded near the coronal sulcus. The largest *b* potentials were evoked when the stimulating electrode was positioned dorsal to the corticospinal tract in the pons and dorsal to the basis pedunculi in the midbrain. The *a* potential was most readily evoked when the stimulating electrode was in the basis pedunculi. The *b* potential was suppressed by conditioning stimulation to the contralateral forepaw between conditioning-test intervals of 20 and 200 msec. The *a* potential was not significantly effected by such conditioning stimulation at any conditioning-test interval. The *a* potential could follow repetitive stimulus rates in excess of 100/sec, while the *b* potential was greatly attenuated at comparable frequencies. The *a* potential showed a greater resistance to asphyxia than the *b* potential.

The results in this study indicate that the *a* and *b* potentials are mediated by different fiber systems. The *a* potential is most likely antidromically mediated by the pyramidal tract, while the *b* potential probably results from activation of an afferent fiber system following midbrain stimulation.

INTRODUCTION

Physiological studies over the past twenty years have attempted to resolve conflicts concerning the organization of the pyramidal tract in terms of fast and slow conducting fiber groups. Some studies have proposed that longer latency potentials result from the antidromic activation of slower conducting pyramidal tract fibers following brainstem stimulation. Other investigations have indicated that such long-latency potentials result from orthodromic activation of afferent fibers adjacent to the pyramidal tract in the brainstem.

In this study, the physiological characteristics of two surface-positive potentials recorded from the cerebral cortex following brainstem stimulation were investigated. These potentials, the *a* and *b* potentials, have latencies of about 0.5 msec and 1.0 msec, respectively, following midbrain stimulation. This study was designed to determine if the *a* and *b* potentials represent the summation of antidromic action potentials mediated by fast and slow conducting pyramidal tract neurons, respectively.

REVIEW OF LITERATURE

General Considerations

The controversy over the functional significance and importance of the group of corticofugal neurons known as the pyramidal tract has existed for over a century. Although the quantitative data accumulated on the pyramidal tract is voluminous, the physiological role of this fiber system still remains speculative.

The pyramidal tract is an anatomical entity, not a physiological one. The term "pyramidal" refers to the passage of the descending axons through the bulbar pyramids in the caudo-ventral medulla. By definition, it comprises "those neurons with descending axons which traverse, longitudinally, the bulbar pyramids" (Patton and Amassian, 1960). Excluded from this definition are the arcuate fibers which transversly cross the ventral surface of the pyramid in route from the arcuate nucleus, which receives corticospinal terminations, to the cerebellum.

At the level of the bulbar pyramids, where the pyramidal tract is anatomically most pure, it is contaminated by functionally dissimilar fiber groups, while fiber groups bearing a closer functional relationship are not present. Inappropriately excluded from this definition are corticofugal fibers which terminate on the cranial motor nuclei. Although these fibers depart from the pyramidal system

at the level of the pons and, therefore, do not traverse the pyramids, they bear a close relationship in terms of motor function to the corticospinal fibers which terminate in the spinal cord nuclei.

Inappropriately included are those corticofugal neurons leaving the pyramids to terminate in the more dorsally located reticular formation. These fibers are potentially part of the "extra-pyramidal" system, since they do not constitute a direct projection system from the cerebral cortex to the spinal cord. These facts indicate the difficulty in obtaining a satisfactory functional definition for the pyramidal tract.

A thorough historical account of the early scientific investigations on the pyramidal tract (PT) is given by Marshall (1936). Turck first described the PT in 1851, dividing it into two fiber components based on the location of the fibers as they descend in the spinal cord. These components were identified as the capsular-lateral-column tract, known contemporarily as the crossed PT, and the capsular-anterior-column tract, which is equivalent to the uncrossed PT. Turck proposed that both of these fiber components originate in the basal ganglia.

Flechsig, in 1876, called the two components described by Turck the 'pyramidal tract', but held to the previous assumption that they originate in the basal ganglia. By use of the myelogenetic method, Flechsig later showed the origins of the PT to be in the cerebral

cortex in the monkey, particularly the precentral gyrus and the paracentral lobule. The pyramidal tract is unique in this respect since it is the only long descending tract to originate in the cerebral cortex; the other major descending tracts take origin in sub-cortical nuclei and the brainstem.

Origin of the Pyramidal Tract

The origin of the pyramidal tract (PT) in the mammalian cerebral cortex has been investigated by a variety of anatomical and electrophysiological techniques which have yielded varying results. As reviewed by Marshall (1936), Campbell in 1905 and Holmes and May in 1909 proposed that the PT originates exclusively from the giant Betz cells of the cytoarchitecturally defined motor area. This conclusion was based upon observations of retrograde chromatolysis in the Betz cells in a variety of mammals, including the monkey, following hemisection of the cervical spinal cord. Postcentral cortical areas were not observed for retrograde reactions. Since Lassek (1941) has shown that only approximately 18,000 Betz cells exist in the cerebral cortex of the monkey in comparison to the presence of about 500,000 fibers in the pyramids, it is apparent that the giant Betz cells account for less than 5% of the PT fibers.

Between 1905 and 1925, several anatomical reports demonstrated PT fibers originating in other cortical areas, principally the premotor

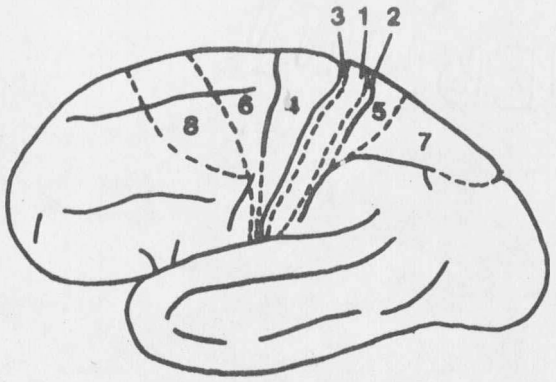
and postcentral areas (Marshall, 1936). Following cervical hemisection in the monkey, Levin and Bradford (1938) traced about 20% of the degenerating PT fibers to areas 3, 1, 2, and 5 of Brodmann; the rest were reported to originate in Brodmann's area 4 (Fig. 1). Using the same technique, Walberg and Brodal (1953) reported pyramidal origins in the temporal and occipital lobes in cats.

The extirpation of selected cortical areas followed by a histological examination of the pyramids for the presence of fiber degeneration is another anatomical technique used to determine the cortical origins of the PT. Barnard and Woolsey (1956) reported that about 60% of the PT fibers in the monkey, take origin anterior to the central sulcus, while 40% originate from more posterior regions, mostly from areas 3, 1, 2, 5, and 7 of Brodmann (Fig. 1). Peele (1942) reported degeneration in the pyramids of monkeys following ablation of Brodmann's areas 3, 1-2, 5, and 7.

Lassek (1942) reported degeneration of only 27-40% of the pyramidal axons following the extirpation of Brodmann's area 4, most of which were larger diameter PT fibers. More recently, Lassek (1952) reported that approximately one-third of the PT fibers were intact following ablation of the complete frontal lobe in the monkey; the remaining fibers were of small diameter. These latter results suggest that PT fibers from the parietal cortex of the monkey are of a smaller caliber than those originating anterior to the central sulcus.

Figure 1. Diagramatic representations of Brodmann's cortical areas for (A) man, (B) monkey, and (C) cat. These areas are numerically labeled and enclosed by broken lines. The major sulci on the cerebral surface are represented by solid lines in all cases. In (C), the cruciate sulcus is represented by the solid line between Brodmann's area 4 and 6. Figure 1 (A) is taken from Barr (1974), 1 (B) is taken from Ariens Kappers *et al.* (1967), and 1 (C) is taken from Papez (1929).

A



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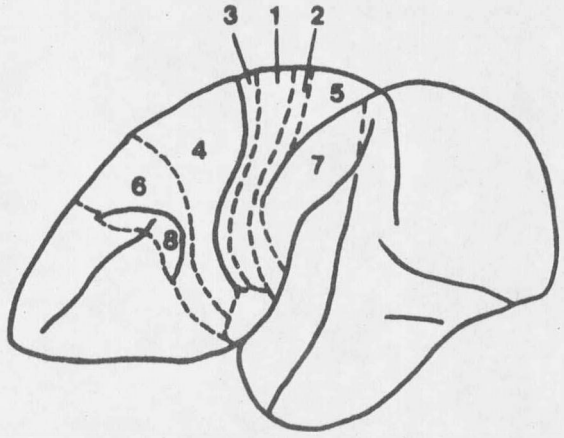

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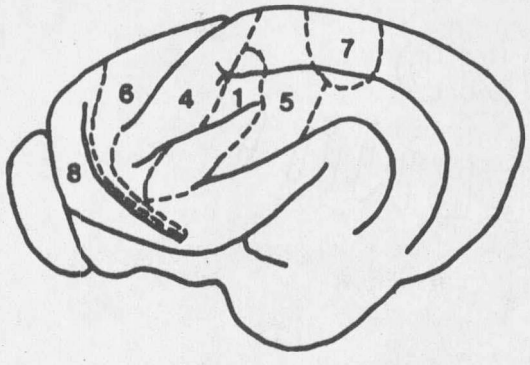

Electrophysiological techniques have been used more recently to study the cortical origins of the PT. Patton and Amassian (1954) reported that stimuli to the pericruciate cortex in the cat, including both somatosensory areas, evoke orthodromic discharges in cortico-spinal (PT) fibers in the bulbar pyramids. Lance and Manning (1954) recorded the largest orthodromic responses in the spinal cord of cats when stimulating on the lateral two-thirds of the anterior sigmoid gyrus or the entire posterior sigmoid gyrus.

By stimulating in the pyramids, impulses can be generated in the axons of PT neurons and conducted to the cell soma in the cortex, where a potential can be recorded from the surface of the brain. This phenomona is referred to as antidromic conduction, and has also been used to map the cortical origins of the PT. In studies on rabbits, cats, and monkeys, Woolsey and Chang (1948) recorded antidromic cortical potentials from Brodmann's areas 8, 6, 4, 3, 1, 2, 5, and 7 following stimulation of the medullary pyramids (Fig. 1). Lance and Manning (1954) reported that about two-thirds of the PT neurons originate anterior to the rolandic homologue (about 2 mm posterior to cruciate sulcus) in the cat, the remaining one-third in the 'sensory' cortex. Both Lance and Manning (1954) and Towe and Kennedy (1962) reported that the largest antidromic cortical potentials were recorded near the lateral tip of the cruciate sulcus in the cat following stimulation in the pyramids.

Based upon histological studies of the cerebral cortex in a variety of mammals, Lorente de No (1949) reported that Betz cell axons arise mainly from layer V (Fig. 2). As reviewed by Patton and Amassian (1960), electrophysiological studies on cats have demonstrated corticospinal units in all layers of the cerebral cortex except layers I and II. Towe *et al.* (1963), Towe *et al.* (1964), and Towe *et al.* (1968) segregated PT neurons in the cerebral cortex of the cat into two major groups based on (1) depth and (2) their latency of antidromic firing following bulbar stimulation. An early firing population of PT neurons, activated 1 to 2 msec following bulbar stimulation, is concentrated in layer V of the cortex, 1100-1700 microns below the surface (Fig. 2). A later firing group is activated 4 to 5 msec following stimulation of the pyramids and is concentrated in layer III, 700-1000 microns deep.

In summary, although neurons contributing to the pyramidal tract are found over a wide area of the cortex, they are concentrated for the most part in the sensorimotor area in all species which have been studied.

The origin of the pyramidal tract in man is not exactly established. In a fiber analysis of the pyramids in a 51-year-old female who had been subjected to a complete ablation of the precentral gyrus 20 years prior to death, Jane *et al.* (1967) reported that about 60% of the PT fibers had degenerated. Wiesendanger (1969) concludes that data

Figure 2. Laminar organization of the cerebral cortex. The six major layers of the cortex are labeled with Roman numerals at the left and separated by broken lines. The name of each principle layer is at the right. The small letters at the left identify the sub-divisions of layers IV, V, and VI. The lower solid line demarcates the cerebral cortex from the underlying white matter, which is labeled. Superficial and deep pyramidal tract (PT) projection efferent neurons and a thalamo-cortical afferent fiber are illustrated.