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NEURONAL CODING OF LOW FREQUENCY COMPLEX STIMULI AT THE COCHLEAR NUCLEUS AND INFERIOR COLLICULUS OF CAT BRAIN

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This Dissertation submitted by James L. Walker in partial fulfillment of the requirements for the Degree of Doctor of Philosophy from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

Edward S. Halas

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A special debt of gratitude is due to my wife, Lilly, who has offered encouragement and understanding throughout the year necessary to complete the experiment. The psychological consequences of several major equipment failures were considerably lightened by her presence.

This dissertation is dedicated to the memory of my mother, Phyllis Jaeger Walker, who helped create a family atmosphere placing great esteem on intellectual pursuits. Perhaps untimely loss of life from brain pathology will be reduced as we learn more about the central nervous system.

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ABSTRACT

Articles have recently appeared by Erickson (1968) and Pfaff (1969) which propose that the study of the activity of a large population of neurons may contribute information about sensory coding which is supplementary to data obtained from single neuron studies. These authors propose that there are not enough neurons in the primary sensory pathways so that every stimulus can be represented by a separate neuron. They maintain that over-all measures of neuronal activity will be more fruitful in the study of sensory coding. The present study used such a measure (multiple unit techniques) to monitor the over-all discharge characteristics of neuronal pools at the cochlear nucleus and inferior colliculus of cat brains to aural stimulation.

Measures of spike discharge frequencies were obtained from four adult cats. Stimuli consisted of recorded male and female voices presenting the words "one" through "ten". Data was collected from four sites: left and right cochlear nuclei and left and right inferior colliculi. The dependent variable was the number of neuronal spike discharges counted during each 500 millisecond recording period. The basic hypothesis of the experiment was that the large multiple unit spike bursts to aural stimulation consistently observed at the sites investigated represented a stimulus coding mechanism. If such a mechanism was operating, it was predicted that analysis of discharge patterns would reveal that the subcortical auditory nuclei discharge differentially to the different stimuli. It was also thought that different voices presenting the same stimuli would evoke very similar patterns of activity both within and between anatomical sites tested. The following effects were investigated: laterality of stimulation; stimuli; voices presenting the stimuli; and anatomical sites both within and between cats.

Results clearly indicated that at the level of the cochlear nuclei ipsilateral stimulation evoked a sustained multiple unit spike burst while contralateral stimulation had no observable effect on the on-going neuronal activity. The importance of laterality of stimulation was also clearly confirmed at the inferior colliculi level. Only rarely did ipsilateral stimulation at the inferior collicular level cause any detectable change in the on-going level of neuronal discharge. Contralateral stimulation, however, was consistent in evoking a sustained spike burst.

The experiment demonstrated that the multiple unit spike bursts observed at the cochlear nucleus and inferior colliculus have a functional significance. Different stimulus words generated discharge patterns which differed from each other. Different voices presenting identical stimuli also generated responses having a moderate to very high similarity to each other. The spike discharge patterns were highly similar at both cochlear nucleus and inferior colliculus in all experimental animals. There was also a very close association between anatomical sites within each cat.

The results contributed evidence that the original hypothesis of the existence of a neuronal coding mechanism was confirmed. This phenomenon appeared to be a prominent feature of the neuronal response to low frequency complex stimuli through the level of the inferior

colliculus. Low frequency sounds which are coded at the cochlear nerve by frequency of nerve fiber discharge appear to be encoded in the same way by groups of neurons at the dorsal cochlear nucleus and the inferior colliculus. The fact that the encoding mechanism occurs only below the level of the thalamus suggested that pitch discrimination may be essentially completed before the neuronal discharges arrive at the medial geniculate body of the thalamus.

CHAPTER I

STATEMENT OF THE PROBLEM

Introduction

The impetus for this research was derived from laboratory observations made while implanting electrodes in the subcortical auditory pathway of both anesthetized and conscious but paralyzed cats. The multiple unit neuronal activity of the electrodes designated for auditory sites was monitored as the electrodes were slowly lowered into position. At 0.5 mm steps one of the experimenters would speak into the cat's ear and the neuronal activity was observed for responsiveness to auditory stimulation. Using this method it was possible to detect when the electrode tip entered the auditory pathway. In the dorsal cochlear nucleus and the inferior colliculus two phenomena were readily apparent during vocal stimulation. The well-known cochlear microphonic effect was clearly present at both sites in the brainstem, and a sustained burst of multiple unit activity corresponding to the onset and termination of the stimulus was also observed. The limited appearance of the complex multiple unit neuronal discharge during the stimulus period seemed to suggest that the spikes were associated with or reflective of a sensory transmission process. The sustained spike burst was also specific to auditory sites, that is, sounds did not elicit spike bursts from non-auditory structures. The hypothesis that the multiple unit activity reflected neuronal encoding of sensory information was further strengthened after observing photographic records of the activity obtained using different stimuli. An examination of the photographs strongly suggested that different verbal stimuli tended to generate distinctive patterns of multiple unit activity. Again, a neuronal method of encoding complex auditory stimuli was suggested.

The present research represented a systematic effort to isolate and identify the frequency characteristics of the discharge patterns in the cochlear nucleus and inferior colliculus of cats to sensory stimulation with human speech. It was predicted that specificity of multiple unit patterns would emerge for each stimulus word and that there would be a high degree of communality between different speakers for each stimulus word across the tested sites. Standard electrophysiological implantation and recording techniques were used to monitor neuronal activity from macroelectrodes in six chronic adult cats. Voices of three males and three females were used in the experiment with each stimulus word being presented five times. Although an N size of five is rather unimpressive statistically, it was dictated by technical requirements. Galambos, et al. (1952), however, have reported that neuronal measures obtained from the first five responses do not differ statistically from samples as large as 75. The data were recorded on a seven track tape recorder. Two of the tracks were occupied by the stimuli and marker pulses, and five tracks remained for neuronal responses. Each stimulus situation was presented to the animals left ear, right ear and then bilaterally. The resulting data were computer analyzed and cast into appropriate form for interpretation.

In research on the neurophysiology of audition the choice of a complex stimulus such as human speech is quite unorthodox. More usually, researchers select an auditory stimulus of a simpler dimension such as a pure tone or click. The rationale behind the selection of such a stimulus is, of course, that the independent variable in the experiment possess a sufficient simplicity that it can be readily manipulated in the experimental situation and be free from possible confounding effects. The selection of such a stimulus for this experiment was contra-indicated by several factors. The presentation of the complex stimuli used in the experiment seemed to elicit both larger spike bursts and also more distinctive patterns of multiple unit activity than pure tones in a comparable frequency range. Since the purpose of the experiment was to investigate the possible role of the neuronal firing patterns in sensory coding, stimuli were chosen which generated neuronal activity most amenable to analysis.

human voice

Another, and perhaps more important, reason for selecting a complex stimulus for the experiment was to make the results more generalizable to everyday situations encountered by hearing organisms. In a natural environment man, or for that matter cats, seldom experience pure auditory signals. Auditory experience is a mixture of noise and complex sound of changing frequency and amplitude. In perceiving human speech, for example, words can be perceived as identical even though spoken by different speakers with widely different vocal characteristics. What is the neurophysiological mechanism that allows such differentiation? The choice of human speech as an experimental stimulus was partly determined by this consideration. The purpose of the experiment was to determine if a particular word, presented by several people, generated the same pattern of neuronal activity among sites in the cochlear nucleus and the inferior colliculus. It was assumed that a specific pattern of "communality" would emerge for each spoken word and it was hypothesized that it was this "communality" which makes the word intelligible even though spoken by different people. For technical reasons and to avoid introducing an excessive degree of stimulus complexity, short one and two syllable stimulus words were used.

Multiple Unit Recording Techniques

During the past several years, a number of experiments have been published using multiple unit neuronal recordings during behavioral and neurophysiological experiments (Buchwald, Halas and Schramm, 1965; Buchwald, Halas and Schramm, 1966; Starr and Livingston, 1963; Halas, Kalbfleisch and Beardsley, 1969; Halas and Beardsley, 1968; 1969a, 1969b, 1970; Galin, 1965; and Weber and Buchwald, 1965). It is not the purpose of this paper to provide a review of these experiments, however, several highly relevant papers will be briefly discussed. Using multiple unit recording techniques, Halas and Beardsley (1968) demonstrated that presentation of auditory and visual stimuli to curarized cats elicited neuronal responses from appropriate auditory and visual nuclei but not from inappropriate sensory systems. The same stimuli did not result in neuronal responses from non-sensory systems. In the same study it was demonstrated that the multiple unit recording technique yielded a low level of electronic interference or noise, resulting in a large signal to noise ratio. The maximum recording distance from each electrode tip was found to be about 1.0 mm.

A second relevant study recently appeared concerning the origin of the large neuronal spikes that are observed in multiple unit recordings (Halas, Kalbfleisch and Beardsley, 1969). It was thought that the large spikes represented either large spike potentials from single neurons or the summation of spike potentials from many neurons firing in unison. Two electrodes were implanted 1.0 mm apart in the sensory nuclei of a number of cats. The spacing of the electrodes allowed each to sample overlapping pools of neurons. If the neuron pools had some neurons firing in synchrony, it was reasoned that a large summated electrostatic field would have been generated and the electrodes in this field would record the same amplitude at the same time. The results supported the position that the large neuronal spikes were generated by the summation of many neurons firing in synchrony.

Methods of Studying Neuronal Encoding of Afferent Stimuli

The electrophysiological activity of the brain has been investigated for a number of years in the hope that it will provide one of the keys to unlocking some of the mysteries of brain function. Nearly 100 years ago Caton first described the low-amplitude fluctuating potentials of the central nervous system (Caton, 1875). This ongoing electrical activity has been extensively studied for the past 50 years and scientists are still uncertain as to where or how the rhythmic oscillations originate. Electroencephalogram (EEG) is the general term referring to these recordings. Despite intensive research attempting to associate EEG activity with behavioral changes or the activity of specific brain structures, few clear examples of such correlations have been demonstrated. The sole relationship which seems reasonably unequivocal is the association between high-voltage slow EEG activity and a behavioral state best characterized as "relaxation." As soon as the organism becomes attentive and orients toward a stimulus, the slow-wave high voltage activity is blocked and replaced by fast low amplitude asynchronous wave patterns (Grossman, 1967, p. 29). The EEG as an experimental technique for studying neuronal encoding of sensory input does not appear especially adequate since such basic questions as how the activity is produced still remain unanswered.

With the refinement of equipment and experimental technique, neurophysiologists began using the evoked potential to study the effect of sensory stimulation on various brain structures. Additional refinements resulted in the development of microelectrode recording techniques enabling the activity of single neurons to be monitored. In recent years the bulk of research on sensory coding in the central nervous system has utilized single unit recordings.

Several authors have recently criticized the fruitfulness of this approach (Erickson, 1968; Pfaff, 1969; Uttall, 1969). Erickson has proposed (1968, p. 459) that "information in the nervous system exists in the form of relative amounts of neural activity across many neurons..." Single unit research has shown that neurons in some sensory systems respond to a relatively large proportion of the relevant stimulus dimension (Adrian, 1943; Granit, 1955; MacNichol and Svaetichin, 1958; Brown and Wald, 1964; Hubel and Wiesel, 1962) while neurons in other sensory systems respond to a smaller segment of the stimulus dimension (Hartline, 1940; Mountcastle, 1957; Galambos and Davis, 1943; Katsuki, 1961). Erickson maintains that in both types of sensory system stimuli are encoded not by the activity of any single neuron, but by a "general pattern of activity" (Erickson, 1968; p. 459) among a cluster of parallel neurons. Two basic arguments are presented in support of this position. There are simply not enough neurons in the central nervous system so that every stimulus can be carried by a separate neuron. There are, for example, only 12,500 hair cells in the cat cochlea (Schuknecht, 1960). It is known that the cat can hear sounds ranging from 30 Hz to 70,000 Hz (Thompson, 1967). At each subsequent point in the auditory pathway there is an increase in the number of afferent neurons. Within the cochlear nucleus, for example, there are about 2.9 times as many afferent neurons as there are ganglion cells in the Corti (Chow, 1951). With such a relative scarcity of neurons at the receptor level of the auditory system, an assumption of narrow specificity such as is implicit in much single unit research would seem to curtail the number and complexity of stimuli that can be encoded by the auditory system. (1)

Erickson's second objection to the implicit view that the activity of single neurons reflect sensory coding involves the responsiveness of any single unit. In all sensory modalities it is found that each neuron responds to a fairly broad range of the relevant stimulus dimension. The data from such experiments are often interpreted only in terms of the point of maximum sensitivity. Unless the rest of the curve is classified as "noise" it is difficult to conceptualize any one neuron as representing a particular stimulus. Erickson assumes that "the nervous system works in an orderly manner being innocent of expending such large proportions of its energy in the production of noise." (1968, p. 457). (2)

The multiple unit recording techniques utilized in this study permit the activity of a large pool of neurons in the sensory nuclei to be monitored. The technique thus provides for a direct empirical test of Erickson's hypothesis that it is the relative amount of neuronal activity over a number of units that ultimately represents stimulus coding rather than the activity of any particular single unit.

CHAPTER II

REVIEW OF THE LITERATURE

Peripheral Mechanism of Auditory Coding

The middle and inner ears are the receptor organs responsible for the sensation of audition. Together with the sense organs of equilibrium, stretch, touch, and pressure, they are classified as mechanoreceptors. Since the source of the auditory information is external to the body, the ears are exteroceptors. Below 20 to 50 Hz hearing tends to merge gradually to the sensation of vibration. In young human ears the upper limit of hearing is approximately 20,000 Hz and 70,000 Hz seems to be the upper frequency limit for cats. With age the upper limit of frequency tends to drop. The difference between frequencies necessary to perceive two stimuli as different is less than one percent. The physical separation of the acoustic receptors allows lags in time of stimulus arrival at each ear as small as 10 msec. to be detected. Sounds as weak as the physical noise of thermal energy can sometimes be perceived and the range of auditory sensitivity extends up to levels intense enough to injure the sensory organ (Davis, 1959). For over 100 years scientists have investigated the properties of the sensory system that allows such widespread sensitivity and discrimination.

Basic Anatomy of the Ear

The peripheral aspect of the auditory mechanism is composed of three components; the external ear (auricle) and external auditory canal; the middle ear; and the inner ear. In animals with movable auricles the external ear may function to "funnel" sound energy into the system. In humans, however, the auricle appears to have little functional significance. The middle ear is filled with air and connected by the Eustachian tube to the nasopharynx. The tube allows for periodic equalization of air pressure between the middle and outer ear. Three bones, the malleus, incus, and stapes, form a system of levers in the middle ear which serve to connect the tympanic membrane with the oval window leading into the inner ear. It is believed that the chief function of the middle ear is to provide an impedance match between the air of the external auditory canal and the fluid filled inner ear (Davis, 1959). This equalization device helps insure that the acoustic energy is effectively delivered to the sensory receptor cells of the inner ear. The auditory receptors of the inner ear are located in the fluid filled cochlea. The sensory organ itself, is called the organ of Corti and it contains the sensory cells called "hair cells."

Peripheral Coding Mechanisms

Historically, the dominant concern of auditory theory has been to determine how the frequency and intensity of the acoustic stimulus is encoded in the nervous system. Several classical theories have been generated from research findings. Helmholtz (1862) originated the resonance or place theory of frequency discrimination (pitch is the psychological correlate of stimulus frequency). Basically, this theory maintains that each tone frequency activates a different segment of the organ of Corti. We are able to discriminate frequencies because different sensory cells are activated by different frequencies.

The second classic theory of pitch discrimination is the volley or frequency principle (Rutherford, 1886), which proposes that the frequency of the tone is coded by the frequency by which the auditory nerve discharges. This hypothesis maintains that the sound waves are not even analyzed in the cochlea. The acoustic signal was thought to be relayed to the auditory cortex with the analysis being made completely in the brain.

It is believed that intensity information may be coded by the total number of auditory fibers that are discharging or by a systematic grading of thresholds within the receptors (Davis, 1961). For the localization of a sound source, the parameters of binaural intensity differences and differences between ears in time of arrival are both known to be significant in the sensory coding of temporal differences (Davis, 1961).

Recent developments in auditory physiology seem to suggest that a more correct view of pitch discrimination lies somewhere between the views of the two classic theories. In 1943 von Bekesy first demonstrated a technique making it possible to observe the actual vibratory movement of the cochlear partition (Bekesy, 1943). According to von Bekesy's work, sound analysis in the cochlea results when a region of the cochlear partition vibrates as a result of auditory stimulation. Tasaki, Davis and Legouix (1952) have confirmed von Bekesy's findings. It has been demonstrated that when a tone of a particular frequency is presented, a traveling wave of fluid is created in the cochlea. Depending on the frequency of the eliciting tone, a maximum displacement occurs in a particular region of the basilar membrane. High frequency tones selectively displace regions of the membrane close to the base of the cochlea, intermediate tones distort intermediate regions of the membrane, and low frequency stimuli tend to affect the entire membrane. In general, the higher the tonal frequency, the closer the distortion of hair cells will be to the cochlear base. The cochlea is thus seen to function as a rather complex mechanical analyzer of the acoustic stimulus.

Although Bekesy's work appears only to support the place theory of pitch discrimination, upon closer inspection it also lends some support to the frequency theory. As was mentioned, the basilar membrane does not appear to exhibit differential sensitivity for low frequency tones. Since there are no apparent mechanisms at the cochlear level to account for pitch discrimination of low frequency stimuli, some principle other than the place theory must be operating. At least for low frequencies, some type of frequency coding must be occurring other than distortion of the basilar membrane.

It is well established (Bekesy, 1959; Bekesy and Rosenblith, 1951) that below 2000 Hz nerve impulses in the auditory nerve tend to fire in volleys. Volleys of action potentials at the frequency of the original sound wave have been observed as the discharges pass up the auditory nerve. This evidence tends to support a frequency theory of pitch discrimination. The "frequency-following" response will be discussed in greater detail in the section on central coding mechanisms.

If a macroelectrode is placed on the cochlea (Wever and Bray, 1930) an electrical potential can be observed which follows the intensity and frequency of the acoustic stimulus. This response, the cochlear microphonic, was originally believed to represent spike discharges of the eighth nerve. This would indicate that the discharges of the auditory nerve exactly match the input frequencies and would lend strong support to the frequency theory of pitch discrimination. Unfortunately, the matter was subsequently found to be much more complex. The microphonic was found to be a mixture of two phenomena: neuronal action potentials and the aural microphonic itself (Geldard, 1953). Except for the addition of harmonics to the original stimulus, the cochlear microphonic response is said to exactly reproduce the waveform of the eliciting stimulus, at least at the peripheral level. Unpublished observations by Walker, Halas and Oring (1970) suggest that at the cochlear nucleus and inferior colliculus a considerable degree of distortion is introduced into the microphonic. Unlike auditory action potentials, the cochlear microphonic does not show a time lag appropriate to the recording site in the auditory pathway, and does not have a true threshold in the sense that the nerve response has one. Another distinction between neuronal action potentials and the microphonic lies in responsiveness to a broad range of stimulus frequencies. Neuronal action potentials never have the very high frequencies recorded in the microphonic. The cochlear microphonic response has also been found to be highly resistant to adverse conditions such as anoxia and anesthetics (Davis, 1959). The fact that a weak microphonic response may be recorded up to an hour or so after death has suggested to some workers that the cochlear microphonic is a purely physical electro-mechanical byproduct of auditory activity. Other authorities view the cochlear microphonic as a generator potential which excites the afferent nerve endings of the auditory receptors electrically (Tasaki, 1954; Davis, 1961).

A much slower potential, the summating potential, can also be recorded from the cochlea (Davis, 1959). This potential appears as an envelope of the cochlear microphonic activity. A negative and positive aspect of the summating potential is observed. The negative summating potential is thought to be generated by the internal hair cells, while the cochlear microphonic and the positive component of the summating potential are attributed to the cuticular surface of the external hair cells (Davis, 1961).

In summary, it would appear that both frequency of neuronal discharge and place of excitation in the cochlea are important factors in the peripheral coding of tonal frequency. For frequencies below 4000 Hz synchronous neuronal discharges play a role, while the place principle is most important for high frequency stimulation. Intensity seems to be encoded both by the activation of fibers with selectively different thresholds and by the total number of fibers which discharge. The cochlear microphonic and negative summating potential produced by the bending of hair cells may act as a generator potential which ultimately is responsible for initiation of action potentials in the auditory fibers.

Central Coding Mechanisms

Certain arbitrary limits are placed on the description of the "classical" auditory pathway, since neuronal activity may be elicited in many systems of the brain by stimulation of the organ of Corti. The classical pathway of Ramon y Cajal is usually used as the standard anatomical series of connections between the organ of Corti and the cerebral cortex (Ades, 1959). The sequential series of connections are as follows: organ of Corti, cochlear nerve, cochlear nucleus, trapezoid body, superior olivary nucleus, lateral lemniscus and its nuclei, inferior colliculus, brachium of the inferior colliculus, medial geniculate body and the acoustic fibers radiating to Brodmann cortical auditory areas 22, 41, and 42 (House and Pansky, 1967). The projection pathways in the auditory system tend to differ from other sensory systems in the number of neural elements in the pathway. The somatic sensory system, for example, is characterized by a three neuron chain from the sensory receptor to the cortical projection area. In the auditory system there is a much more complex system of interruptions, and there are at least four or more neurons in the sequence. Ades (1959, p. 587) has speculated that

> ...one factor leading to this situation must have been that, since the cochlea and its central connections developed phylogenetically late as compared with other sensory systems, the ascending pathway had to be constituted from such scattered elements as were still open to modification in a neural matrix otherwise too fixed in pattern to permit of a new through pathway.

Several observations have been reported which are difficult to explain with a strict adherence to the classical auditory pathway. Galambos, et al. (1952) have reported, for example, the presence of single units in the medial geniculate with a response latency far too long for the impulses to be carried over the classical auditory pathway. Erulkar, et al. (1956) have reported similar longer than usual latencies from regions in the cerebral cortex. Another finding suggesting the existence of additional auditory pathways is that evoked responses can be elicited from cerebellar units by sound stimulation (Ades, 1959) and also from the lateral geniculate body (Hotta and Kameda, 1963) and primary visual areas of the cat cortex (Spinelli, et al., 1968; Kornhuber and Fonseca, 1964).

Descending fibers in the auditory pathway are known to exist from the acoustic cortex to the cochlea. These fibers generally run parallel with the ascending system although they seem to bypass many of the nuclei of the ascending system. Reviews on the descending pathways have been published by Livingston (1959) and Galambos (1954).

Central Mechanisms of Frequency Coding

Studies of single neurons in the auditory pathway have yielded a great quantity of evidence on the coding of acoustic stimuli (Galambos and Davis, 1943; Galambos, 1944; Thurlow, et al., 1951; Gross and Thurlow, 1951; Galambos, et al., 1952; Hilali and Whitfield, 1953; Katsuki, et al., 1958; Katsuki, et al., 1959; Rose, et al., 1963; Hind, 1953). Many of the results of these and other studies can be summarized by saying that single units can be found at all levels of the auditory system which fire to a tone onset, or decrease discharging when a tone is presented, or discharge continuously during the duration of a stimulus. Spontaneous discharge of neurons is also observed at the cochlear nucleus, trapezoid body, inferior colliculus, and medial geniculate body. At the upper levels of the auditory pathway neurons exhibit less spontaneous firing, and at the cortex most neurons are found to be silent (Katsuki, 1961). In the cochlear nucleus and the medial geniculate body the spontaneous activity can be reduced by presenting an auditory stimulus (Galambos and Davis, 1943; Galambos, et al., 1952). At the superficial layers of the auditory cortex most neurons do not respond continuously to pure tones, but tend to exhibit only brief responses at the beginning or termination of the tone.

At the cochlear nerve and the trapezoid body a sigmoid relationship is obtained between frequency of neuronal discharge and sound intensity (Katsuki, 1961). At the auditory cortex and the thalamic level the sigmoid relation is not maintained. In general, the higher the recording level in the auditory pathway, the lower the rate of neuronal discharges as a function of stimulus intensity.

Most of the work on stimulus coding in the auditory pathway has involved systematic investigation of the range of stimulus frequencies which elicit discharges from single units at various levels. Once a single cell has been experimentally isolated in the laboratory, a frequency curve is obtained by presenting a range of tones with differing frequencies and intensities. The response curve is a frequency-threshold curve, and the "best frequency" is that frequency where the cell can be fired with stimuli of the lowest intensity. Two types of response areas are generally obtained in the auditory pathway (Katsuki, 1961). The first response type is asymmetrical against the axis of the "best frequency." The upper frequency limit of this type of response area is a sharp cut-off and the lower frequency side of the threshold shows a gradual rise toward the lower frequency which will elicit a response. The second type of response area mentioned by Katsuki is one where the curve is symmetrical against the axis of the "best frequency." Most of the units which show this type of response area have low "best frequencies."

The response areas of cells at progressively higher levels of the auditory pathway are progressively sharper. The narrowest area tends to be obtained at the medial geniculate body of the thalamus. Cortical response areas tend to be wider than the thalamic patterns. Thus, as we ascend the system, it appears that the discriminability of cells is sharpened. Thompson (1967, p. 271) has suggested that this effect may occur as a result of inhibitory synaptic interaction between cells at all regions of the auditory system.

Response Latency in the Auditory Pathway

A great deal of evidence has accumulated concerning the time relationships involved in the central auditory pathway. Significant delays are introduced as the auditory impulse travels up the brain. Traditionally, investigators have measured this response latency by measuring the reception of a strong stimulus indicated by the appearance of the microphonic and the appearance of action potentials at various auditory sites. Latency in the auditory system is a function of the sound intensity and a considerable degree of variation appears between units and animals. The data of Katsuki et al., (1958) seem to agree with reports by other workers. At the auditory nerve the latencies range from less than one to two milliseconds (msec.). In the dorsal cochlear nucleus latencies ranging from one to five msec. are reported and two to five msec. delays are observed at the trapezoid body. The latencies obtained at the inferior colliculus vary between five and eight msec. At the medial geniculate body of the thalamus, Galambos et al., (1952) have reported responses occurring as early as seven msec. and as late as 125 msec. As mentioned earlier, the longer latencies observed at the medial geniculate cannot readily be explained by a strict adherence to the classical auditory pathway. The latencies of evoked cortical response to sound lies within a range of 10 to 15 msec. (Galambos et al., 1952).

In general, the latency findings agree reasonably well with the four or five element model of the central auditory pathway. When allowance is made for the delay in conduction time in the neuron, it appears that the primary delay is that at the synaptic junction. The time lost at each synapse appears to be around 0.8 msec. (Geldard, 1953, p. 146). These findings agree with measurements made at synaptic junctions in other sensory systems.

Frequency-following Neuronal Responses

In the section on peripheral coding of frequency information it was seen that in the auditory nerve low frequency stimuli cause volleys of action potentials corresponding to the frequency of the original sound wave. This phenomenon can also be seen at the cochlear nucleus of the medulla and to a limited extent at high levels of the auditory pathway. At the trapezoid body the "frequency-following" response (FFR) appears to show some limitation. The maximum stimulus frequency which will reproduce itself at the trapezoid body appears to be 2500 Hz (Kempt et al., 1937) although tones as high as 4000 Hz tend to produce an asynchronous discharge at this level. At the acoustic cortex no "frequency-following" responses are observable with pure tones, however, a series of distinct click stimuli can be reproduced up to 100 Hz. The neuronal response breaks down beyond this frequency. Part of the reason for not obtaining volleying responses at the upper levels and particularly at the cortex undoubtedly stem from the use of anesthetics.

Neurologically, a general anesthetic first innervates the higher brain regions extending its influence progressively downward.

The FFR in the central auditory pathway has been relatively neglected in the recent literature. Studies by Boudreau (1965a, 1965b), Rose (1966, 1967) and Tsuchitani and Boudreau (1964) describing FFR-like neuronal responses have recently appeared. Boudreau (1965a) has inferred from his results that information coded in the auditory nerve by a volleying action is coded in a similar manner by the fibers of the trapezoid body which ennervate the superior olivary complex. Recent work by Rose et al., (1967) has also reported a phase-locking of the auditory nerve of the squirrel monkey where the discharges are grouped at intervals around integral multiples of the tone period. The phase-locking is characteristic of sites up to the inferior colliculus and has been observed for stimulus frequencies up to 5000 Hz. In isolated instances, however, the single unit phase-locking response has been observed to frequencies as high as 12,000 Hz. Two other papers which are highly relevant to the present research because of their recording techniques, neuronal responses, and recording sites (Worden and Marsh, 1968; Marsh and Worden, 1969) are also reported in the recent literature.

Worden and Marsh (1968) have recorded from gross electrodes in the central auditory pathway and observed a neuronal response which, like the cochlear microphonic, reproduces the sine wave of the eliciting sound. Recording from chronically implanted macroelectrodes in adult cats, Worden and Marsh observed a neuronal response at the cochlear nucleus which tended to reproduce the sine wave of the stimulus and continued throughout the duration of the stimulus. The FFR did not reproduce the stimulus as accurately, however, as the cochlear microphonic. While the amplitude of the cochlear microphonic remained constant throughout the stimulus duration, the FFR amplitude was greatest at the tone onset and gradually decreased as the tone continued. After the first ten msec. of the response the amplitude was found to decrease by approximately 72-75 percent.

Unlike the cochlear microphonic, which has a graded onset corresponding to the stimulus onset, the FFR is reported to appear with a threshold-like abruptness. The FFR also differs from the cochlear microphonic in showing an onset latency appropriate to neuronal latencies of the recording site. As the frequency of the eliciting stimulus is increased, the amplitude of FFR is reduced and its variability is increased. Using a stimulus of 70 db SPL, reference sound pressure level, re: 0.0002 dynes/cm^2. The peak of the amplitude curve was found to generally occur at 2000 Hz. At the cochlear nucleus the maximum frequency range for the FFR could be extended to 500-5000 Hz using a stimulus intensity of 80 dB. No significant differences were found for the upper frequency limit of FFR between conscious and anesthetized cats.

Worden and Marsh's data suggest that the upper frequency limit for FFR tends to decrease at higher levels in the auditory pathway. At the inferior colliculus, for example, the upper frequency limit for FFR was 1000 Hz or less. The amplitude of FFR was larger at the cochlear nucleus than in higher auditory sites. The upper limit for recording FFR seemed to be the afferent side of the inferior colliculus close to the lateral lemniscus. Sites at the brachium of the inferior colliculus and the medial geniculate did not yield FFR.

As would be expected from anatomical pathways, contralateral stimulation does not evoke FFR from the cochlear nucleus. At the lateral lemniscus, contralateral stimulation evokes a larger amplitude FFR than ipsilateral stimulation. Within the same neural structure considerable variation occurs across electrodes in the form of the FFR. A neuroanatomical mapping of these differences was not attempted in the study.

In a subsequent study on FFR, Marsh and Worden (1969) demonstrated the presence of both phasic and tonic FFR amplitude suppression. Their findings suggested that FFR modulation depends on peripheral rather than central factors. The action of the acoustic reflex of the intrinsic ear muscles was implicated. When the inner ear muscles were inactivated by a neuro-muscular blocking agent (Flaxedil) or by tenotomy (the stapedius and tensor tympani tendons were cut) no modulation of FFR was observed at the cochlear nucleus, trapezoid boyd, or medial accessory olivary nucleus.

Tonotopic Organization of the Auditory Cortex

It is well-known that the auditory system is a topographic sensory modality (Woolsey and Waltz, 1942; Rose, et al., 1963; Tunturi, 1944; Galambos and David, 1943; Katsuki, 1961). What this means, essentially, is that there is a clear spatial projection of acoustic frequency at all levels of the system, from the Corti to the acoustic cortex. At each level in the auditory system frequency is represented in a spatial manner.

Since the present research involves cats, the discussion will be limited to a summary of what is known about projection of the auditory signal to the cat's brain. At least six different auditory areas have been described in the cat (Woolsey, 1961). The primary auditory region in the cat (AI) lies in the temporal lobe, occupying the greatest part of the middle ectosylvian gyrus. Woolsey and Waltz (1942) demonstrated a topographic organization in AI. High frequency stimuli were found to project to anterior portions of AI and low frequency sounds projected to the posterior portion. Tunturi (1952) has reported that stimulus intensity also appears to be projected topographically to the primary auditory cortex with intensity being represented spatially at right angles to the corresponding frequency area. The differential intensity representation was found to be maintained, however, only for contralateral stimulation.

Tunturi (1960) and Hind, et al., (1961) have reported similar topographic projections to the primary auditory cortex in unanesthetized dogs and cats. As mentioned in the section on central coding mechanisms, individual cortical cells in the primary auditory area generally have a "best frequency." The breadth of the response area for these cortical units is generally smaller than at the inferior colliculus or lower in the pathway, but larger than the response areas observed at the medial geniculate body.

Woolsey and Waltz (1942) have also demonstrated a tonotopic projection in a second auditory area (AII) of the cat brain. AII lies slightly ventral to the primary auditory cortex. Low frequencies are projected anteriorly in AII and high frequencies are projected posteriorly (exactly opposite the projection pattern found in AI). The existence of a third major auditory area in the cat cortex was demonstrated by Downman and Woolsey (1954) and Sindberg and Thompson

(1962). The region occupies the posterior ectosylvian gyrus and is referred to as auditory area "Ep." High frequencies tend to project on the dorsal aspect of Ep and low tones are projected ventrally.

Tunturi (1945) and Bremer (1953) have reported auditory evoked potentials in somatic sensory area II. An auditory response area in the insular cortex has also been demonstrated (Loeffler, 1958; Sendberg and Thompson, 1962; Desmedt, 1960; Thompson, et al., 1963). Responses to somatic sensory, auditory, and visual stimulation can be observed in the insular region. Thus, the area is often referred to as a "polysensory" cortical region. The topographic projection to the insular cortex seems to be high tones dorsally and low tones more ventrally. The work of Desmedt (1960) has shown that stimulation of the insular cortex inhibits cochlear nucleus responses. The insular cortex is, therefore, implicated in the descending efferent auditory system.

The work of Woolsey (1961) has pointed to the existence of a sixth auditory area having a topographic organization. The area lies on the lower aspect of the suprasylvian sulcus and overlaps to the surface of the cortex, and is referred to as the "suprasylvian fringe" (SF). High frequency tones are projected to the dorsal aspect of SF just above AI. Low tones are projected to the surface of the anterior ectosylvian gyrus slightly below the primary auditory cortex. For a neurobehavioral analysis of the various auditory areas the interested reader may refer to Meyer and Woolsey (1952), Butler, Diamond and Neff (1957), Thompson (1960), Neff (1961), Thompson (1964), Randall (1965), and Axelrod and Diamond (1965).

Central Mechanisms of Temporal Coding

As mentioned in the discussion on peripheral coding mechanisms, binaural intensity differences and differences between ears in time of stimulus arrival are both known to be important peripheral variables in localizing a sound source. The binaural intensity differences are known to be especially important for high frequencies, while the differences in time of stimulus arrival at the ears is very important for low frequency sounds (Stevens, 1938). It is well-known that the auditory system projects bilaterally with perhaps a slight preference for the contralateral side of the brain. Auditory stimuli presented to only one ear tend to influence auditory cells differently than stimuli delivered to both ears.

It is beyond the scope of this report to present a detailed review of the literature in this area. Excellent papers have recently appeared by Boudreau, et al. (1968), Goldberg, et al. (1963), Hafter, et al. (1968), Hall (1965), Hall, et al. (1968), Hind, et al. (1963), Moushegian, et al. (1964), Nelson, et al. (1966), and Whitworth and Jeffress, (1961). A brief review of some pertinent research findings follows.

In 1964 Rosenzweig demonstrated that gross evoked potentials of the auditory cortex differ depending upon the ear that is stimulated. Contralateral presentation of stimuli generated an evoked potential of greater amplitude than ispilateral stimulation. A difference of less than 0.5 msec. in the time of binaural stimulation was found to produce significant differences in the amplitude of evoked auditory potentials.

Stotler (1953) has described specialized cells in the superior olivary complex of the cat which apparently encode differential time of arrival of stimuli at the ears. The cells are described as having two large dendrites. One dendrite is directed laterally and the other is directed medially. The afferent connections to the latter come from the contralateral side of the auditory system and most connections to the former originate from the ipsilateral side. Similar specialized cells have been reported by Galambos, et al., (1959).

Goldberg and Brown (1969) have also reported the presence of units in the superior olivary complex which contribute to sound localization. Two kinds of binaural cells are reported by these workers: "excitatory-excitatory" neurons which receive excitatory inputs from both ears, and "excitatory-inhibitory" cells which are activated by stimulation of one ear and depressed by activation of the other ear. The two types of cells were found to respond differently to binaural intensity differences. The "excitatory-excitatory" cells are reported to be very sensitive to "variations of average binaural intensity, but may be relatively insensitive to the introduction of interaural intensity differences" (Goldberg and Brown, 1969, p. 629). The "excitatory-inhibitory" cells are influenced by inter ear intensity variations, but are relatively insensitive to changes in the average binaural intensity of the stimulus. The presence of these types of neurons has also been reported at the medial geniculate body, inferior colliculus, and auditory cortex (Adrain, et al., 1966; Hall and Goldstein, 1968; Hind, et al., 1963; Rose, et al., 1966).

At the inferior collicular level, Hind (1963) has demonstrated the presence of units which are relatively unresponsive to ipsilateral stimulation. Curiously enough, binaural stimulation caused these units to fire more frequently than stimulation of either ear alone. Cells responding in this manner appeared to have a "best frequency" of 850 Hz. It has been emphasized by Rose, et al., (1963) that each inferior colliculus neuronal unit seems to have its own distinctive discharge pattern. Using an evoked potential technique Hirsch (1968) has demonstrated similar findings in the amplitude of the auditory cortex evoked response. She has found that the evoked response is much greater when contralateral stimulation leads ipsilateral tone presentation. When the ipsilateral stimulus was presented before the contralateral tone, the evoked response was minimal. Using ipsilateral tones above 2000 Hz it was, in fact, difficult to evoke a cortical response. In speaking of the evoked potential technique Hirsch maintains that

> ...a study of the slow-wave potential can offer important complementary data to those obtained from single-unit studies, since the slow-wave potential provides an overall view of what is presumably occurring in a large unit population (1968, p. 925).

The same advantages could, of course, be ascribed to the multiple unit recording technique utilized in this research. Since the multiple unit recording technique provides an index of neuronal activity in a large cluster of cells, it provides advantages in the study of sensory coding over those obtainable from single unit techniques. However, until much more work has been completed on firing patterns of both individual cellular units and groups of cells we will still not completely comprehend how the brain encodes auditory information.

CHAPTER III

METHODS

Subjects

Six adult cats were used in the experiment. Cats Lz, Lg, Pg, and Rp were male, and cats Do and Ge were female. Chronic electrode implantation was completed one year prior to data collection. Several months prior to this experiment the animals had completed long-term instrumental avoidance conditioning. All of the cats remained healthy and were docile.

Implantation Procedure

Standard electrophysiological techniques were used for chronic implantation of monopolar macroelectrodes. Cats were anesthetized with ether and a tracheal cannula was positioned. The right foreleg was shaved and an intravenous cannula was inserted. The cat was then placed in a Kopf sterotaxic instrument and after the cranium was shaved, a longitudinal incision was made on the scalp. When the cranium had been cleaned of connective tissue and muscle, sites were marked on the skull and small holes were drilled in the appropriate locations. Electrode sites were marked using standard Horsley-Clarke coordinates (Ajmore and Marson, 1960; Snider and Niemer, 1961).

At this stage the ether anesthetic was terminated and the animal was paralyzed with gallamine triethiodide (Flaxedil). The cat was artificially respired (15-20 strokes/min.) throughout the period of paralysis. Multiple unit neuronal activity was monitored while each electrode was lowered into position. Each electrode was cemented to the skull with Cadon and referenced to an indifferent stainless steel screw mounted in the skull. At the completion of implantation, the cat was anesthetized with sodium pentobarbital (Nembutal). The electrode leads were soldered to a Cannon plug mounted on the skull with Cadon. The wounds were perfused with Zephiran and tightly drawn together with surgical thread. At the completion of surgery animals received intramuscular injections of procaine penicillin G (Duracillin).

Electrodes were constructed from 00 gauge stainless steel insect pins and insulated with Epoxylite. Each electrode tip was bared for a distance of 0.1 to 0.3 mm. Cats Lz and Lg had electrodes positioned in the right dorsal cochlear nucleus and the left inferior colliculus. The remaining four cats had electrodes in both right and left dorsal cochlear nuclei and left and right inferior colliculi. Horsley-Clarke stereotaxic coordinates for cochlear nuclei placements are presented in Table 1. In all cats left inferior colliculus coordinates were P 2.0, L 4.0, H 11.0, and right inferior colliculus coordinated P 2.0, R 4.0, and H 11.0 were used. The cochlear nuclei electrodes were angled 30 degrees toward the anterior and the inferior colliculi electrodes were angled 20 degrees toward the posterior.

Recording Procedures

All experiments were conducted in a sound deadened room adjoining the equipment room. The cats were anesthetized with intraperitoneal injection of Nembutal. Ear phones calibrated and matched on a Bruel and Kjaer Model 1613 Precision Sound Level Meter were used for stimulus

TABLE 1

STEREOTAXIC COORDINATES FOR COCHLEAR NUCLEI PLACEMENTS

Cat	Left Dorsal Cochlear Nucleus			Right Dorsal Cochlear Nucleus		
Lz	--	--	--	P 7.5	R 7.0	H .15
Lg	--	--	--	P 7.5	R 7.0	H 3.5
Pg	P 6.5	L 8.0	H 3.0	P 7.5	R 7.0	H 3.0
Rp	P 7.5	L 7.0	H 2.6	P 7.5	R 7.0	H 3.0
Do	P 7.5	L 7.0	H 2.0	P 7.5	R 7.0	H 0.0
Ge	P 7.5	L 7.0	H 3.0	P 7.5	R 7.0	H 3.0

presentation and were placed in the external auditory meatus. The neuronal activity was picked up from the electrode tip, and fed into a Tektronix 122 preamplifier. The signal was then passed through an electronic filter which removed slow wave EEG activity. The neuronal activity was then relayed to a Tektronix 565 oscilloscope for visual display. A parallel circuit relayed the neuronal activity into a Minnesota Mining and Manufacturing (3M) C100 tape recorder where it was permanently recorded.

Stimuli

Stimuli consisted of the spoken words "one" through "ten" presented by three female and three male voices. The stimuli were recorded by student announcers at the campus radio station in a sound deadened room. The words were recorded once onto a tape loop which was used to transfer the stimuli to track three of the 3M-C100 tape.

The words were presented to the animals at an intensity of approximately 65 dB.

Each stimulus tape was recorded prior to collection of the neurological data. The tape contained six complete stimulus "loops." Loops one to three were presented to the left site under conditions of left, right, and bilateral aural stimulation. Loops four to six were presented to the right side under the same stimulational conditions. Track four of each tape was reserved for the clock pulses. Clock pulses were recorded on every tape after the stimulus words had been recorded. The voices were relayed to a specially constructed "automatic triggering" electronic circuit. The energy conveyed by the onset of each voice triggered the clock pulse generator which then generated and recorded a 500 msec. series of clock pulses. The pulses bracketed the onset and termination of the stimulus words. Photographic records of the spike bursts elicited by the stimuli indicated that the bursts did not exceed the 0.5 second recording time.

Neurological Recording Procedures

After the animals lost consciousness, they were placed on a table in the sound-deadened room and the ear pieces were positioned in the external auditory canal. Each stimulus tape included two recording sites, either left and right cochlear nuclei, or left and right inferior colliculi. Trials began on recording track one to the end of the tape, then to track two, five, six, and seven. Each track thus represents a replication of identical stimulus situations. During the neurological recording situation a direct lead from playback track three (voice track) to the ear phones was maintained. At the same time the neurological activity was recorded on a parallel track. Thus, at all times track three was on playback and one of the other tracks was recording live neurological data. The completion of recording on all five tracks required about eight hours of recording time. Cats were given one week of rest between the first and second recording session. Because of the lengthy recording period at each session, it was necessary to interrupt the tape approximately every three to five hours to administer small doses of Nembutal. .A technician remained in the recording room throughout each session in order to observe the level of anesthesia, and to change recording sites and aural stimulation when appropriate. Whenever an animal showed muscular movement lasting longer than approximately one minute, Nembutal was readministered. Recording was resumed after the cessation of all but respiratory movement.

Analog to Digital Conversion Procedure

All neurological data was recorded direct onto the analog tape recorder. Data analysis did not commence until all of the experiments were completed. The data was converted from analog to digital one track at a time. The neurological information was played from the recorder to the oscilloscope, relayed to a specially constructed digital data analyzer and then automatically punched into IBM cards by a IBM 024 key punch. Each of these steps are subsequently explained in somewhat more detail.

No formal measurement or validation of the fidelity of the neurological recordings on the 3M tape recorder was undertaken. Experienced observers were unable to detect any qualitative difference between recorded neurological data and on-line data. Comparison of photographs made from the tape and directly from the cat have indicated that no distortion, either in time base or in clarity of the signal, was introduced by the tape recorder.

The neurological signal was relayed from the oscilloscope to a specially designed solid state digital data analyzer. Figures 1 and 2 present the basic outline of instrumentation for recording and analyzing the neurological signal. The data analyzer counted the frequency of the neuronal spikes during the 0.5 second stimulus period. The stimulus period was divided into 18 equal time intervals. Immediately following each stimulus period the data were automatically punched on IBM cards by the IBM 024 key punch.

The digital data system was constructed so that the threshold of measurement was set at the central hash mark on the Tektronix 565 oscilloscope. By adjusting the position of the beam carrying the multiple unit activity, the effective threshold of measurement can be manipulated. If all ongoing neurological activity is above the central hash mark, the digital data system will record all zeros. As the beam carrying the neuronal signal is lowered below the threshold, the numerical counts become progressively higher until an asymptotic level is attained. The effect of adjusting the beam location in relation to the threshold is presented in Figure 3. The neurological activity represented in the figure was generated in cat Pg, left inferior colliculus by female one presenting the stimulus word "eight" under conditions of contralateral stimulation. The ordinate represents frequency of neurological spike activity in number of spikes per unit time. The horizontal axis contains 18 independent observations made during the 500 msec. recording duration. Traces A through H each

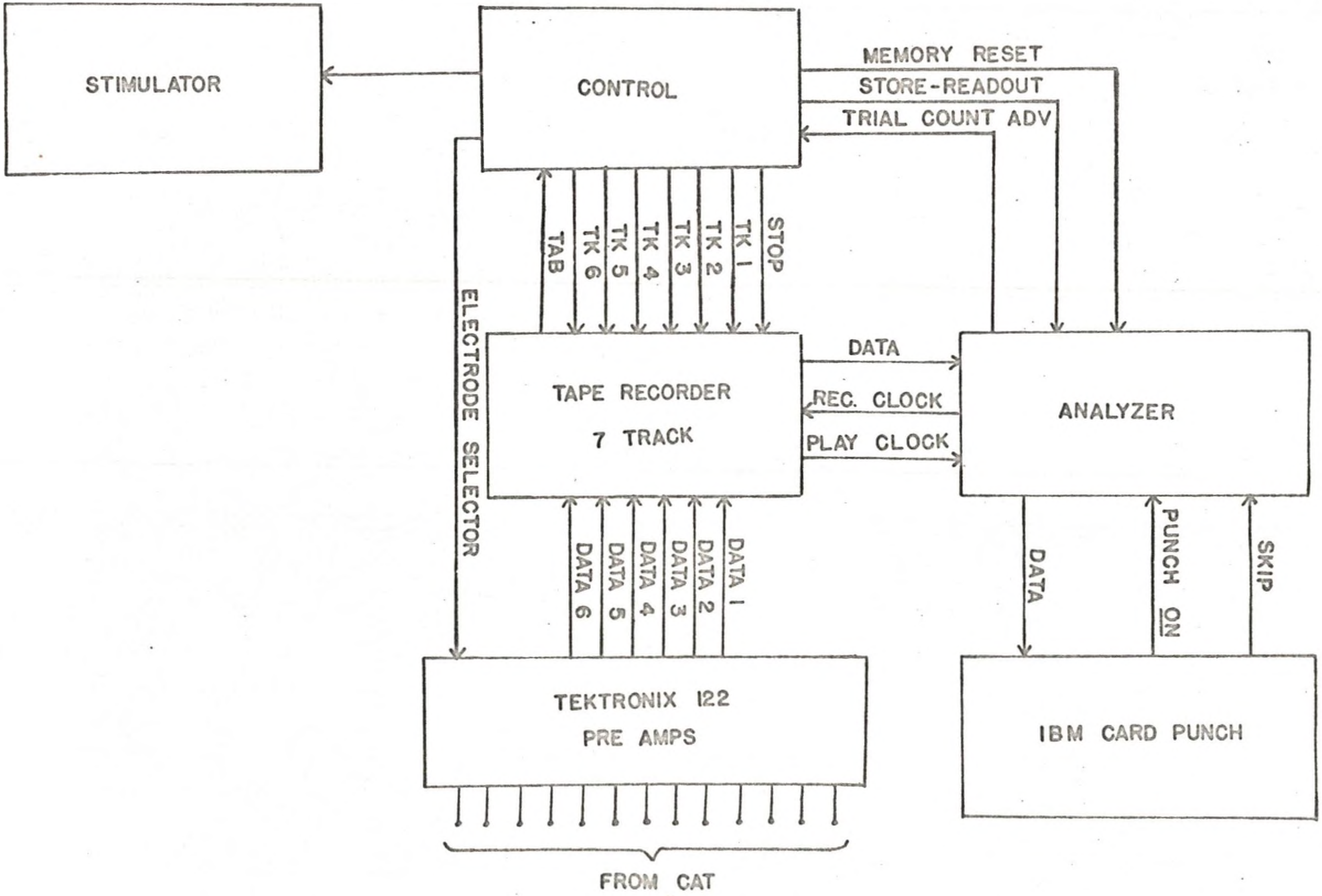


Figure 1. Block diagram for stimulating, recording and analyzing multiple unit neuronal activity.

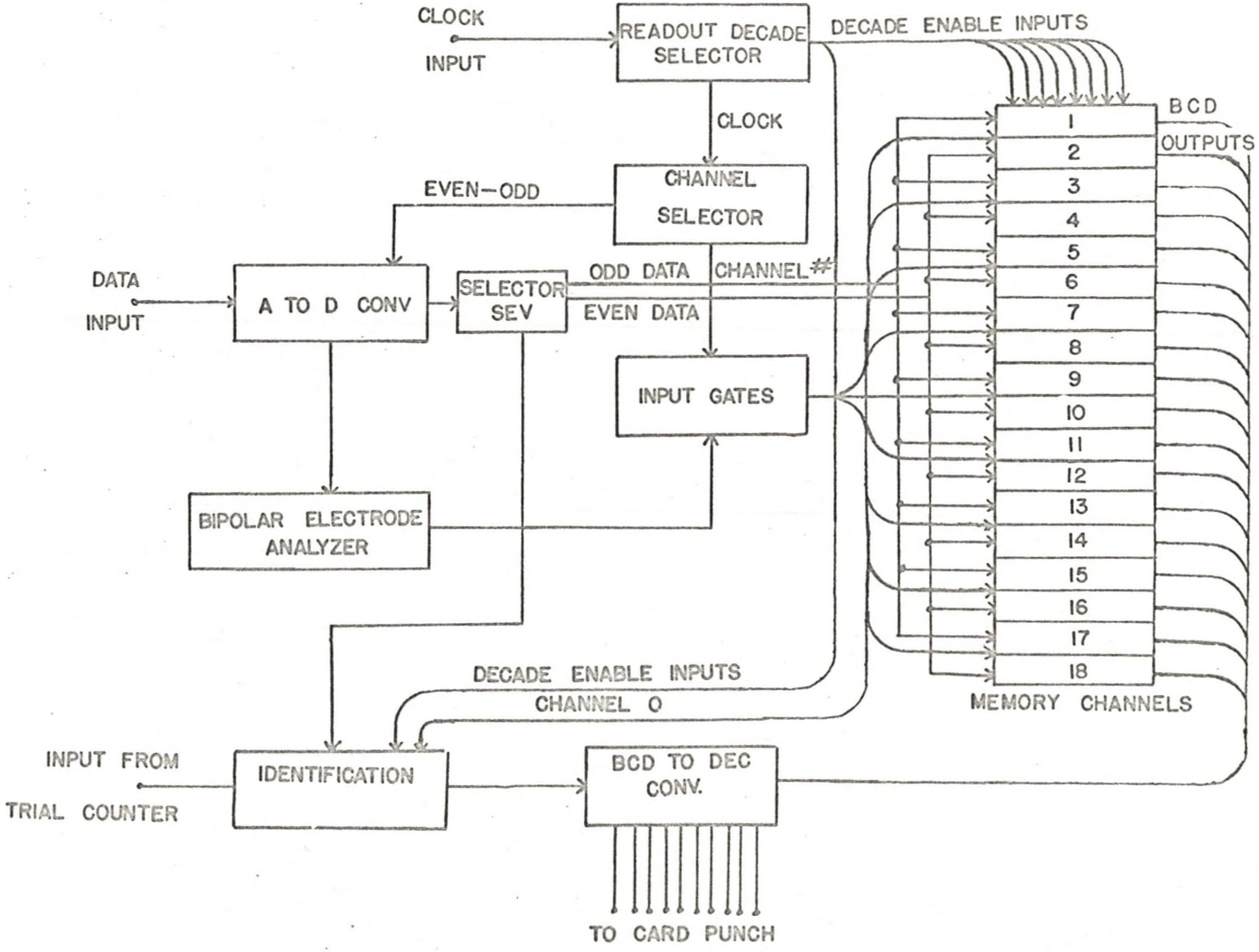


Figure 2. Block diagram for 18 channel digital data analyzer.

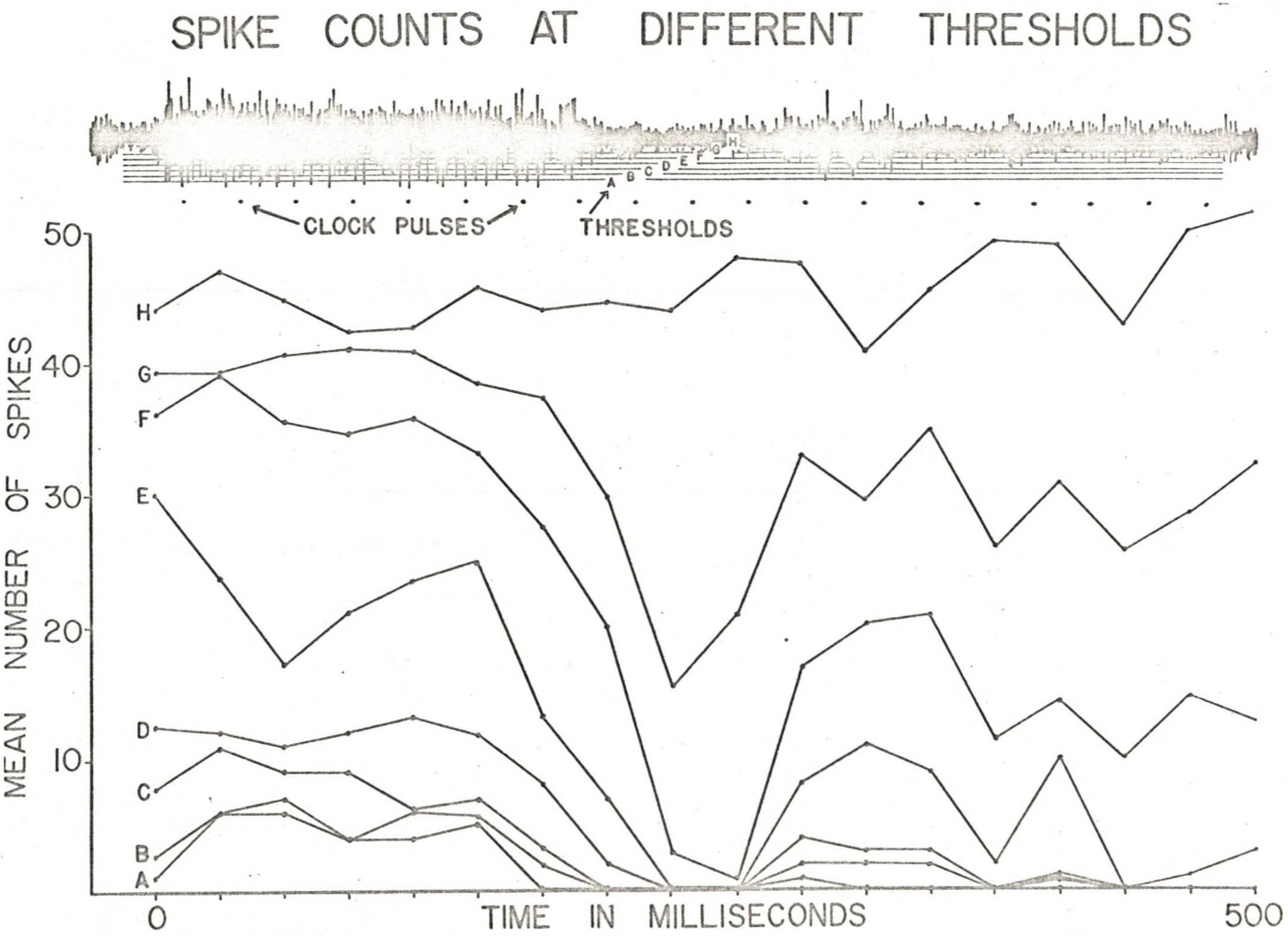


Figure 3. Mean number of spikes at eight different recording thresholds. Each data point represents the mean of ten independent observations.

represent the same data monitored at different threshold levels, with trace A reflecting the highest threshold and trace H the lowest. In trace A the ongoing multiple unit activity was well above threshold level. Only portions of the evoked activity in both A and B were below threshold. Traces D and E were the first locations which reflect measurement of the multiple unit neuronal burst elicited by the stimulus. Traces F and G represent the point at which the tip of the spontaneous ongoing activity was below the recording threshold. In trace H, all aspects of the neurological response were well below threshold value, and the data system was recording ongoing activity. It is apparent from this data that if the recording threshold is too low, the frequency discharge pattern generated by the stimulus would be completely obscured. For the purposes of data collection in this experiment, the beam was adjusted so that the tip of ongoing activity rested on the measurement threshold.

A reliability check of the digital data system yielded the results presented in Table 2. The neuronal spike burst was from cat Pg, left inferior colliculus, elicited by a female speaker presenting the word "eight" under conditions of contralateral stimulation.

The neuronal signal was relayed through the digital data analyzer ten times and intercorrelations were computed between the resulting ten IBM cards. It can be seen from the table that the data analyzer presented a highly reliable set of measurements of the neuronal signal. The reliability measures range from .993 to .999. The very small degree of discrepancy between the ten measures apparently was generated when two spikes appeared so close temporarily that on one trial the analyzer

TABLE 2

PEARSON PRODUCT MOMENT CORRELATIONS AMONG TEN INDEPENDENT COUNTS OF A 500 MILLISECOND MULTIPLE UNIT SPIKE BURST (N=18)

	Cards								
	2	3	4	5	6	7	8	9	10
1	.996	.997	.996	.996	.996	.993	.995	.997	.994
2	--	.997	.997	.996	.996	.996	.995	.997	.995
3	--	--	.997	.997	.997	.993	.996	.998	.995
4	--	--	--	.997	.999	.997	.997	.998	.997
5	--	--	--	--	.997	.995	.997	.998	.996
6	--	--	--	--	--	.996	.996	.997	.998
7	--	--	--	--	--	--	.998	.997	.998
8	--	--	--	--	--	--	--	.998	.998
9	--	--	--	--	--	--	--	--	.997

counted them as a single spike while on another trial they were resolved as two spikes.

Data Analysis

At the completion of the analog to digital conversion procedure the neuronal data from each anatomical site had been coded on 900 IBM cards. Since a total of 20 sites were investigated, 18,000 data cards were available for analysis. The great bulk of this data dictated that computer programming be developed to handle the analysis.

The experiment was basically designed to answer two questions: will different words generate different neurological discharge patterns, and how much communality of neuronal discharge will be present between different voices presenting the same word. To assess the degree of communality between speakers product-moment correlations were computed for the multiple unit activity evoked by different speakers presenting identical stimuli at the same ear and site. Since the frequency range of the male voices was significantly lower than that of the female voices, intercorrelations were limited to female voices as a subgroup and male voices as a separate subgroup.

In order to compare multiple unit activity between different stimulus words, the five independent observations of each stimulus for each of the three same-sex voices were averaged and plotted by a IBM 360 computer. Each point on the polygon represented an arithmetic mean of 15 scores.

Treatment of the total data in this manner resulted in the production of 1200 different polygons. It would be very difficult to present this mass of data in a comprehensive manner. Therefore, it was decided in advance of data analysis that one cat would be selected and complete sequential data for one cochlear nucleus and inferior colliculus site presented. The figures for this sequential presentation were organized so that male and female voices for both contralateral and ipsilateral stimulation could be compared on the same figure. Additional polygons are presented for comparisons between sites and cats.

Intercorrelations between different voices were calculated using the mean of the five observations available for each data point. Using this procedure 18 pairs of scores were used to compute each intercorrelation. With an N of 18 any correlation coefficient of .59 or larger will be significantly different from zero (t=2.921) beyond the .01 level of confidence (McNemar, 1962, p. 138).

CHAPTER IV

RESULTS

Neuronal data was collected for all stimulus conditions from six adult cats. Oscilloscopic inspection of neuronal responses from both the dorsal cochlear nuclei and inferior colliculi sites in cats Do and Ge revealed a complete lack of responsiveness to auditory stimulation. This lack of neuronal responsiveness to sound was also indicated by the computer print-out for these cats. All sites showed essentially random on-going neuronal activity. The data from cats Do and Ge were, therefore, not subjected to further analysis, and are not presented here. Since neuronal responsiveness to sound at both the cochlear nucleus and the inferior colliculus has been such a common observation in our laboratory, it was probable that the recording sites in these animals were outside the auditory pathway.

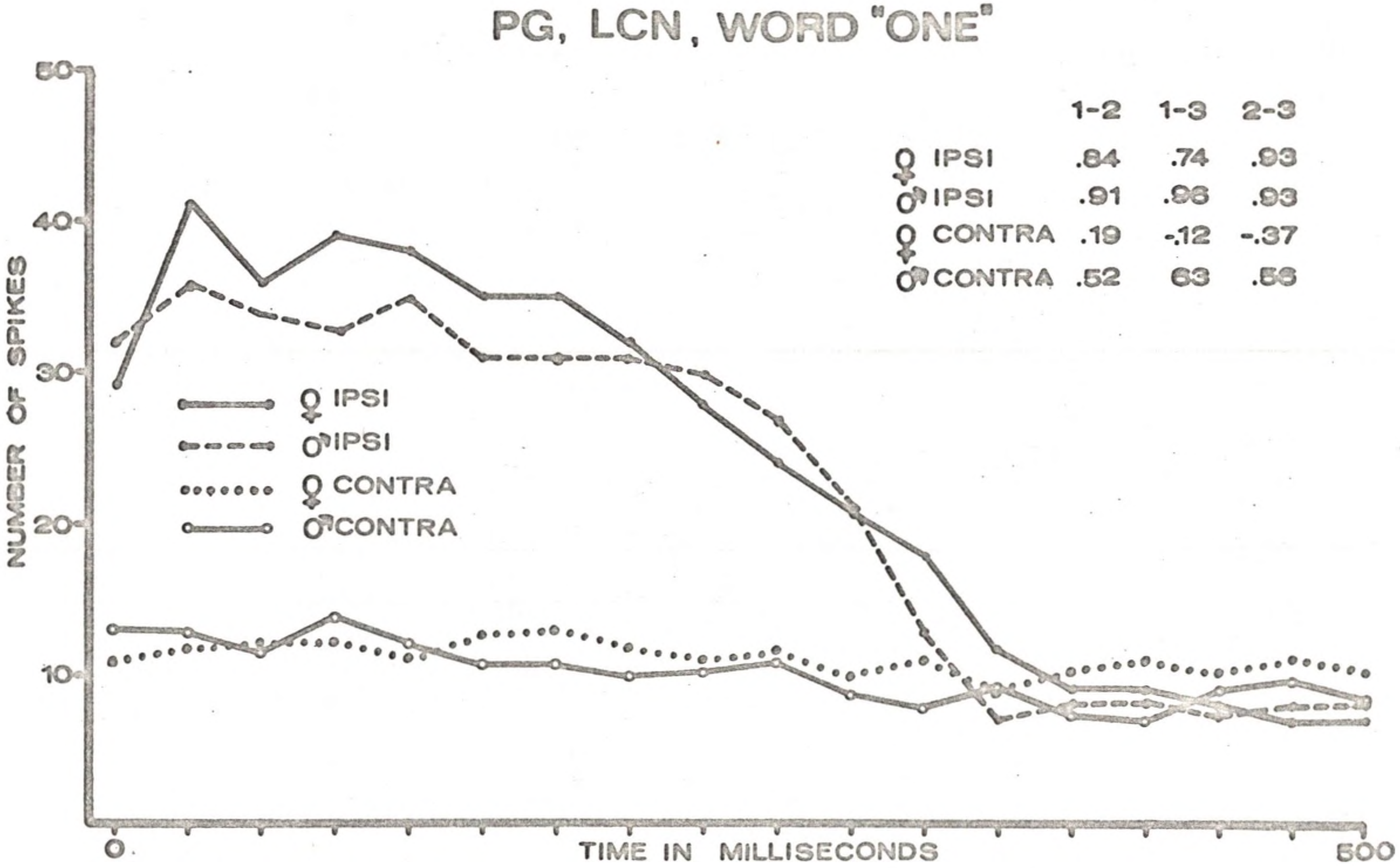
Even with the elimination of two subjects, 10,800 data cards were still available for analysis. Each of these cards contained 18 independent spike counts. The great bulk of these data dictated a selective presentation of results. An attempt was made to select data impartially, and the data presented in this section was representative of the larger population from which it was drawn. The intercorrelations between neuronal responses for cats Pg, Lz, Lg, and Rp are presented in the Appendix.

Of the 10,800 data cards that were potentially available for analysis, 209 or 1.9 percent of the total represented erratic data measures. At certain apparently random times during the course of the experiment electronic noise appeared on the tapes. These artifacts were transmitted faithfully through the ear pieces to the cat causing highly irregular spike bursts. During the presence of static the clock pulses were also frequently obliterated and the digital data system could not be triggered. In these situations a specially marked card (containing all zero counts) was placed in the deck so that the orderly sequence of data could be preserved. The majority of the erratic data was generated in this manner. However, in a few instances highly erratic results were recorded in a few columns of the IBM cards when the counters in the data analyzer apparently failed to reset from the previous trial.

Prior to data collection it was decided to select one cat and present complete sequential data for one dorsal cochlear nucleus site and one inferior colliculus electrode placement. This data is presented for the left dorsal cochlear nucleus and the right inferior colliculus of cat Pg. The results from this cat were representative of data obtained from the other animals.

Dorsal Cochlear Nucleus

Figure 4 presents the neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "one" presented by male and female voices under conditions of both ipsilateral and contralateral stimulation. In this and all subsequent figures the ordinate represents the mean number of spikes and the horizontal axis reflects



	1-2	1-3	2-3
♀ IPSI	.84	.74	.93
♂ IPSI	.91	.96	.93
♀ CONTRA	.19	-.12	-.37
♂ CONTRA	.52	63	.56

Figure 4. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "one." The ordinate represents the mean number of spikes and the horizontal axis gives time in milliseconds. Each data point reflects the mean of 15 observations for the three voices of the same sex. The upper responses were evoked by ipsilateral stimulus presentation, and the lower traces by contralateral presentation. The inset presents the intercorrelations between the three voices of the same sex comprising each plotted response.

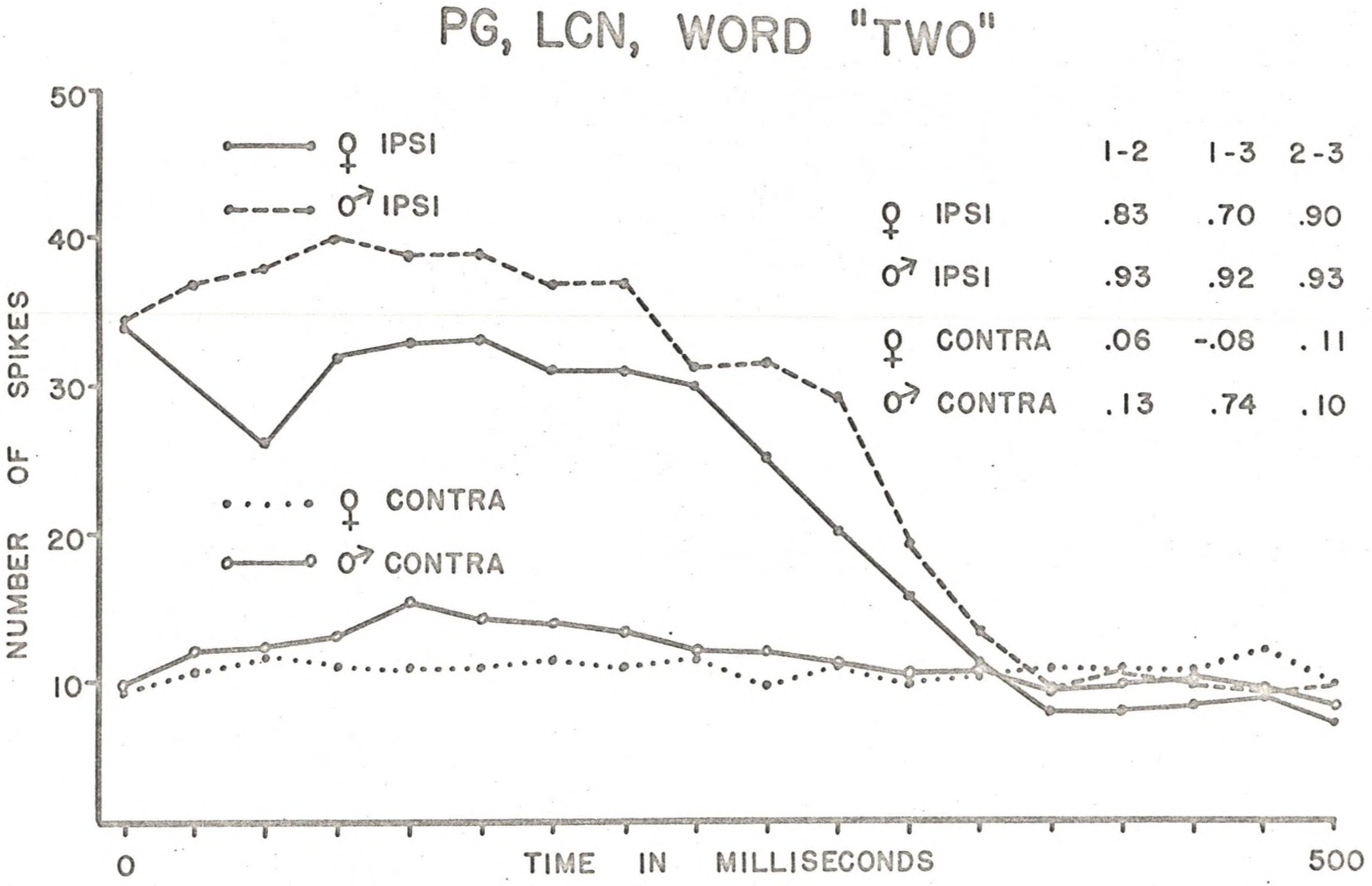
the time base in milliseconds. Each neuronal measure had a duration of 500 milliseconds with 18 independent observations recorded during this period. In Figure 4 and the other figures each data point represents the mean of 15 observations for the three voices of the same sex. The upper traces represent multiple unit neuronal activity generated by ipsilateral stimulus presentation and the lower traces reflect contralateral stimulation. The extent of similarity between the three voices of the same sex comprising each plotted response is given in the table of intercorrelations between voices in the upper right of each figure.

An outstanding feature of the neuronal response at the dorsal cochlear nuclei level involved the fact that contralateral stimulus presentation did not elicit a multiple unit neuronal spike burst. In Figure 4 ipsilateral stimulation by both male and female voices elicited a sustained burst of multiple unit activity. Contralateral stimulation by the same voices did not produce a spike burst. The neuronal activity under this latter stimulus condition resembles random on-going activity in the absence of auditory stimulation. These results do not represent a new finding, but rather a verification of past work, since it has been known for some time that there are no direct anatomical connections between the cochlear nucleus and the contralateral ear (House and Pansky, 1967).

It can be observed from Figure 4 that with ipsilateral stimulation the word "one" elicited a multiple unit neuronal response that was very similar for both male and female speakers. It is also apparent that the relationship between neuronal responses evoked by same-sex voices is substantial under ipsilateral stimulation. The intercorrelations between male voices in this situation ranged from .91 to .96 (N=18, p .01 and .74 to .93 (N=18, p .01) for female voices. With an N of 18, any correlation of .59 or larger is significantly greater than a zero correlation at or beyond the .01 level of confidence. The intercorrelations between voices in the contralateral stimulational situation are not significantly different from zero at the .01 level, with the exception of the correlation between male voices one and three. The insignificant correlations suggest that the neuronal response elicited by contralateral stimulation is, in fact, random on-going activity.

Figures 5, 6, and 7 present the multiple unit neuronal responses obtained at the left dorsal cochlear nucleus in cat Pg with stimulus words "two", "three", and "four". The neuronal activity in the figures are consistent in exhibiting the differences between contralateral and ipsilateral stimulation. Ipsilateral stimulation elicited a sustained spike burst while contralateral stimulation did not elicit more than on-going activity.

All the intercorrelations between neuronal patterns generated by both male and female voices presenting the stimulus words "two", "three", and "four" to the ipsilateral ear are significantly different from a zero correlation at or beyond the .01 level. For the stimulus word "two" the range of intercorrelations for ipsilateral stimulation extend from .70 for female voices one and three to .93 for the intercorrelations between male voices one and two and two and three. The intercorrelations for stimulus word "three" in Figure 6 range from .65 for female voices one and three, to .99 for male voices one and two. In Figure 7 with the stimulus word "four" the intercorrelations range



	1-2	1-3	2-3
♀ IPSI	.83	.70	.90
♂ IPSI	.93	.92	.93
♀ CONTRA	.06	-.08	.11
♂ CONTRA	.13	.74	.10

Figure 5. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "two." Each data point reflects the mean of 15 observations for the three voices of the same sex.

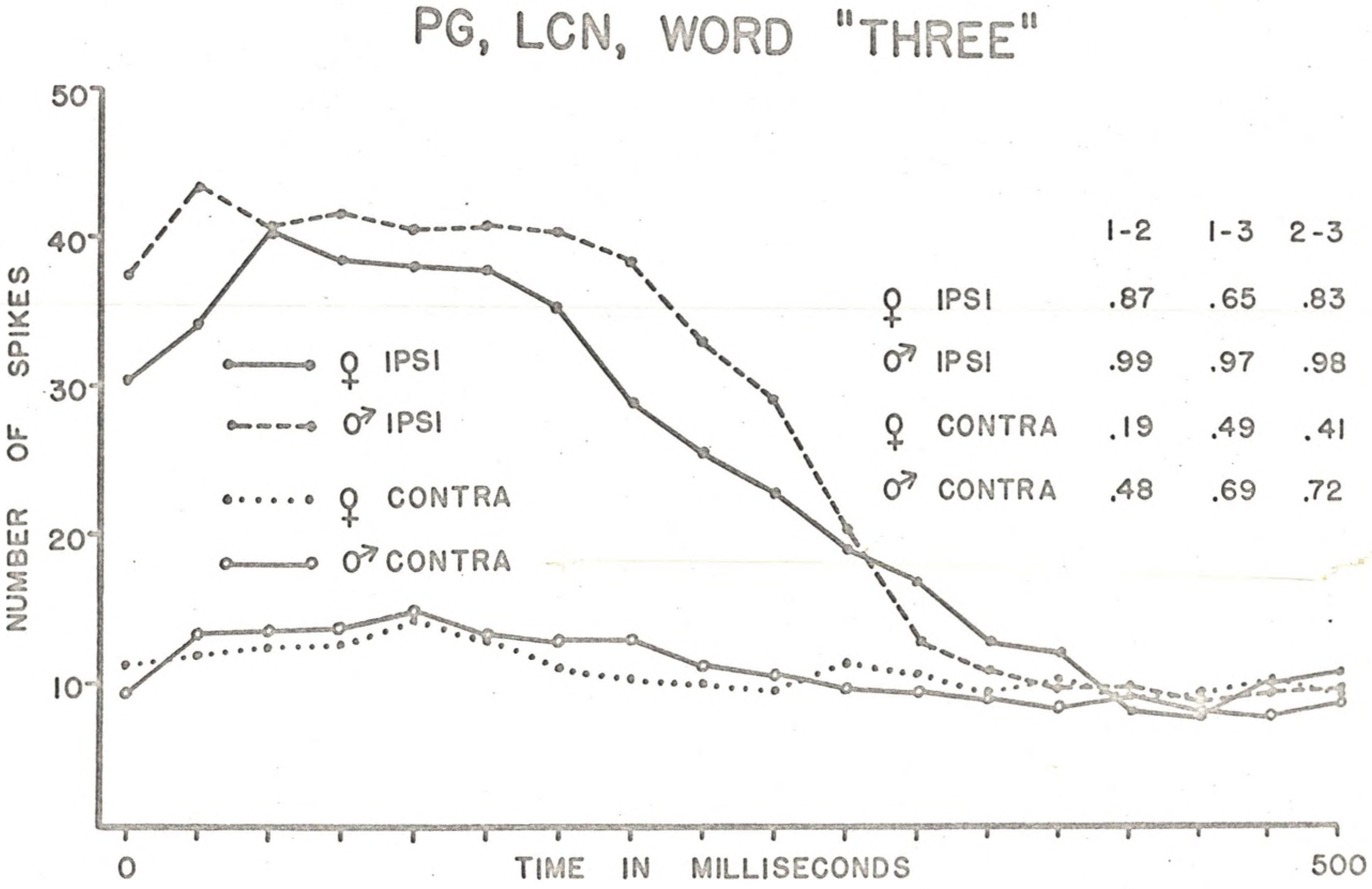


Figure 6. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "three."

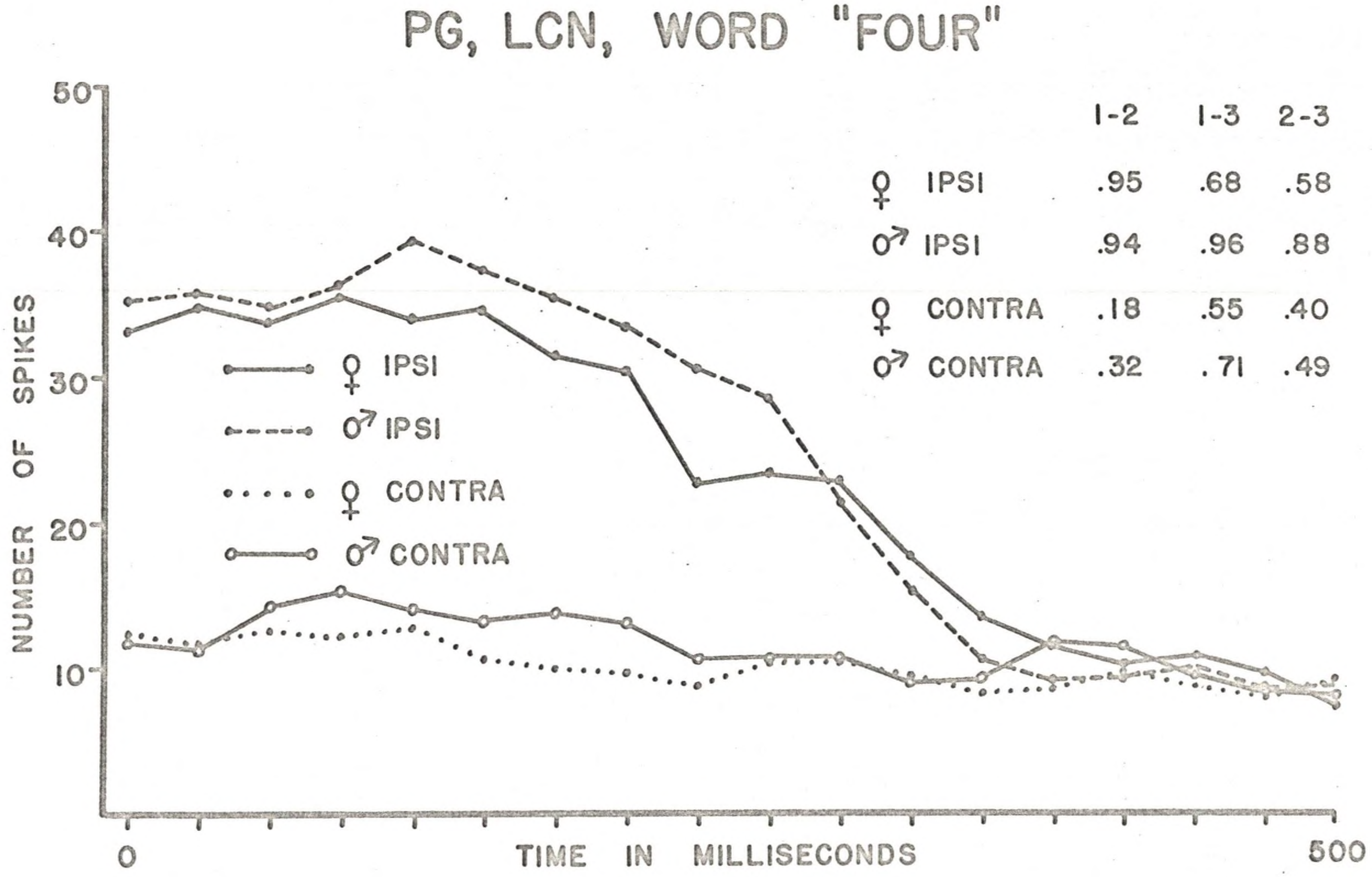


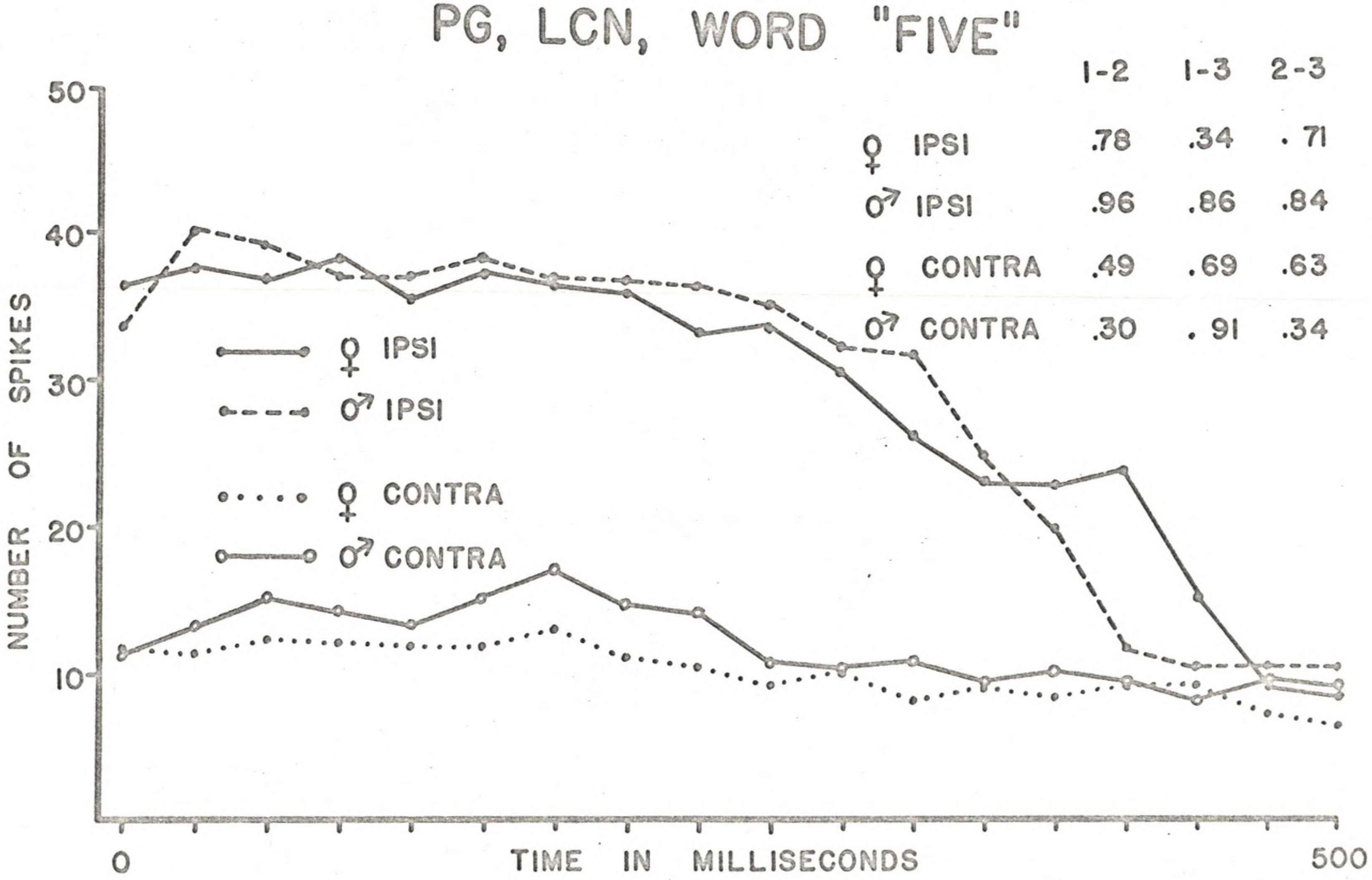
Figure 7. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "four."

from .58 for female voices two and three to .96 for male voices one and three. The intercorrelations for contralateral stimulation in Figures 5, 6, and 7, suggest, once again, patterns of essentially random neuronal activity.

Figures 4 through 7 are consistent in showing a gradual decline in spike count from the onset of the stimulus words to approximately the thirteenth count, where the spike burst has returned to the level of spontaneous on-going neuronal activity. The general configuration or neuronal pattern generated by the stimulus words "one" through "four" appears quite similar. Maximum spike bursts are observed at the onset of the words with a gradual decline at around the thirteenth count.

Figures 8, 9, and 10 present the multiple unit spike counts in cat Pg left dorsal cochlear nucleus for the stimulus words "five", "six", and "seven". Once again, the marked distinction between neuronal activity during ipsilateral and contralateral stimulation may be observed. The intercorrelations between ipsilaterally evoked responses in Figures 8, 9, and 10 tend to be lower than those previously reported with nine correlations failing to reach significance at the .01 level. In Figures 9 and 10, the lower intercorrelations between voices may be partially generated by the fact that while the general pattern of neuronal response for different voices is similar, the response tended to peak at different points along the temporal axis. Such a phenomenon would tend to lower the intercorrelations between individual neuronal patterns.

The spike bursts in Figures 8, 9, and 10 resulting from ipsilateral stimulation appear to last slightly longer than those of



	1-2	1-3	2-3
♀ IPSI	.78	.34	.71
♂ IPSI	.96	.86	.84
♀ CONTRA	.49	.69	.63
♂ CONTRA	.30	.91	.34

Figure 8. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "five."

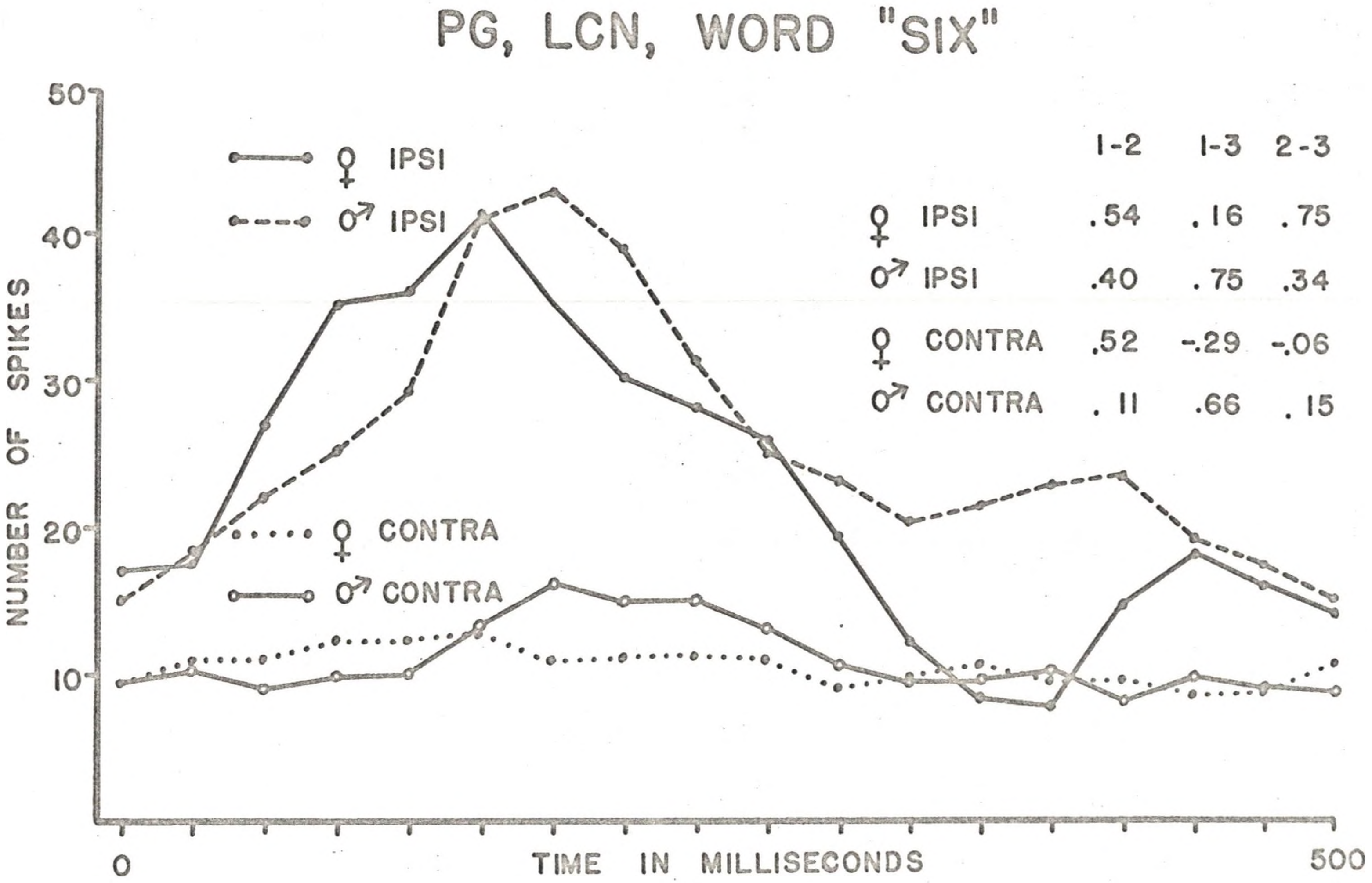


Figure 9. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "six."

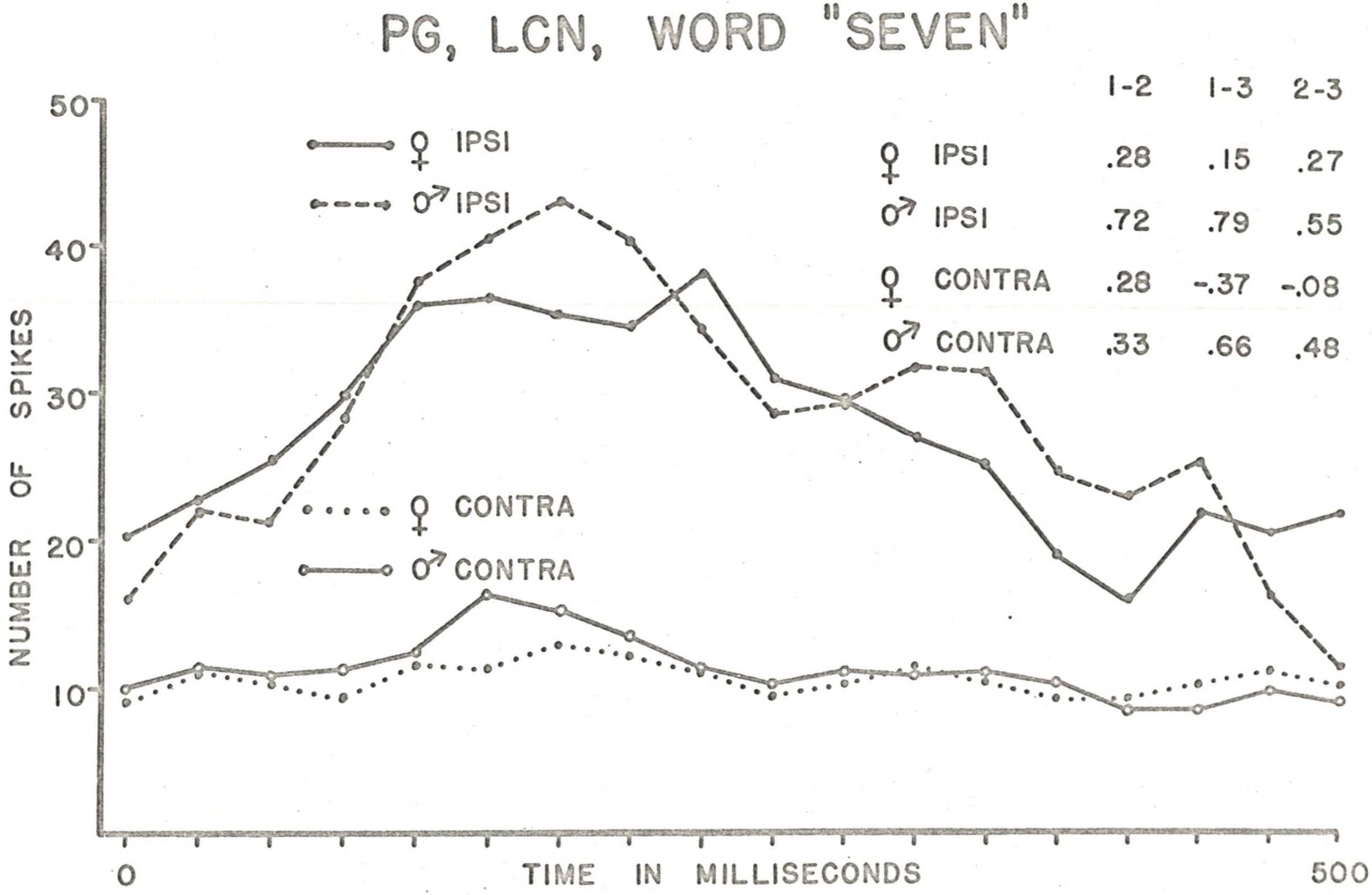


Figure 10. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "seven."

the ipsilateral plottings previously reported. In Figure 8, for example, the ipsilateral neuronal response does not return to the ongoing level until approximately the fifteenth to seventeenth time interval. Figures 9 and 10 also suggest the presence of a small neuronal burst lasting throughout the 500 millisecond recording time.

Compared to responses elicited by the stimulus words "one" through "four", the neuronal responses to stimuli "five", "six", and "seven" in Figures 8, 9, and 10 exhibit a great amount of "pattern differentation". The neuronal responses to the word "five" in Figure 8, for example, started out at a high rate (33-36 spikes) which was maintained with only a very gradual decline. The response tended to return to the level of spontaneous activity between the fifteenth and seventeenth time interval. The sustained period of this response tended to distinguish it from responses elicited by previous stimuli. While the agreement between mean responses for male and female voices appeared to be very great in Figure 8, there was only a moderate degree of similarity between the responses elicited by female voices.

Figures 9 and 10 show a pattern of multiple unit neuronal activity that clearly distinguish them from responses elicited by other stimuli. Ipsilateral stimulation with the stimulus "six" elicited a burst with a peak which occurred at the sixth interval for female voices and the seventh time interval for male voices. The peak with the female voices represented a mean spike count of approximately 41.5 discharges, while the peak for male voices reflects a mean spike discharge of 43. Figure 10, representing the neuronal response to the word "seven", again exhibits a rather unique discharge pattern. For both male and female voices an initial spike peak occurred between the sixth and seventh time interval. The neuronal response to this word exhibited a second smaller spike peak between the ninth and twelveth time interval. The maximum spike count for the neuronal response in the first peak was 43 and a maximum mean count of 32 was observed in the second smaller peak. Both of these counts were elicited by male voices. The female-elicited mean responses reflected a lower frequency.

Figures 11, 12, and 13 present mean spike counts recorded in Pg at the left dorsal cochlear nucleus for the stimulus words "eight", "nine", and "ten". The intercorrelations between the three same-sex voices comprising each mean neuronal response are again presented in the inset.

Averaging all of the intercorrelations of Figures 4 through 13 across stimulus words using the r to z transformation (McNemar, 1962, p. 139), yielded the average intercorrelations between speakers presented in Table 3.

TABLE 3

AVERAGE Z SCORES AND PEARSON PRODUCT MOMENT CORRELATIONS FOR NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES ACROSS ALL TEN STIMULI AT THE LEFT DORSAL COCHLEAR NUCLEUS IN CAT PG

		Laterality of Stimulation		
		ipsi	contra	bilateral
Females	z_{av}	.89	.34	.97
	r_{av}	.66**	.30	.72**
Males	z_{av}	1.45	.60	1.46
	r_{av}	.88**	.54	.88**

**p .01

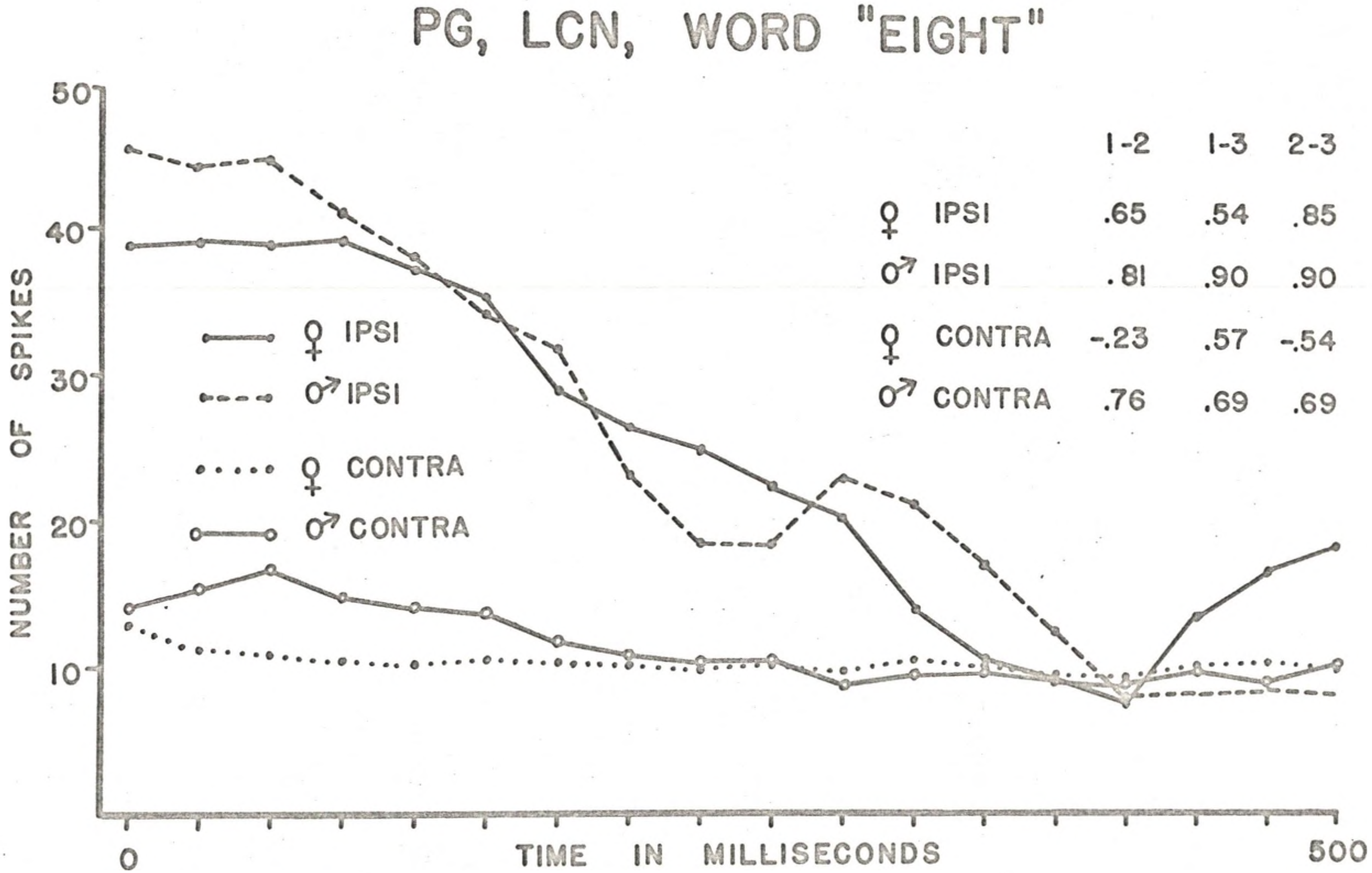


Figure 11. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "eight."

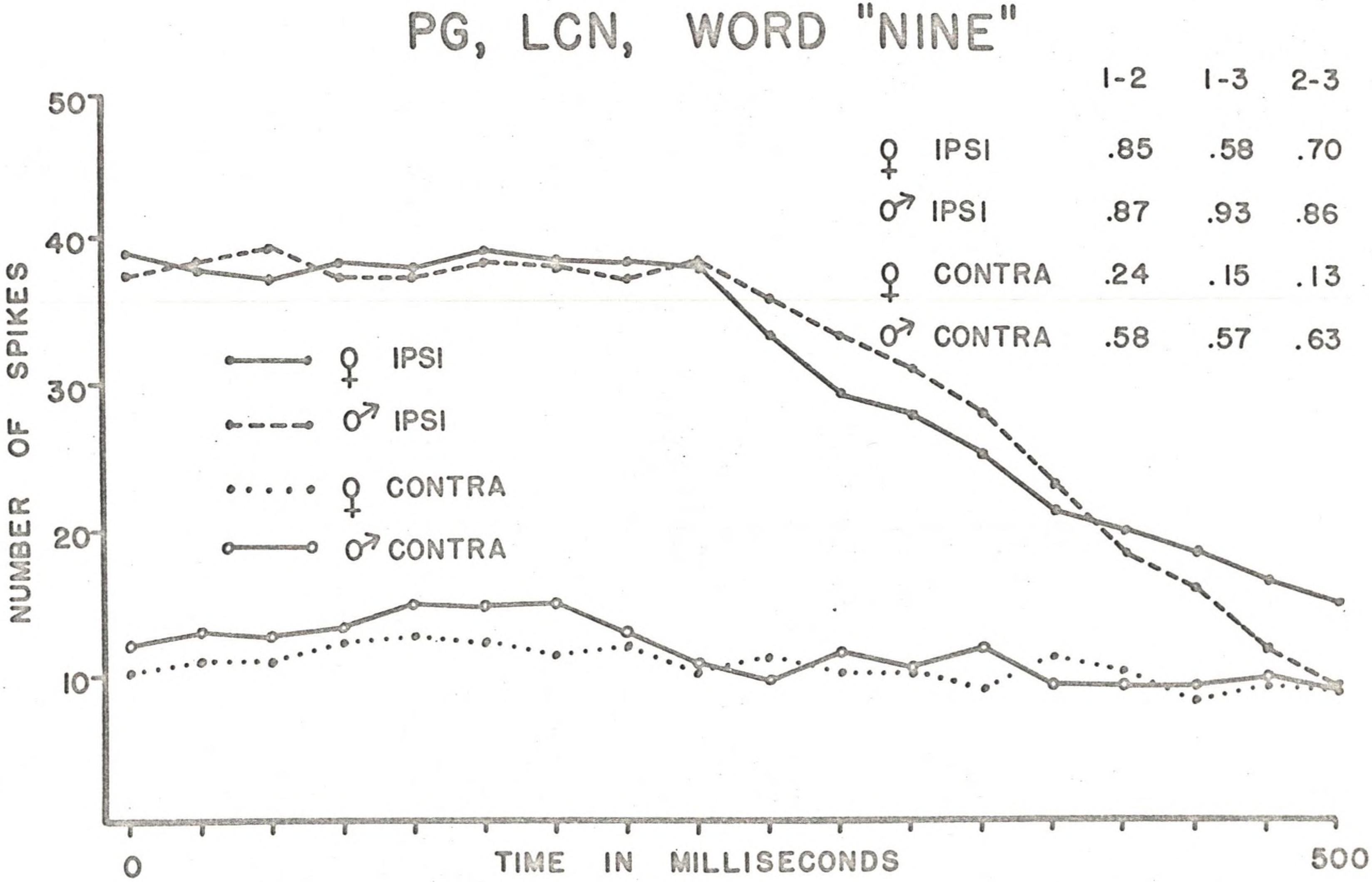


Figure 12. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "nine."

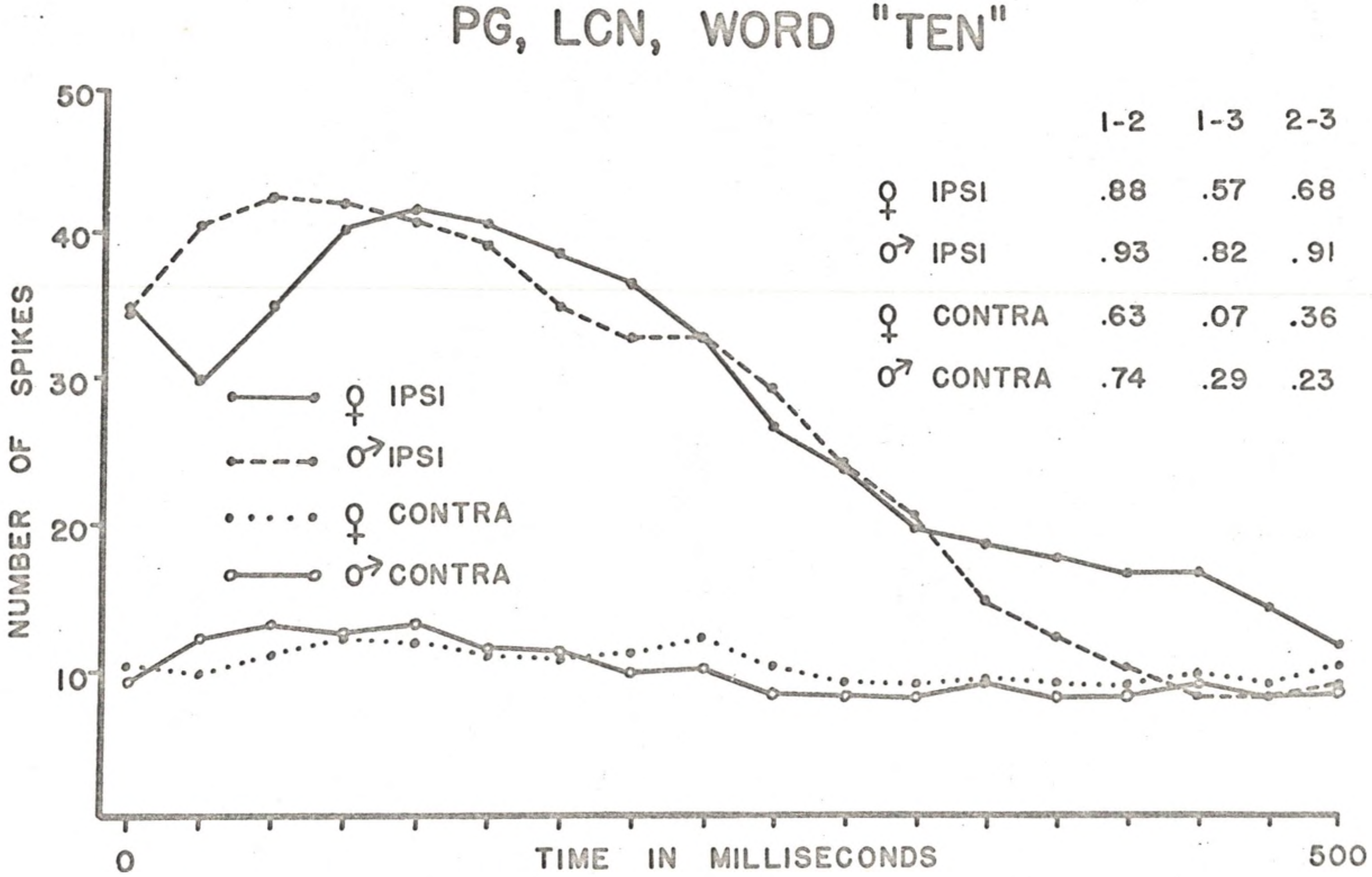


Figure 13. Neuronal responses at the left dorsal cochlear nucleus in cat Pg to the word "ten."

It can be observed from Table 3 that with contralateral stimulation at the left dorsal cochlear nucleus, same-sexed speakers do not elicit multiple unit neuronal patterns that are similar to each other beyond a chance level. On the other hand, ipsilateral and bilateral stimulation generated neuronal patterns having a moderate to high degree of similarity to each other. The difference between the average female correlations with ipsilateral and contralateral stimulation is significant beyond the .05 probability level (t=2.03). The difference between the average correlations with male ipsilateral and contralateral stimulation is significant beyond the .01 level (t=3.10). With both male and female voices there was essentially no difference in inter-speaker agreement between ipsilateral and bilateral stimulation (males: t=.02; females: t=.27 df=57). These findings may be summarized as follows: when averaging across ten stimuli at the left dorsal cochlear nucleus in cat Pg, it was found that a moderate to high relationship occurred for both male and female voices under conditions of both ipsilateral and bilateral stimulation. The neuronal patterns generated by ipsilateral or bilateral stimulation did not differ significantly from each other. The neuronal responses elicited by contralateral stimulation suggest random neuronal activity. The findings suggest a neuronal coding mechanism: very similar neuronal firing patterns were appearing when the same stimuli were presented (ipsilaterally or bilaterally) by same-sexed voices. This coding mechanism, as expected, failed to appear under conditions of contralateral stimulation.

Similarity of Neuronal Responses at the Dorsal Cochlear Nucleus

Earlier in this chapter, it was reported that the data from the dorsal cochlear nucleus in cat Pg was representative of the dorsal cochlear nuclei response in the other experimental animals. Data is now presented to substantiate this interpretation. Figure 14 presents the average neuronal responses elicited by the stimulus word "seven" presented by male voices under conditions of ipsilateral stimulation. The neuronal responses for the right dorsal cochlear nucleus of cats Pg, Lg, Lz, and Rp are presented. As in previous figures, the abscissa represents 500 milliseconds and each data point represents the mean of 15 observations for the three same-sex voices. The inset in Figure 14 presents the intercorrelations between mean data points for each cat (N=18). Any correlation larger than .59 is significantly greater than zero beyond the .01 probability level. It is obvious from an inspection of Figure 14 that there was a high degree of correspondence between the neuronal responses in all four cats. The intercorrelations between cats ranged from a low of .77 to a high of .91. In comparing the neuronal responses between cats the difference between the responses on the vertical dimension is irrelevant. This dimension is contaminated by the fact that the recording threshold of the digital data system had to be readjusted between each experimental animal. This readjustment was necessary since at some anatomical sites the on-going level of neuronal activity was larger or smaller in amplitude than at other sites. In Figure 14, for example, the differences in spike count between cats Lz and Pg could be either partially or totally due to the fact that when analyzing data for cat Lz more of the multiple unit activity was below the recording threshold than when analyzing the

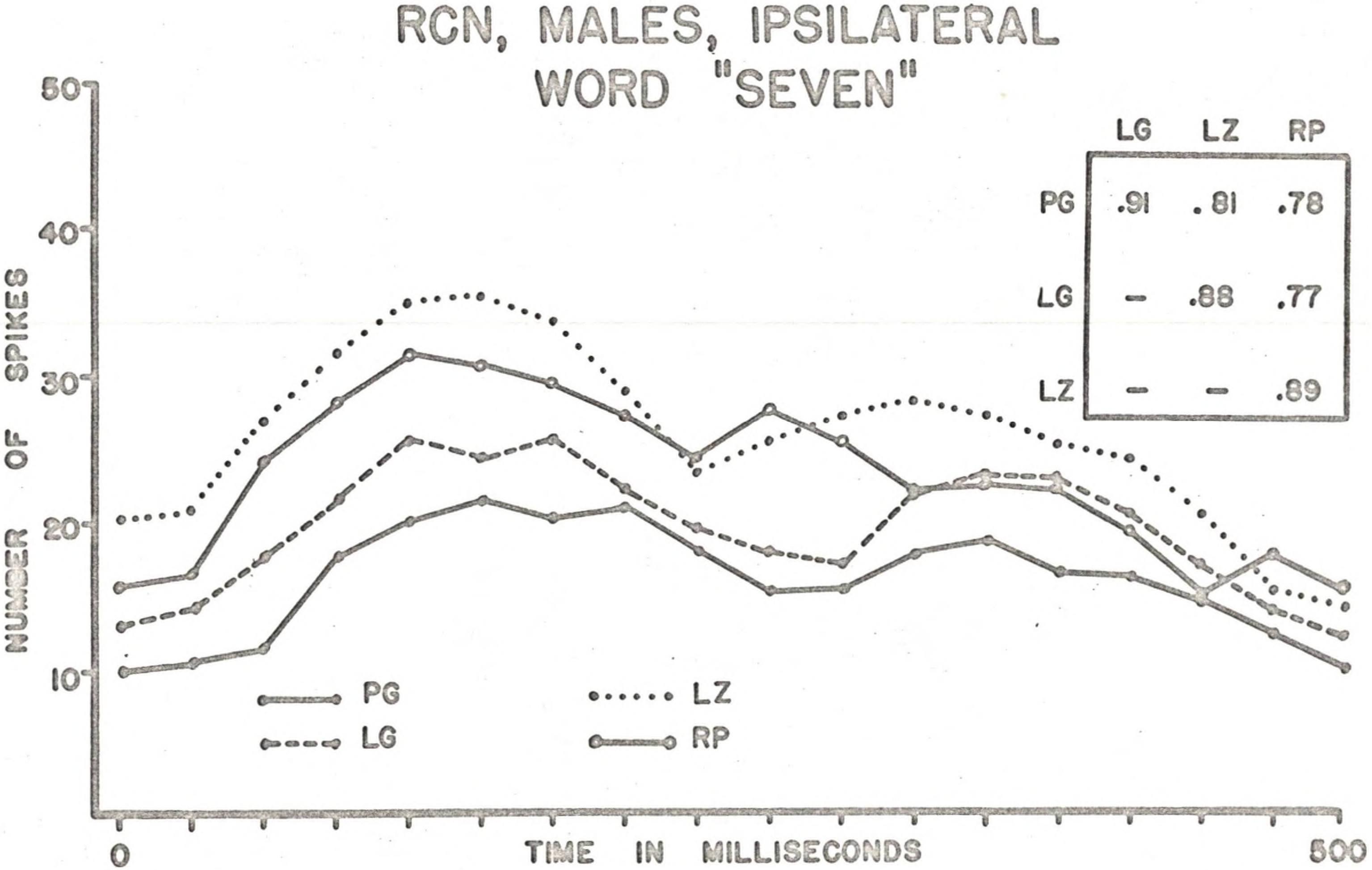


Figure 14. Mean number of spikes elicited at the right dorsal cochlear nucleus in cats Pg, Lg, Lz, and Rp. Stimulation consisted of male voices presenting the word "seven" to the ipsilateral ear. Each data point represents the average of 15 observations for the three male voices. The inset presents the intercorrelations between the plotted neuronal responses of the four cats.

neuronal data for cat Pg. Disregarding differences along the vertical dimension, the general pattern of neuronal activity in Figure 14 shows a high degree of similarity among cats.

Figure 15 presents the response to females presenting the word "six". In this figure all correlations between cats are significant (p .01) except for the intercorrelation between cats Pg and Lz. The intercorrelations for this stimulus word range from .53 to .97 indicating a low to very high similarity between the spike patterns across cats. The correlations between cat Pg and the other animals are quite low by comparison with the other intercorrelations presented in Figure 15. This may be partially due to the fact that, while the neuronal response pattern in cat Pg is very similar to the other patterns, the peak occurs approximately one time interval later than the peak neuronal response in the other animals.

Figure 16 presents the neuronal response in the four experimental animals to ipsilateral stimulation with male voices presenting the stimulus word "six" at the right dorsal cochlear nucleus. The intercorrelations between cats range from .71 to .94 with all correlations significant beyond the .01 level.

Figure 17 presents neuronal responses obtained at the right dorsal cochlear nucleus with male voices presenting the word "eight". The intercorrelations between cats range from .94 to .97 indicating a very high degree of response similarity between all four cats under these conditions of stimulation.

In summary, it can be seen that the coding mechanism that was initially observed in cat Pg at the dorsal cochlear nucleus is also occurring at the cochlear nuclei level in all of the experimental animals.

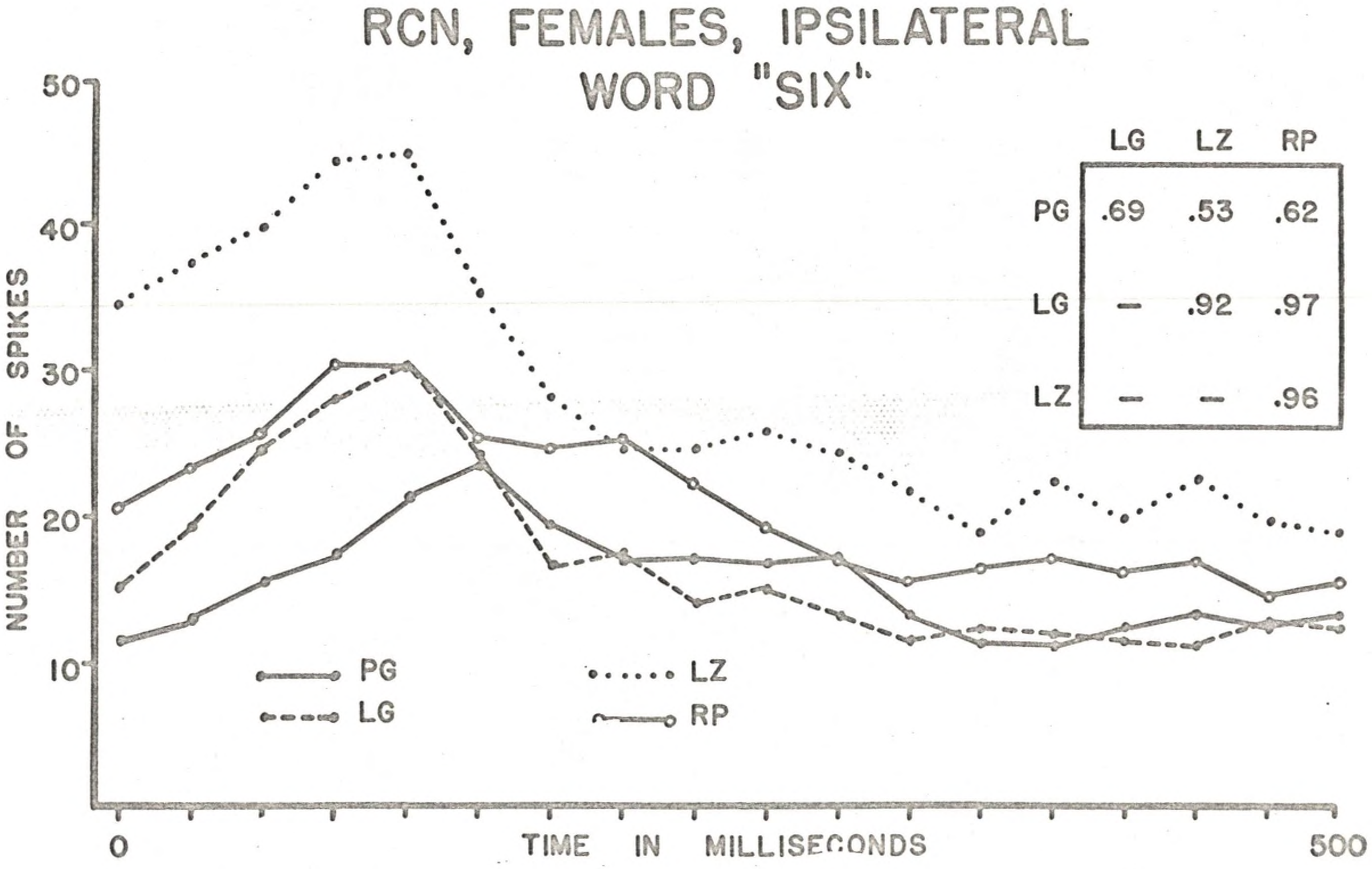


Figure 15. Mean number of spikes elicited at the right dorsal cochlear nucleus in cat. Pg, Lg, Lz, and Rp. Stimuli were female voices presenting the word "six" to the ipsilateral ear. The inset gives intercorrelations between neuronal responses of each cat.

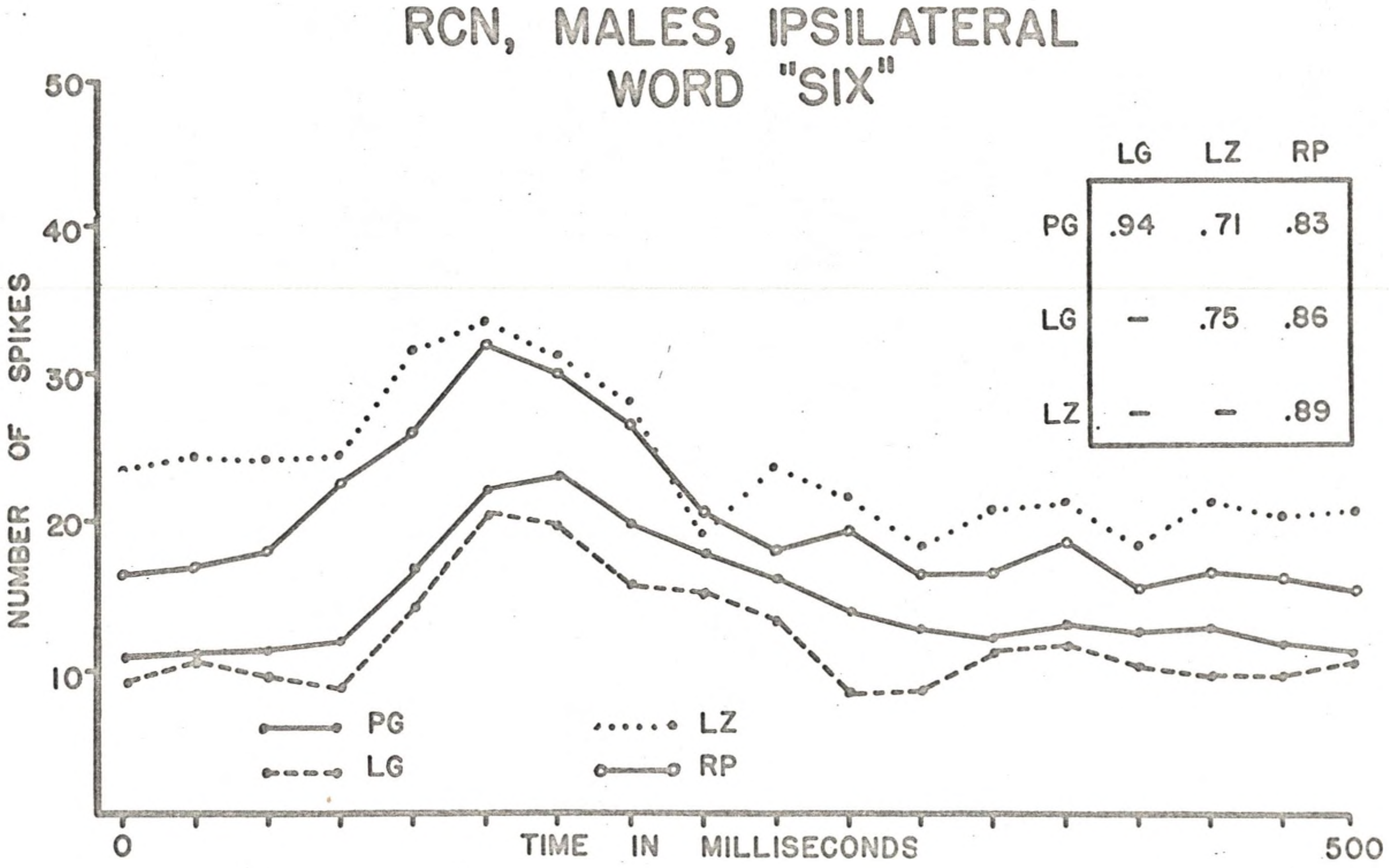
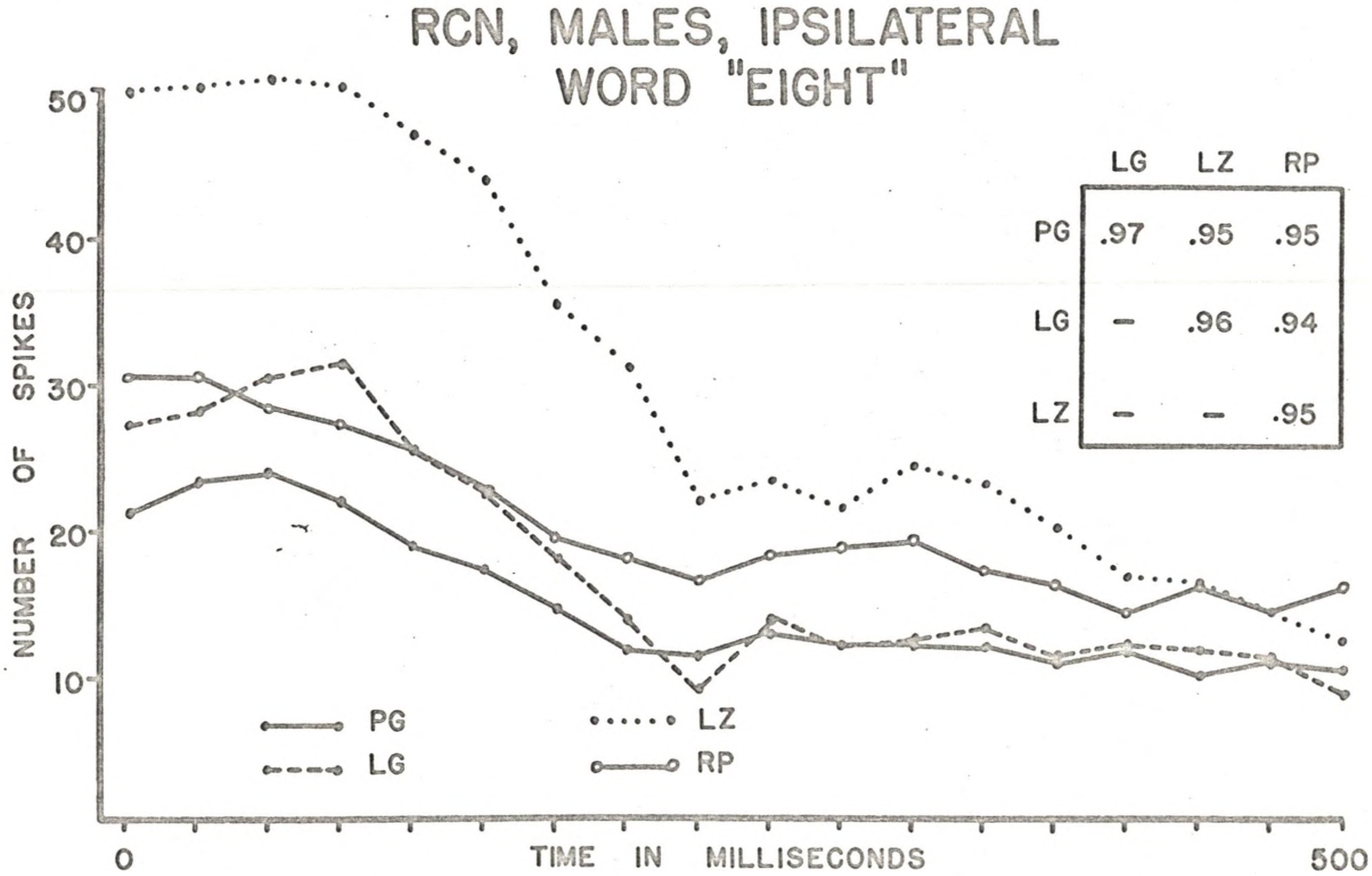


Figure 16. Mean number or spikes elicited at the right dorsal cochlear nucleus. Stimulus word was "six" presented by male voices to the ipsilateral ear.



	LG	LZ	RP
PG	.97	.95	.95
LG	–	.96	.94
LZ	–	–	.95

Figure 17. Mean number of spikes elicited at the right dorsal cochlear nucleus. Stimulus word was "eight" presented by male voices to the ipsilateral ear.

The four stimulus samples selected for presentation appear to be representative of all of the between-cat data at this level of the primary auditory pathway. This data strongly suggests that particular stimulus words elicited very similar patterns of multiple unit spike discharges in all of the experimental animals.

Inferior Colliculus

As previously mentioned, the right inferior colliculus site in cat Pg was selected for sequential presentation of the neuronal responses to the stimulus words "one" through "ten" for both male and female voices. Figures 18 through 27 present these data. As in previous figures, the vertical axis represents mean number of spikes. Each data point is the mean of 15 observations for the three speakers of the same sex. The horizontal axis presents time in milliseconds.

Figure 18 presents the mean neuronal response at the right inferior colliculus of cat Pg to the stimulus word "one". The two upper traces were recorded during contralateral stimulation and the lower traces were recorded during ipsilateral ear stimulation. No observable multiple unit spike burst was elicited by either male or female stimulation of the ipsilateral ear. As in previous figures, the inset of Figure 18 presents the intercorrelations between each of the neuronal patterns of each mean response generated by voices of the same sex (N-18). Once again, a correlation coefficient of .59 was necessary for an obtained coefficient to reach significance at the .01 level of probability. None of the intercorrelations between spike discharge patterns generated by ipsilateral stimulation reach statistical significance. Presentation of the word "one"

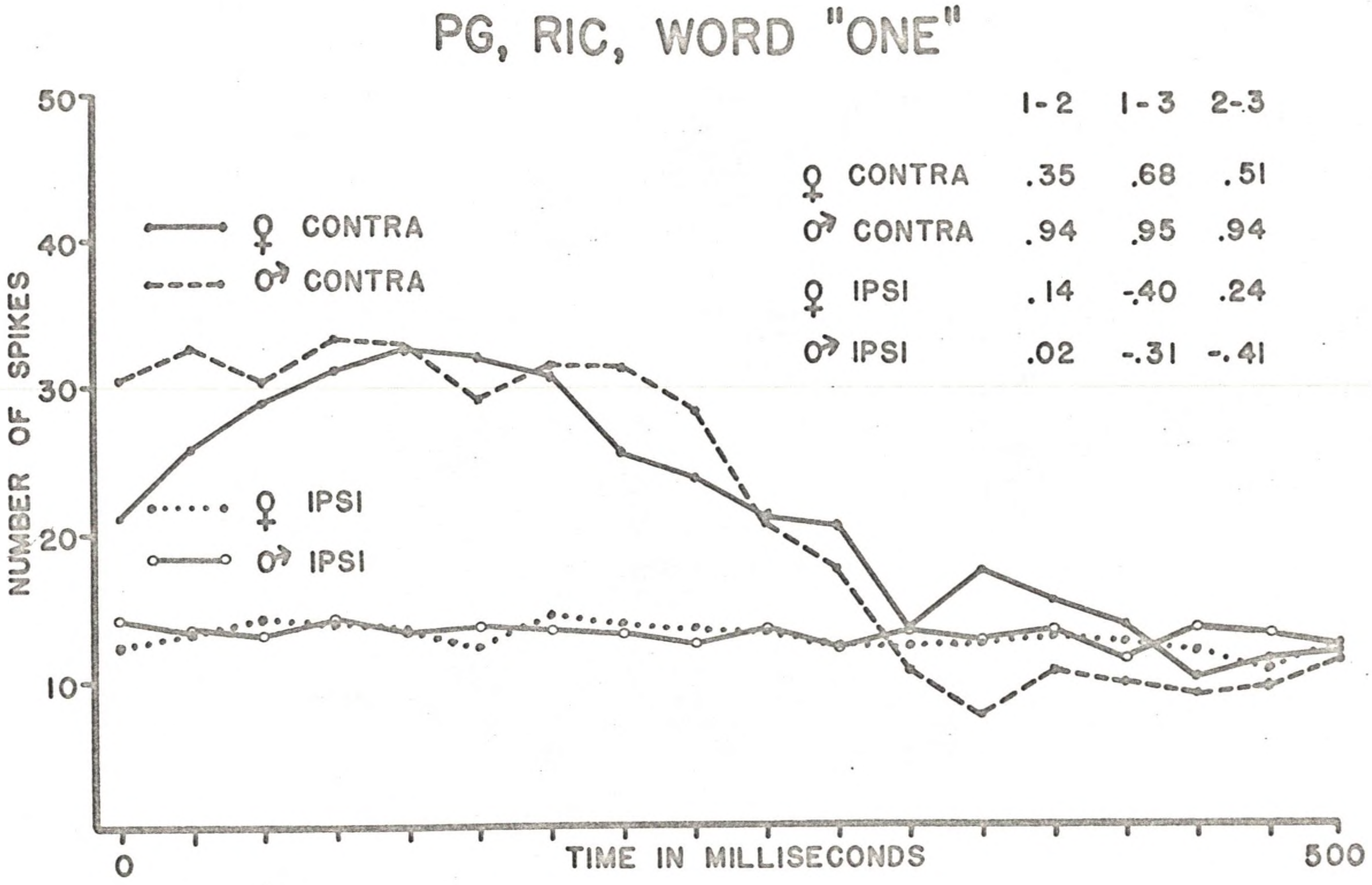


Figure 18. Neuronal responses at the right inferior colliculus of cat Pg to the word "one". The ordinate represents the mean number of spikes and the abscissa gives time in milliseconds. Each data point reflects the mean of 15 observations for the three voices of the same sex. The upper neuronal responses were evoked by contralateral stimulus presentation, and the lower traces by ipsilateral stimulation. The inset presents the intercorrelations of the neuronal responses elicited by the three voices of the same sex which were averaged for each tracing.

apparently did not change the random on-going discharge pattern at this site. Two of the intercorrelations between neuronal patterns evoked by contralateral stimulation also failed to reach significance at the .01 level: the correlation between female voices one-two and female voices two-three. In this situation female voice two was apparently generating a rather unique spike pattern. The remaining correlations for contralateral stimulus presentation range from .68 for female voices one and three to .95 for male voices one and three. The spike burst elicited by the contralateral stimulus returned to the on-going level by approximately the twelfth to fourteenth time period.

Figure 19 gives the neuronal data for the right inferior colliculus of cat Pg to the word "two". With this stimulus word contralateral stimulation again produced a noticeable spike burst while ipsilateral stimulation had no observable effect on the level of spontaneous activity. A moderately high degree of agreement is reflected for neuronal discharges elicited by same-sexed voices for contralateral stimulation. The lowest correlation between neuronal firing patterns occurred between patterns generated by female voices one and three (r=.79) and the highest correlation appeared for the neuronal patterns elicited by male voices one and two (r=.96). The intercorrelations between neuronal patterns generated by ipsilateral stimulation range from a low of -.10 for female voices one and two to .60 for male voices one and two. Of the six correlations for ipsilateral stimulation, only this latter correlation of .60 is significant (p .01).

The neuronal data of the inferior colliculus of cat Pg to the stimulus word "three" is presented in Figure 20. Contralateral

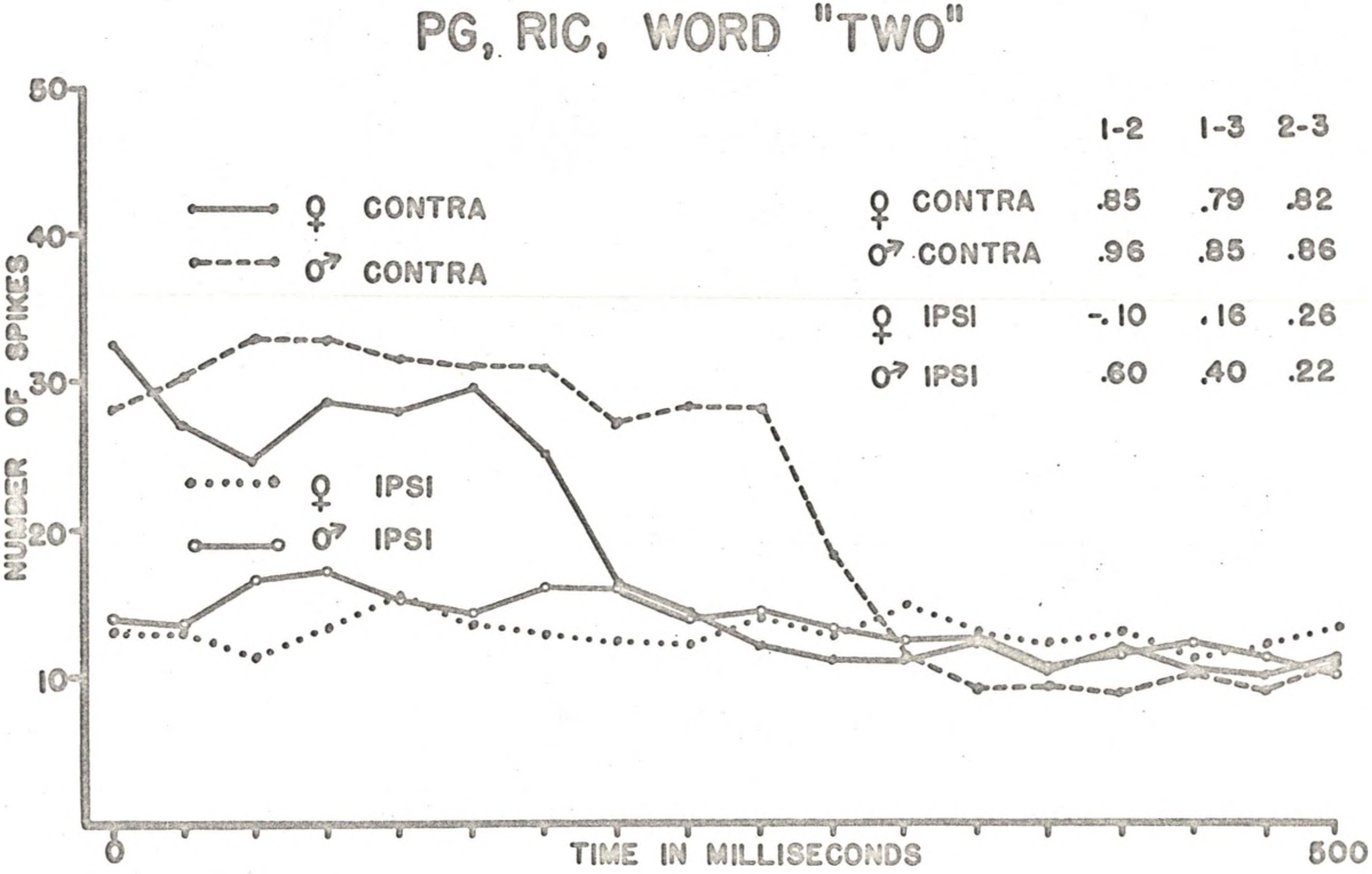
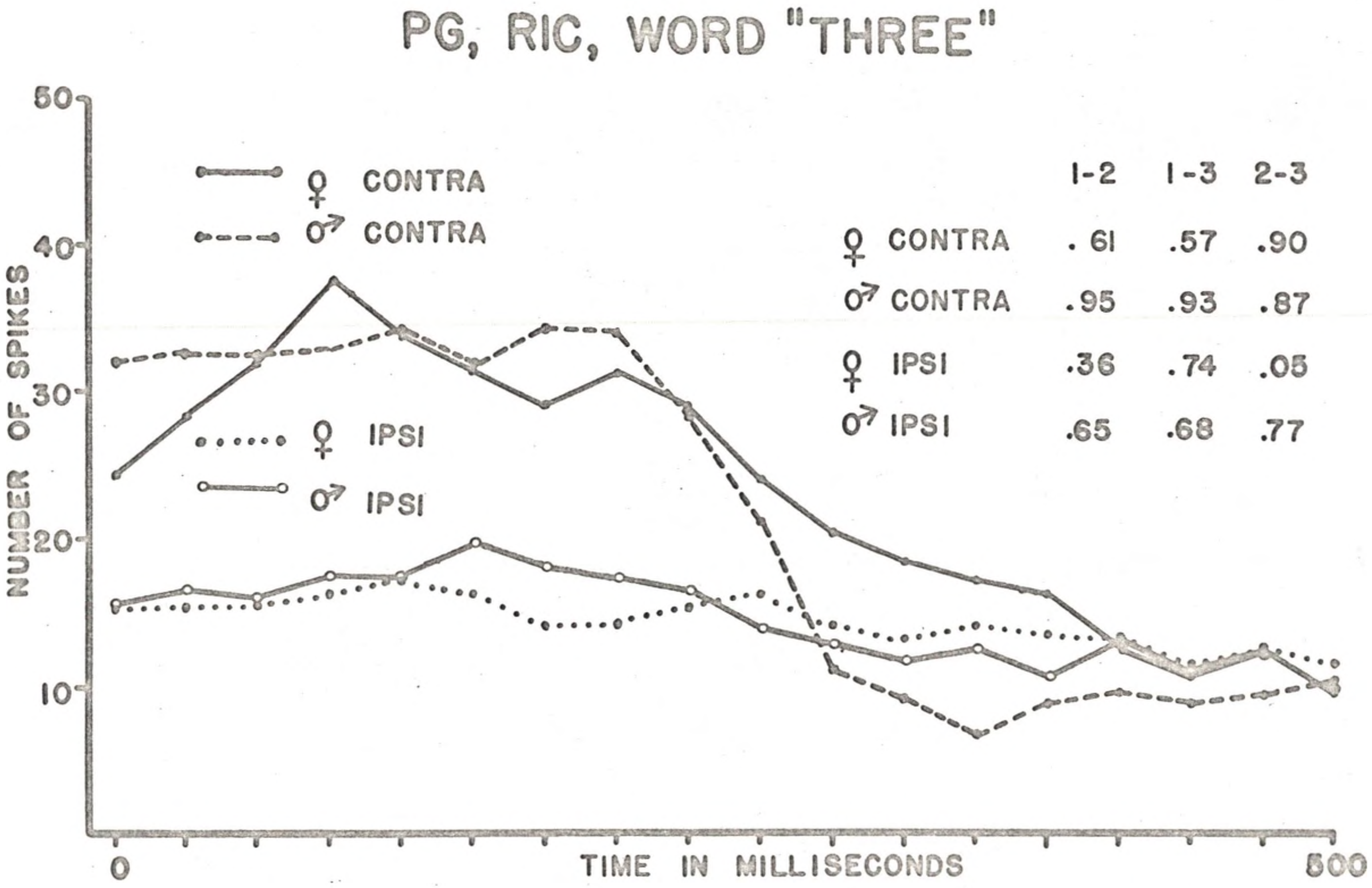


Figure 19. Neuronal responses at the right inferior colliculus of cat Pg to the word "two". Each data point reflects the mean of 15 observations of neuronal responses elicited by the three voices of the same sex.



PG, RIC, WORD "THREE"

	1-2	1-3	2-3
♀ CONTRA	.61	.57	.90
♂ CONTRA	.95	.93	.87
♀ IPSI	.36	.74	.05
♂ IPSI	.65	.68	.77

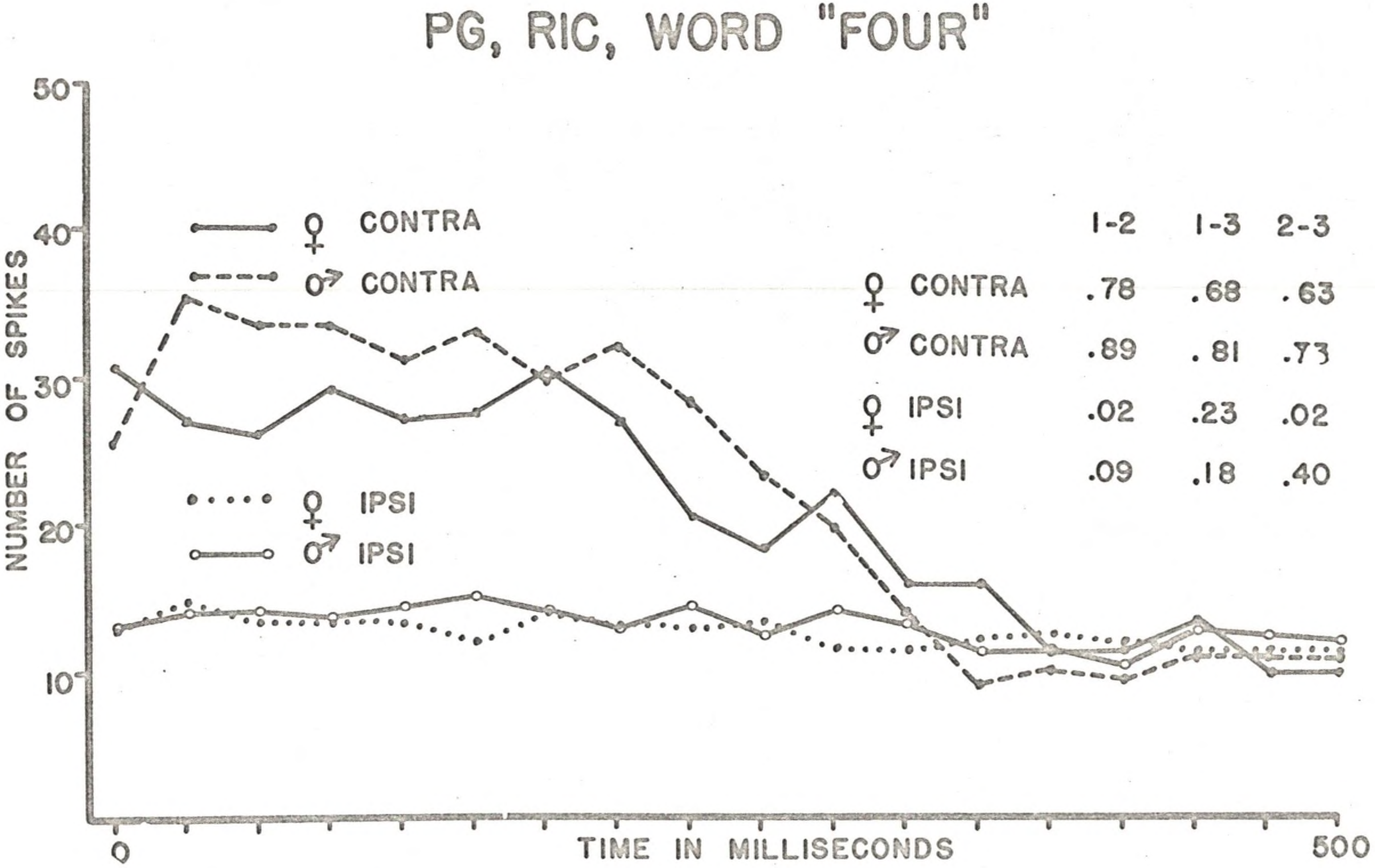
Figure 20. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "three".

stimulation once again evoked a sustained spike burst at this site. The correlations between neuronal patterns to voices of the same sex range from .57 for female voices one and three to .95 for male voices one and three. The former correlation is the only one of the six for contralateral presentation which fails to reach statistical significance at the .01 level.

The plotted neuronal response to the word "three" under ipsilateral stimulation suggests the presence of a very small spike burst, at least for the average male elicited response. The extent of the correlations between neuronal responses generated by ipsilateral male voices also suggested the presence of a neuronal response in addition to the random activity. These correlations between male ipsilaterally evoked responses ranged from .65 for male voices one and two to .77 for male voices two and three (p .01). The intercorrelations between female ipsilaterally evoked responses ranged from .05 for female voices two and three to .74 for female voices one and three.

Figure 21 presents the collicular response in cat Pg to the stimulus word "four". A moderately high relationship is indicated between the contralaterally evoked responses. All of these correlations are statistically significant (p .01). Ipsilateral presentation of the word "four" did not elicit neuronal discharge patterns which were similar to each other. All of the correlations between ipsilaterally evoked responses are insignificant.

In Figure 22 the neuronal response to the stimulus word "five" is presented. The correlations between the neuronal responses are similar in magnitude to those previously reported. Essentially no



	1-2	1-3	2-3
♀ CONTRA	.78	.68	.63
♂ CONTRA	.89	.81	.73
♀ IPSI	.02	.23	.02
♂ IPSI	.09	.18	.40

Figure 21. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "four"

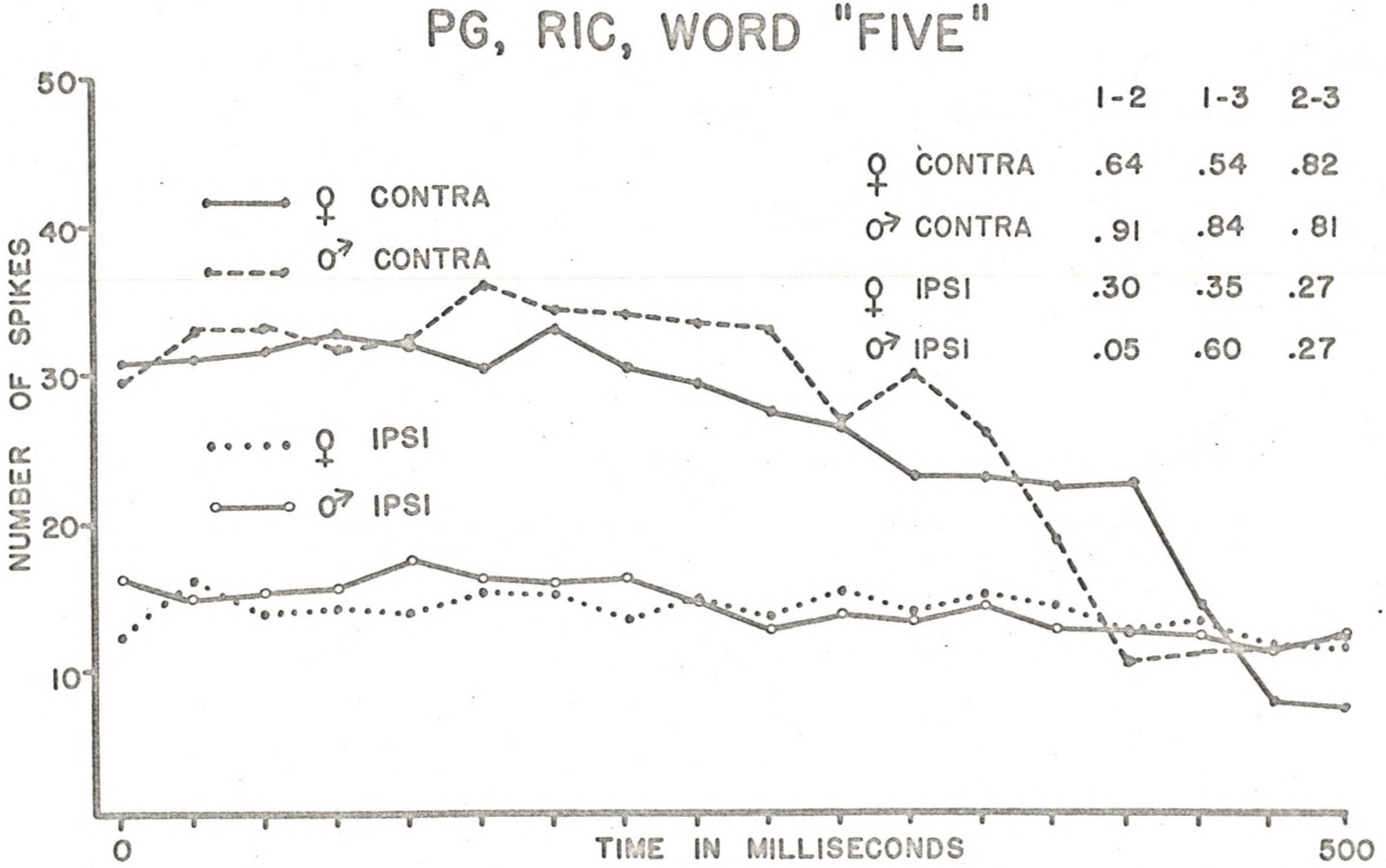


Figure 22. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "five".

correlation appeared for ipsilateral stimulation, and contralateral stimulation resulted in moderately high intercorrelations between spike discharge patterns.

Figures 23 through 27 present the remaining sequence of neuronal responses elicited in the right inferior colliculus of cat Pg to the stimulus words "six" through "ten". The neuronal responses in these figures tends to correspond rather closely with previously reported results at the collicular level.

Table 4 presents the average z scores and correlations for cat Pg at the right inferior colliculus. The r to z transformation (McNemar, 1962, p. 139) was used to obtain average correlations for each condition of stimulation across all ten stimulus words.

TABLE 4
AVERAGE Z SCORES AND PEARSON PRODUCT MOMENT CORRELATIONS FOR NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES ACROSS ALL TEN STIMULI AT THE RIGHT INFERIOR COLLICULUS IN CAT PG

		Laterality of Stimulation		
		ipsi	contra	bilateral
Females	z_{av}	.30	.68	.76
	r_{av}	.30	.54	.61**
Males	z_{av}	.53	1.15	1.17
	r_{av}	.46	.80**	.80**

** p .01

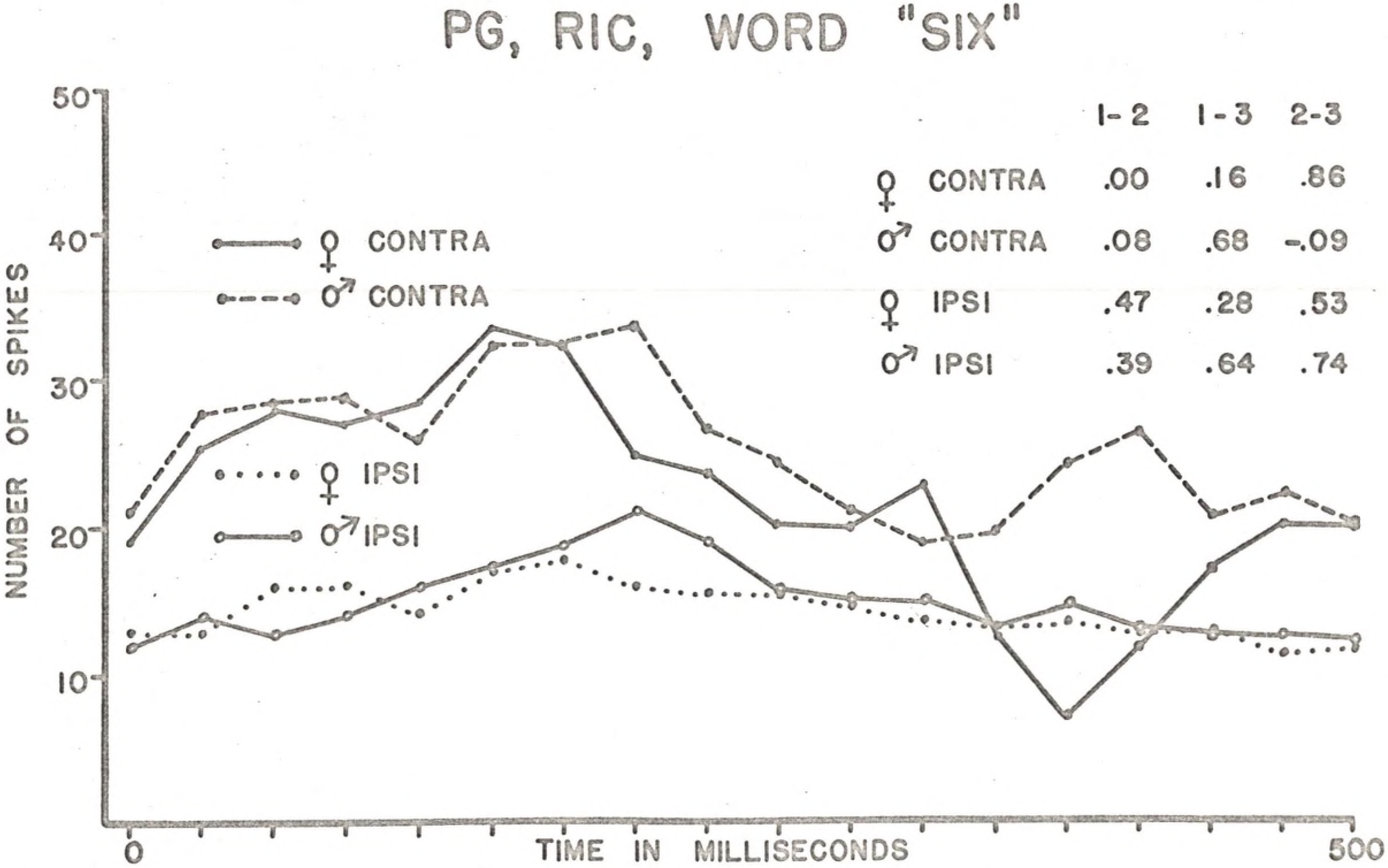


Figure 23. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "six".

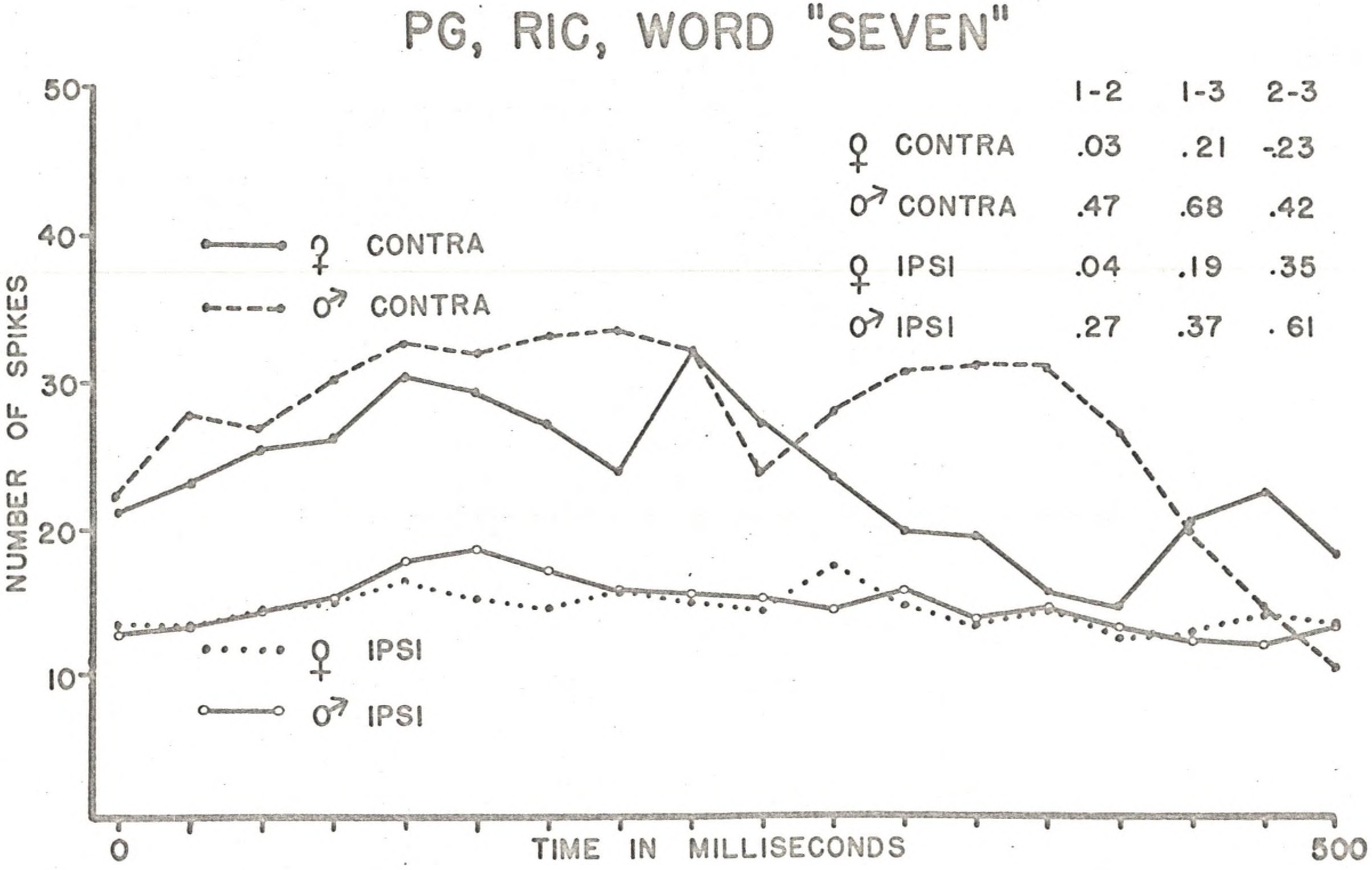
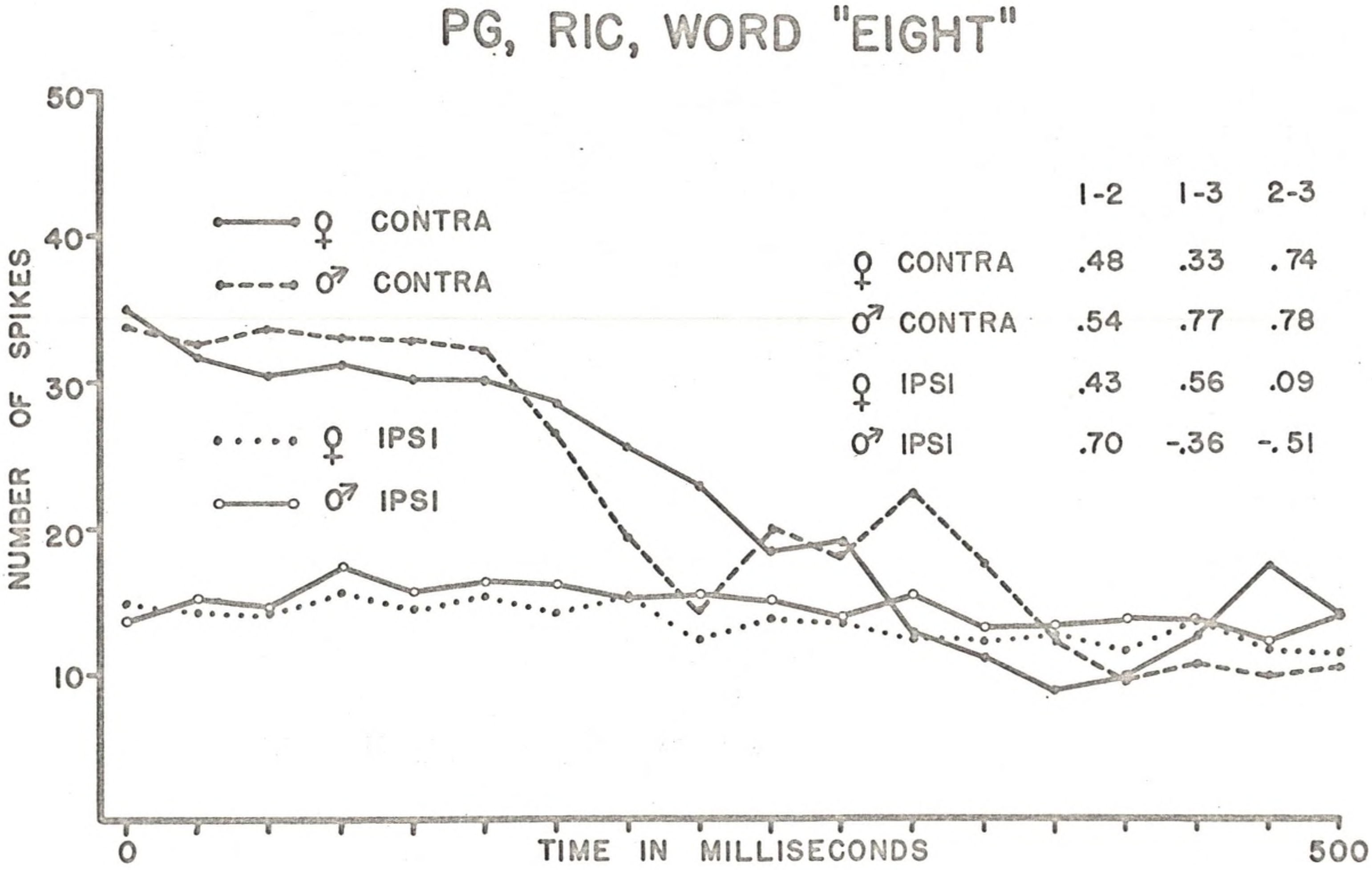


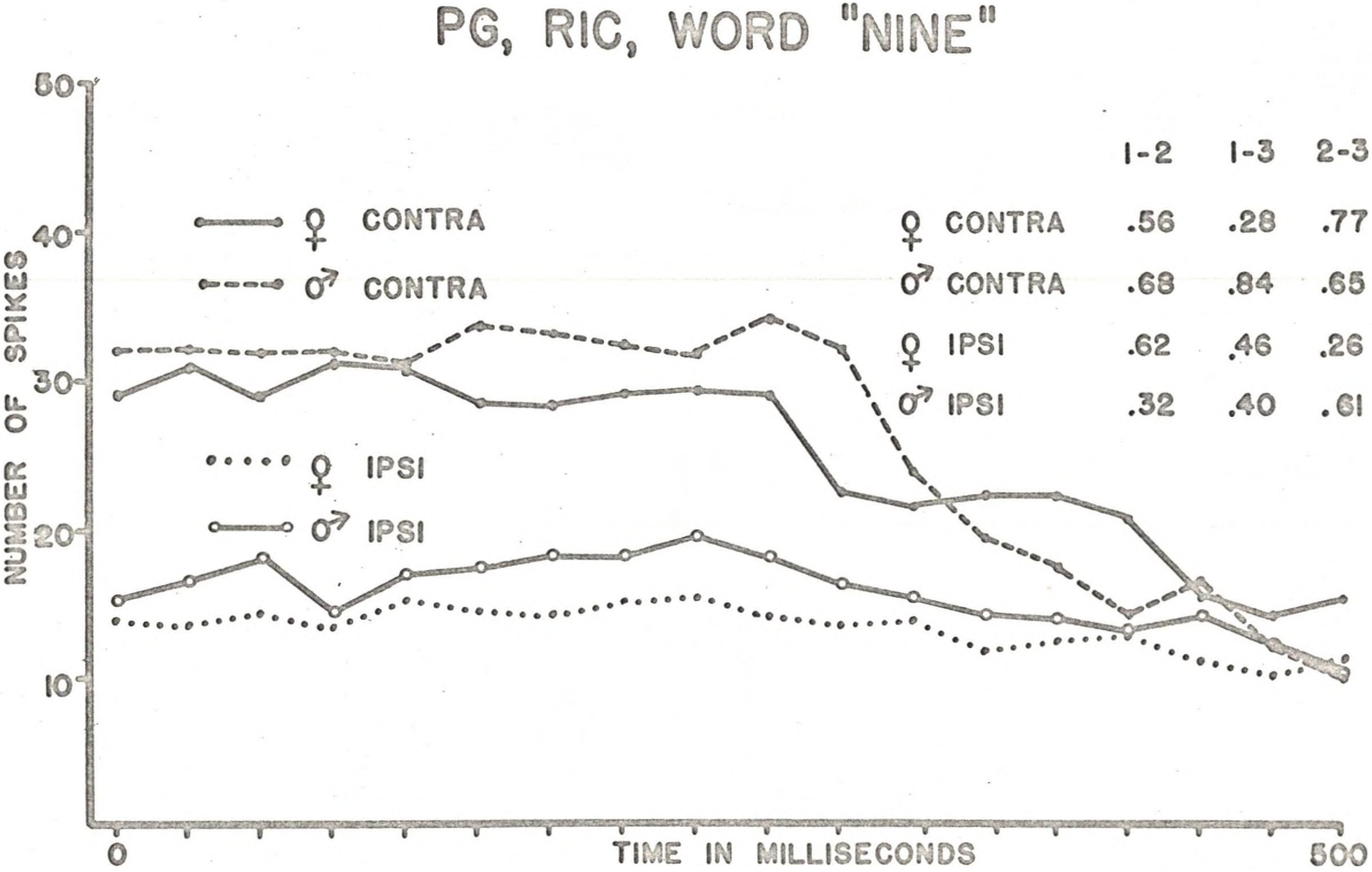
Figure 24. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "seven".



PG, RIC, WORD "EIGHT"

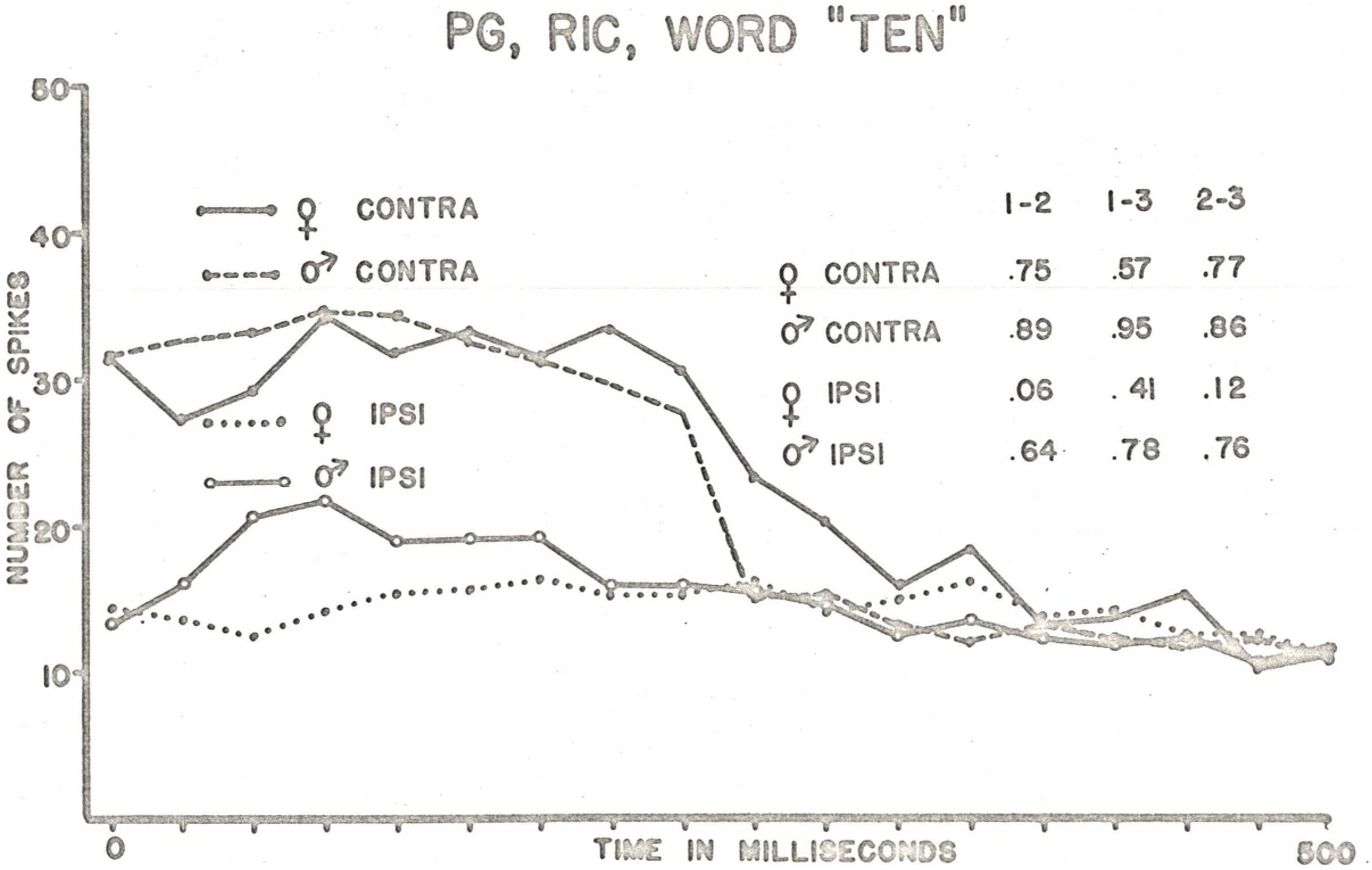
	1-2	1-3	2-3
♀ CONTRA	.48	.33	.74
♂ CONTRA	.54	.77	.78
♀ IPSI	.43	.56	.09
♂ IPSI	.70	-.36	-.51

Figure 25. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "eight".



	1-2	1-3	2-3
♀ CONTRA	.56	.28	.77
♂ CONTRA	.68	.84	.65
♀ IPSI	.62	.46	.26
♂ IPSI	.32	.40	.61

Figure 26. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "nine".



PG, RIC, WORD "TEN"

	1-2	1-3	2-3
♀ CONTRA	.75	.57	.77
♂ CONTRA	.89	.95	.86
♀ IPSI	.06	.41	.12
♂ IPSI	.64	.78	.76

Figure 27. Mean neuronal responses at the right inferior colliculus of cat Pg to the word "ten".

The average correlations presented in Table 4 summarize the trends appearing in the correlations of the previous ten figures. The insignificant average correlations of neuronal responses generated by ipsilateral stimulation demonstrates that the right inferior colliculus of cat Pg was largely unresponsive to ipsilateral stimulation. Such stimulation, on the average, did not appear to change the normal spontaneous activity level of the anatomical site under investigation.

Although the average correlation for neuronal patterns generated by female voices with contralateral stimulation approaches statistical significance, it does not equal or exceed the .01 level of confidence. The remaining three average correlations of Table 4 are significant (p. 01). This leads to the conclusion that at this site, the stimulus words, when presented contralaterally by males or bilaterally by either males or females, evoked patterns of neuronal activity that correlated significantly with each other. In testing the significance of the differences between the average correlations presented in Table 4, the t values (McNemar, 1962, p. 140) of Table 5 were obtained. In all comparisons the degrees of freedom were 57. It is apparent from Table 5 that none of the differences between average female-elicited neuronal responses were significant. This indicates that, on the average, not only did contralateral female presentation not differ significantly from bilateral presentation of the female voices, but the average correlations between female ipsilateral and contralateral stimulus presentation also did not differ significantly. The differences obtained with male stimulus voices conformed more closely to expectation. The average difference between correlations of neuronal responses at the inferior colliculus elicited by male contralateral and ipsilateral

TABLE 5

t STATISTICS FOR THE SIGNIFICANCE OF THE DIFFERENCES AMONG AVERAGE INTER-RESPONSE CORRELATIONS FROM THE RIGHT INFERIOR COLLICULUS OF CAT PG

	Females		Males	
	ipsi	bilateral	ipsi	bilateral
contra	1.38	.31	2.27*	.05
ipsi	--	1.69	--	2.33*

*p .05

stimulation did differ significantly from each other at the .05 level. Likewise, the difference between average correlations of neuronal responses elicited by male ipsilateral and bilateral stimulus presentation also was significant at the .05 confidence level. As was the case at the inferior colliculus with female voices, the average response to male voices was not significant when comparing the bilateral and the contralateral response. This finding suggests that at the anatomical site monitored in the right inferior colliculus, there was no facilitation or inhibitory effect when both ears received the stimulus as opposed to only contralateral or ipsilateral stimulation. (This finding refers to inter-response similarity under these conditions of stimulation and not to absolute levels of spike discharge.)

Similarity of Neuronal Responses at the Inferior Colliculus

In Figures 28 to 31 neuronal responses to selected stimuli at the inferior colliculus are presented for the experimental animals.

Once again, an attempt was made to select this data impartially, and it is felt that the similarity between inferior colliculi sites represented in the figures was reflective of the total population of data collected in the experiment for inferior collicular responses.

The left inferior collicular neuronal responses to the stimulus word "six" and "seven" are depicted in Figures 28 and 29 for cats Pg, Lg, Lz, and Rp. The neuronal responses in the figures were recorded during stimulation of the contralateral ear. In Figure 28, all of the correlations between the responses elicited by contralateral presentation of the word "six" by male voices were significant (N=18, p .01). The intercorrelations in Figure 28 range from a low of .65 for cats Lg-Rp to .91 between cats Lg-Lz. The correlations indicate a moderate to high relationship between the neuronal responses evoked by this stimulus situation in the experimental animals.

The neuronal responses of the left inferior colliculus of all cats to male contralateral stimulation with the word "seven" are presented in Figure 29. The correlations between the spike discharge patterns range from .53 for cats Pg-Lg to .74 for cats Pg-Lz and Pg-Rp. All correlations are significant (p .01) except for the r of .53 for cats Pg-Lg. While most intercorrelations in this stimulus situation are significant, there appears to be a lower degree of correspondence between cats than in the other figures of this series.

Figures 30 and 31 depict the between-cat results for the left inferior colliculus with female voices presenting the words "four" and "five". In Figure 30 with contralateral presentation of the word "four", the correlations between neuronal discharge patterns range from .66 for cats Pg-Lg to .96 for cats Lz-Rp. All of the correlations

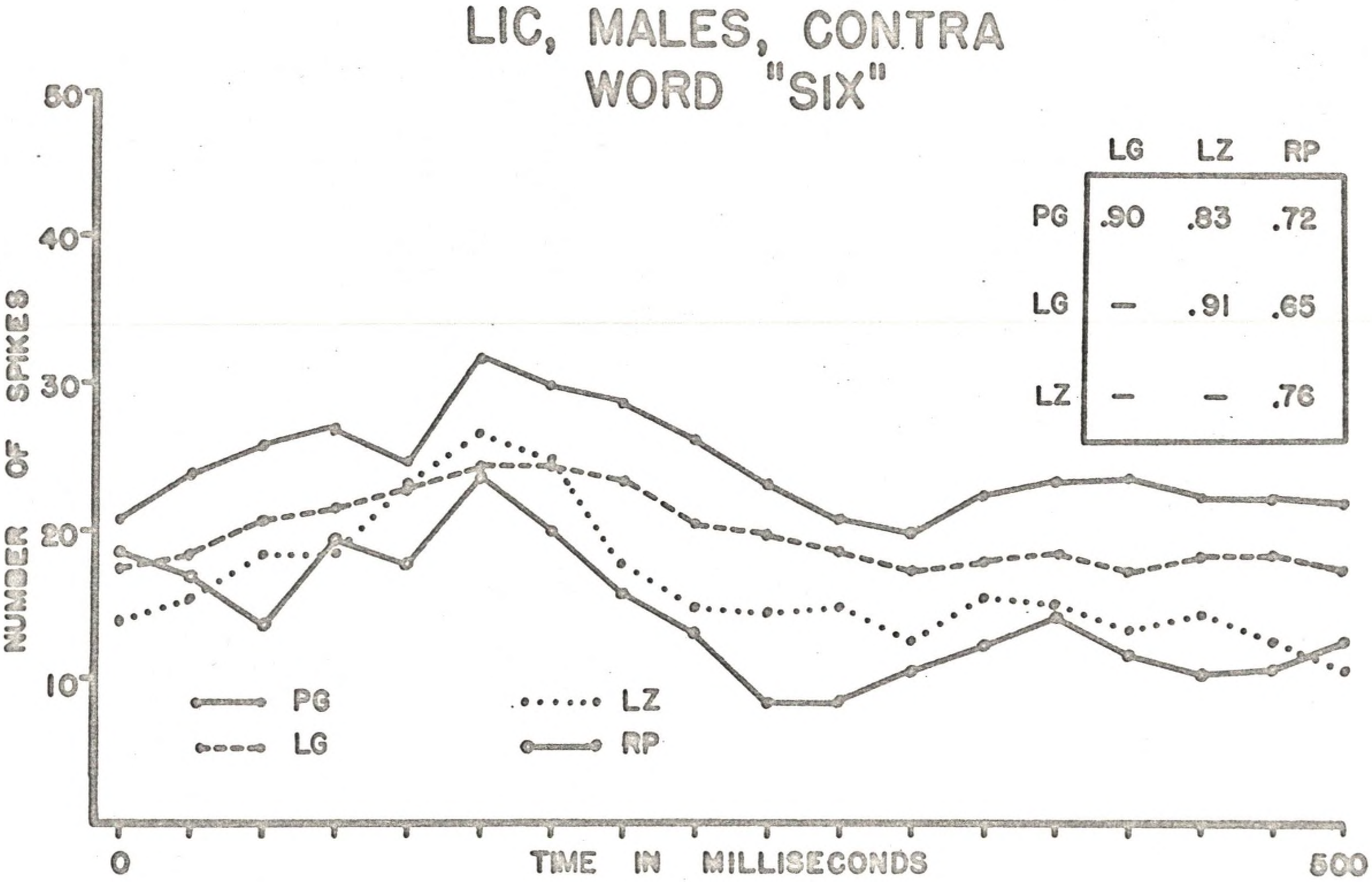


Figure 28. Mean neuronal discharges at the left inferior colliculus of cats Pg, Lg, Lz, and Rp. Responses were recorded during contralateral stimulation with male voices presenting the word "six". The inset presents the correlations between each neuronal discharge pattern.

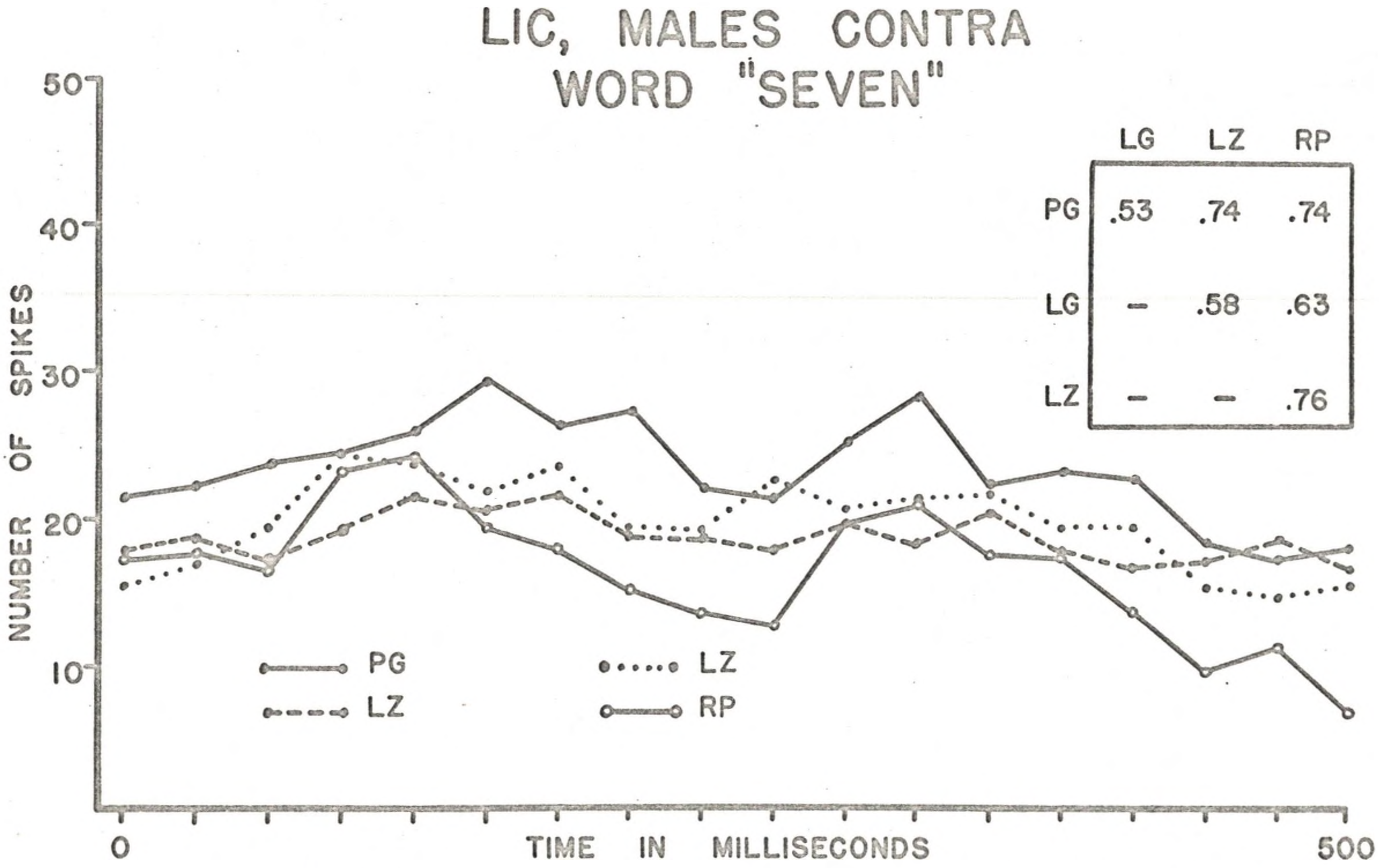


Figure 29. Mean neuronal discharges at the left inferior colliculus. Responses represent the mean number of spikes recorded during contralateral stimulation with male voices presenting the word "seven". The inset gives the intercorrelations between each discharge pattern.

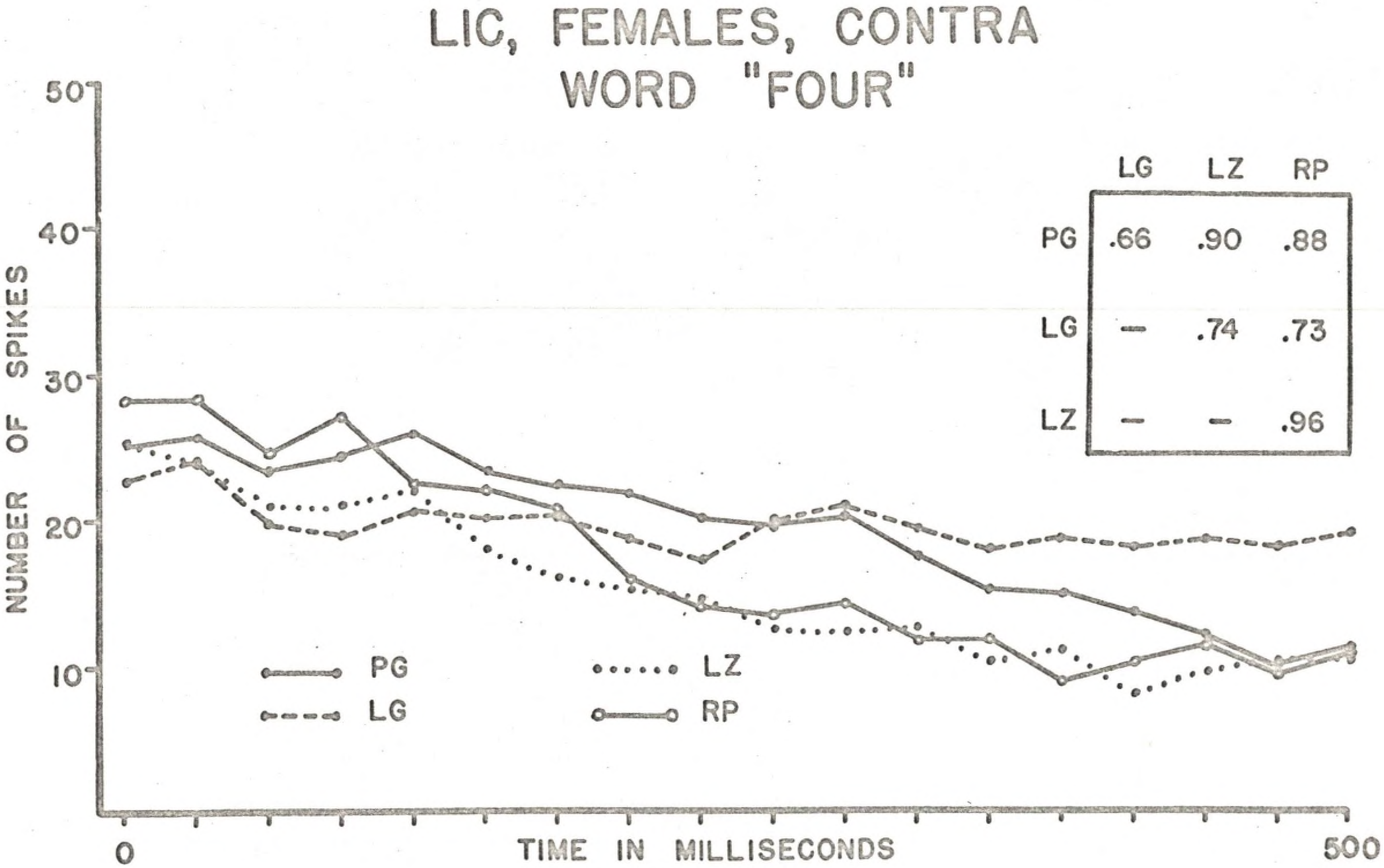
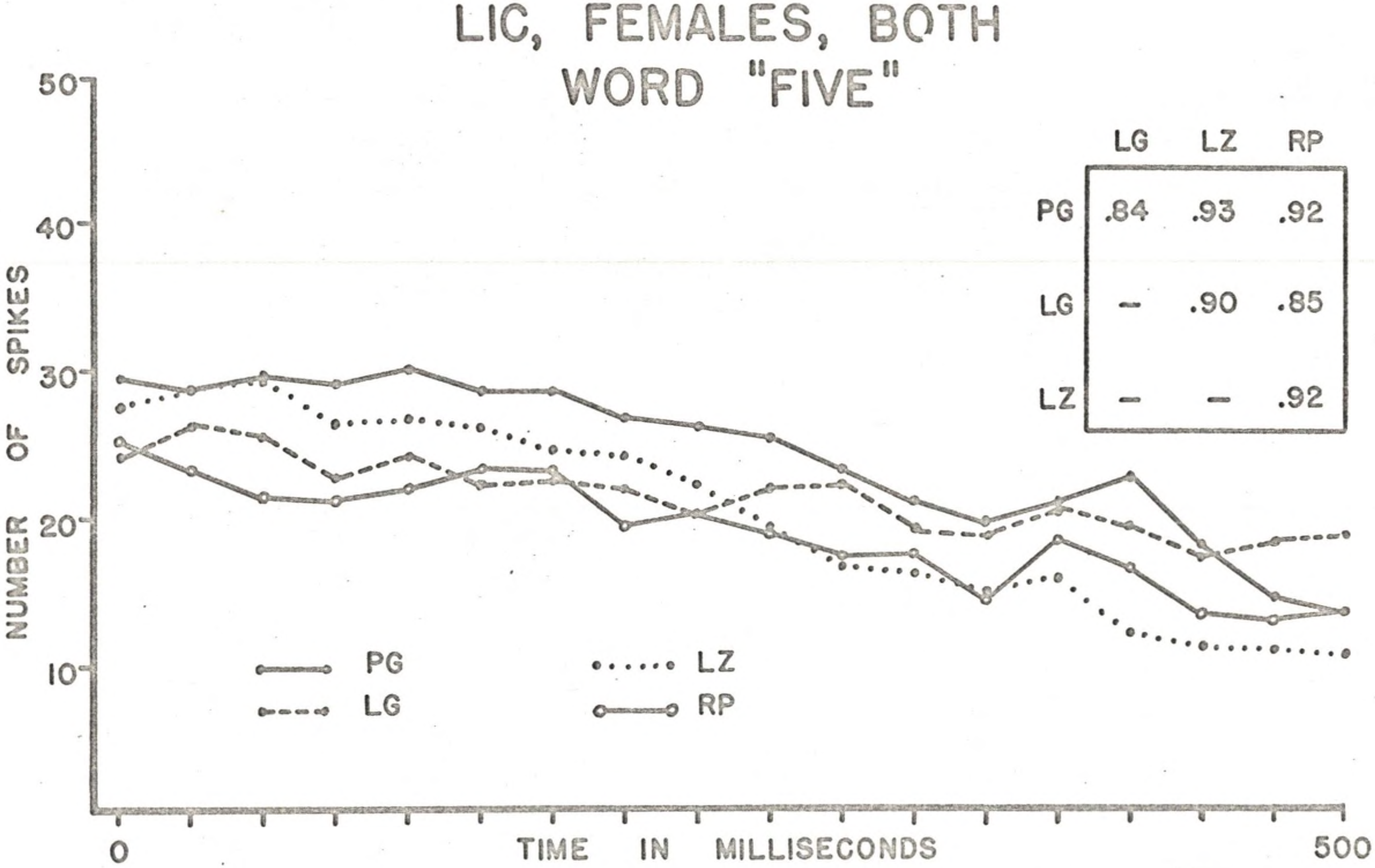


Figure 30. Mean neuronal responses at the left inferior colliculus during contralateral stimulation with female voices presenting the word "four".



	LG	LZ	RP
PG	.84	.93	.92
LG	–	.90	.85
LZ	–	–	.92

Figure 31. Mean neuronal patterns at the left inferior colliculus. Responses were evoked be female voices presenting the stimulus "five" to both ears.

in Figure 30 are significantly different from a zero correlation (p .01). The data suggests the presence of a moderate to very high relationship between the neuronal responses of the four cats under these stimulational conditions.

The neuronal discharge patterns to female bilateral stimulation with the word "five" are presented in Figure 31. All of the correlations between cats are significant beyond the .01 level of confidence. They range from .84 for cats Pg-Lg to .93 for cats Pg-Lz. The correlations suggest a moderate to very high similarity of discharge patterns between cats.

In summary, it appears that there is a moderate to very high degree of similarity of spike discharge patterns at the inferior colliculus between the experimental animals. The sustained spike burst which occurs at the level of the inferior colliculus to contralaterally or bilaterally presented stimuli was a phenomenon which occurred consistently between experimental subjects. This high degree of similarity of neuronal response between cats suggests the presence of the same type of response which was reported at the level of the cochlear nucleus. It is believed that these neural discharge characteristics play a critical role in stimulus coding of low frequency stimuli at both levels of the auditory pathway.

Comparison of Cochlear Nucleus and Inferior Colliculus Responses

Data has previously been reported for the within and between neuronal responses to stimulation at both the cochlear nuclei and inferior colliculi levels of the auditory pathway. At this point, therefore, it is possible to make some summarizing statements concerning the similarities and differences in neuronal spike discharges between these two levels. Using the average correlations for neuronal patterns at the left dorsal cochlear nucleus and the right inferior colliculus in cat Pg (Tables 3 and 4) the significance of the differences between the average correlations at the cochlear nucleus and inferior colliculus were calculated. The resulting t statistics are reported in Table 6 for female elicited responses and Table 7 for male evoked neuronal patterns.

TABLE 6

t STATISTICS FOR THE SIGNIFICANCE OF THE DIFFERENCES AMONG AVERAGE FEMALE EVOKED INTER-RESPONSE CORRELATIONS FROM THE LEFT DORSAL COCHLEAR NUCLEUS AND THE RIGHT INFERIOR COLLICULUS OF CAT PG

		Females, Left Cochlear Nucleus		
		ipsi	contra	bilateral
Females, Right Inferior Colliculus	contra	.79	1.24	1.06
	ipsi	2.17*	.13	2.44*
	bilateral	.99	3.03**	.72

*p .05
**p .01

The degrees of freedom (df) were equal to 57. In assessing the similarity of neuronal discharge patterns at the cochlear nucleus and inferior colliculus one would, of course, be more interested in the average correlations of Table 6 which did not differ from each other statistically. The difference between the average correlation for the right inferior colliculus with contralateral stimulation (r=.54) and the left cochlear nucleus with ipsilateral stimulation (r=.66) was one such difference. Both of these stimulus conditions elicited the maximum spike burst at their respective sites and the average correlations between neuronal responses elicited by female voices does not differ between the sites.

The difference between the average right inferior colliculus correlation with contralateral stimulation (r=.54) and the average left cochlear nucleus correlation under contralateral stimulation (r=.30) also does not reach significance at either the .05 or .01 level of confidence. This finding is somewhat more surprising since contralateral stimulation of the inferior colliculus elicited the maximum spike burst while contralateral stimulation at the cochlear nucleus did not observably change the random pattern of multiple unit neuronal activity. With df of 57 the difference between these two average correlations was not great enough to yield significance although the magnitude of the two correlations corresponded to expectation.

The remaining t statistics of Table 6 which failed to reach significance conform to general expectations based upon a knowledge of the neuronal responsiveness of the sites investigated. In the case of the insignificant difference between the right inferior colliculus with ipsilateral stimulation (r=.54) and the left cochlear nucleus during bilateral stimulation (r=.72), the insignificant difference was expected since both conditions elicit a maximal spike burst at their respective sites. The insignificant difference between average correlations for the right inferior colliculus under ipsilateral stimulation (r=.46) and left cochlear nucleus with contralateral stimulation (r=.30) was also not surprising, since the activity at both sites under these stimulus conditions closely resembled random discharge patterns. The two insignificant differences of the last row of Table 6 were also reasonable in view of the fact that in both stimulus situations maximal spike bursts were evoked at both anatomical sites.

The three t statistics in Table 6 which reflect statistically significant differences all represent situations where apparent random neuronal activity at one site was compared with sustained spike bursts at the other site. It was expected that these differences would reach a significant level.

Table 7 presents t scores for the significance of the differences between average correlations for neuronal responses elicited by male voices at the right inferior colliculus and the left dorsal cochlear nucleus of cat Pg. Table 7 can be interpreted in the same manner as the previous table. An inspection of the t statistics in Table 7 demonstrates that the average neuronal correlation observed with male voices at the left cochlear nucleus did not differ statistically from the right inferior colliculus average correlations when analogous (contralateral or bilateral inferior colliculus stimulation versus ipsilateral or bilateral cochlear nucleus stimulation) comparisons were made.

It appears that when all stimulus words are collapsed and intercorrelations between neuronal patterns are averaged for the appropriate condition of stimulation, the inferior colliculus response does not differ significantly from the cochlear nucleus response. In other

TABLE 7

t STATISTICS FOR THE SIGNIFICANCE OF THE DIFFERENCES BETWEEN AVERAGE MALE EVOKED INTER-RESPONSE CORRELATIONS FROM THE LEFT DORSAL COCHLEAR NUCLEUS AND THE RIGHT INFERIOR COLLICULUS OF CAT PG

		Males, Left Dorsal Cochlear Nucleus		
		ipsi	contra	bilateral
Males, Right Inferior Colliculus	contra	1.10	2.00*	1.13
	ipsi	3.38**	.27	3.46**
	bilateral	.04	2.06*	1.07

*p .05
**p .01

words, the same type of neuronal discharge patterns were observed at the inferior colliculus with contralateral and bilateral stimulation.

Testing the statistical significance of the differences between average correlations for both cochlear nuclei and inferior colliculi neuronal responses provided one technique for making comparative statements regarding evoked neuronal responses at these levels. Another, and perhaps more direct approach, would involve plotting the multiple unit neuronal discharges within several cats at each of the relevant sites within the auditory pathway. Figures 32, 33, and 34 present representative data of this nature. Cats Pg and Rp were selected for these comparisons since they were the only subjects with the complete array of four electrodes. As in all previous figures each plotted point represents the mean of 15 observations for the responses elicited by the three voices of the same sex. The intercorrelations given in the inset of each figure depict the associations between each plotted neuronal response. In these figures the neuronal discharge patterns shown for cochlear nuclei electrode placements were recorded during ipsilateral voice presentation. The inferior colliculi recordings were made during contralateral stimulus presentation.

The neuronal responses recorded at the four auditory sites in cat Rp are shown in Figure 32. The neuronal activity was evoked by female voices presenting the stimulus word "four". Both a visual inspection of the tracings in Figure 32 and the magnitude of the intercorrelations between responses suggest a very high relationship between the neuronal activity within these anatomical sites. The intercorrelations range from .92 to .94. Almost identical discharge patterns occurred at the four sites within this experimental animal.

Figure 33 gives the between site comparison for cat Pg. The mean responses depicted in Figure 31 were elicited by male voices presenting the stimulus word "seven". The lowest intercorrelation between traces was .57 (p .05) for left cochlear nucleus--right inferior colliculus. The highest correlation of this series was the correlation of .83 occurring between the left inferior colliculus--right inferior colliculus sites. The magnitude of the intercorrelations suggests a moderately high degree of similarity between the evoked responses.

In Figure 34 the final comparison of evoked responses within the same cat at all four auditory sites is presented. The responses of Figure 34 were recorded from cat Rp with female voices presenting the word "five". All of the intercorrelations between tracings are significantly different from a zero correlation beyond the .01 level

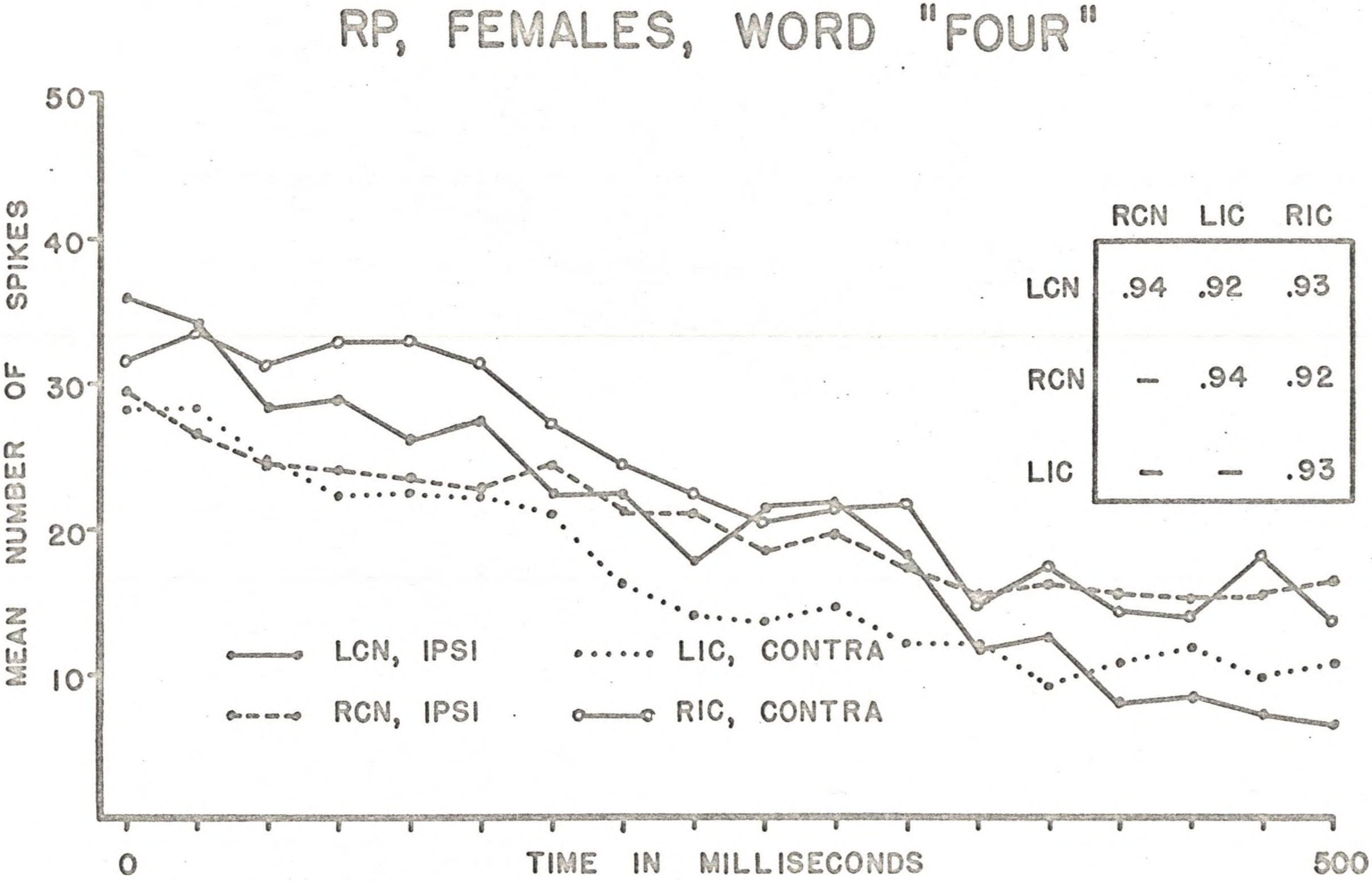


Figure 32. Mean number of spikes at the four recording sites in cat Rp. Responses were recorded during the stimulus "four" presented by female voices. The cochlear nuclei sites were recorded during ipsilateral stimulation and the inferior colliculi sites during contralateral stimulus presentation. The inset presents the intercorrelations between the four neuronal discharge patterns.

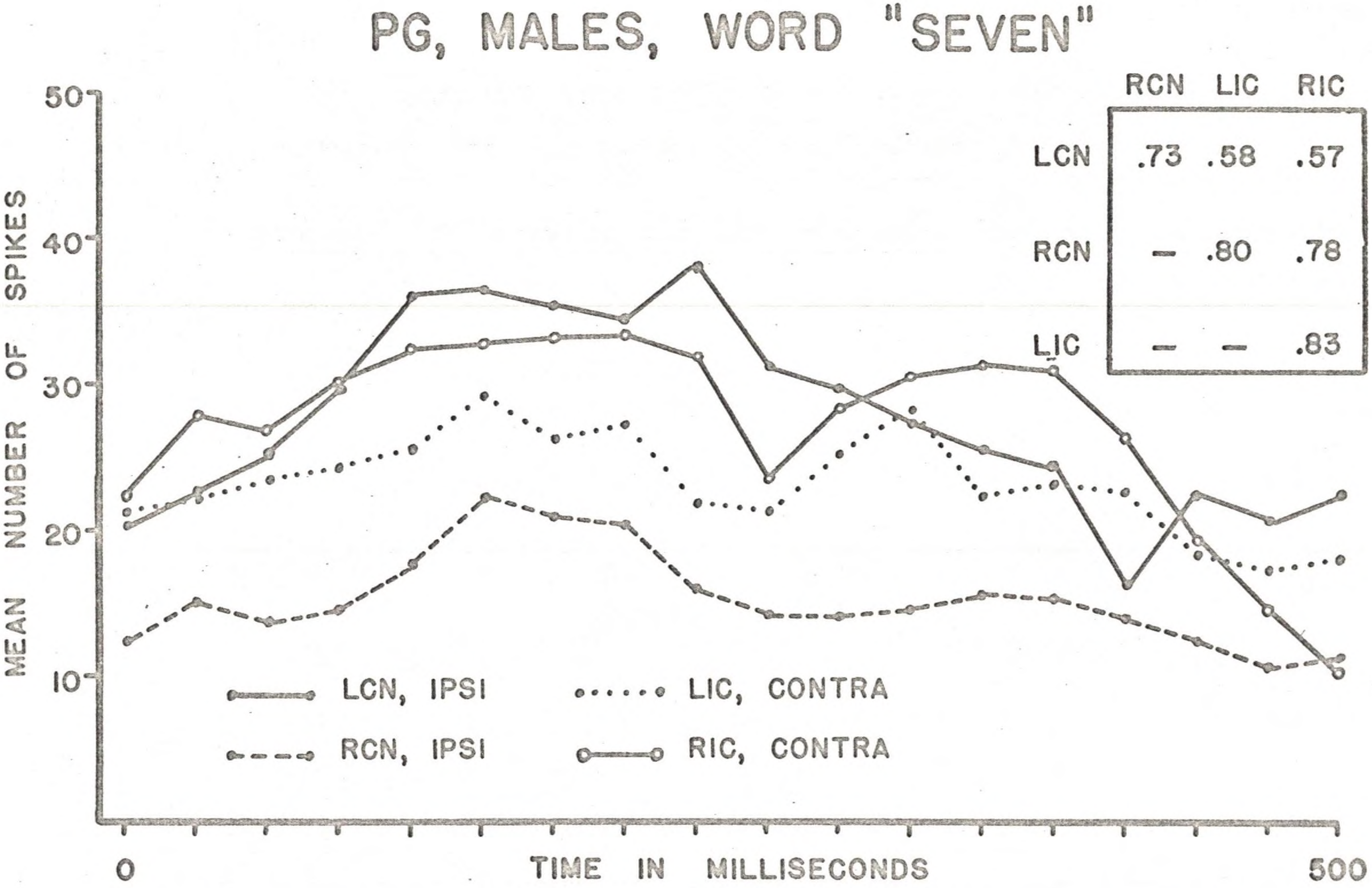


Figure 33. Mean number of spikes at the four recording sites in cat Pg. Responses were evoked by the stimulus word "seven" presented by male voices. Ipsilateral stimulation at the cochlear nucleus is compared with contralateral stimulation at the inferior colliculus.

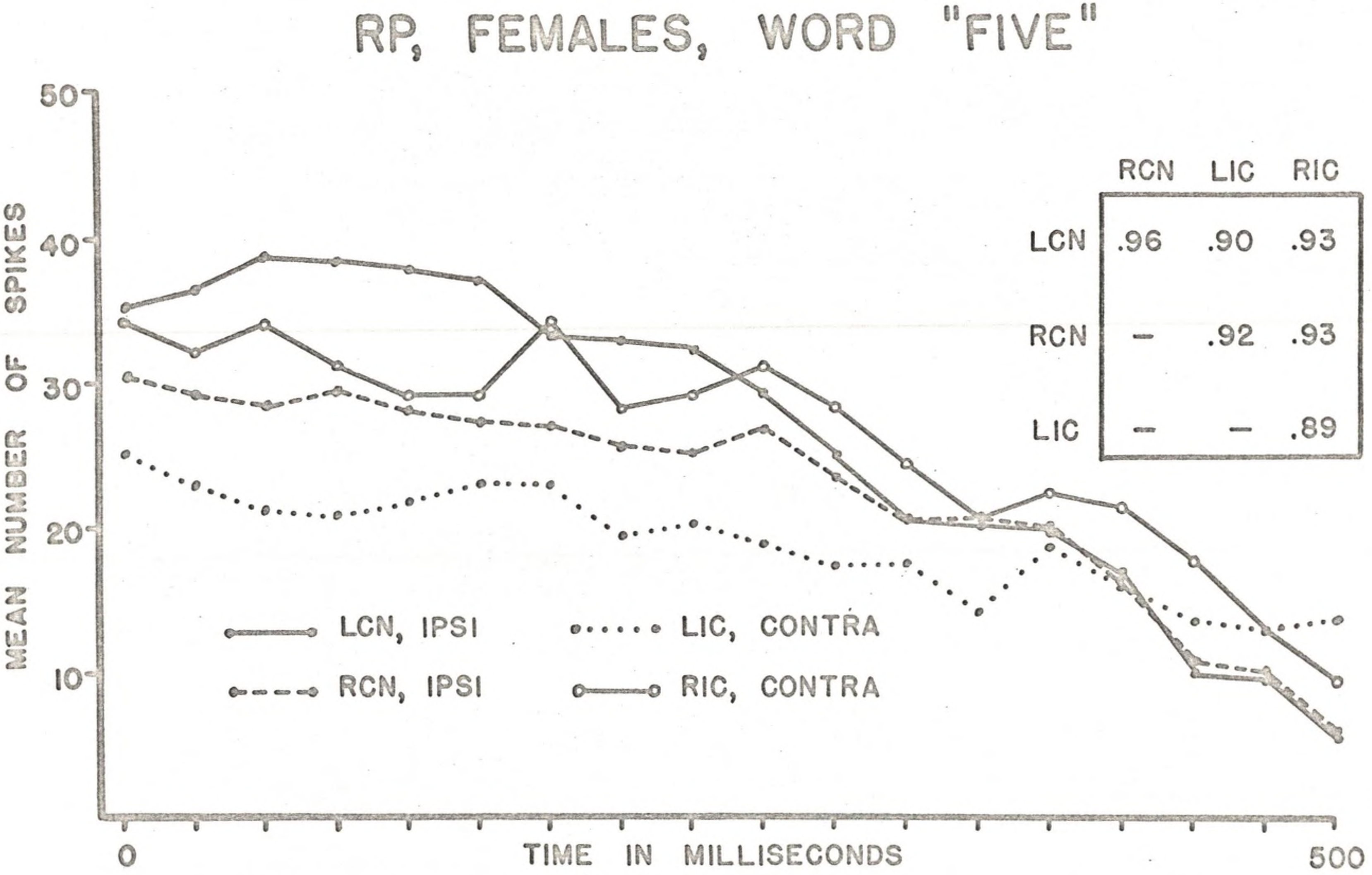


Figure 34. Mean number of spikes at the four electrodes in cat Rp. Responses were elicited by the male voices presenting the stimulus word "five". Ipsilateral stimulation at the cochlear nucleus is compared to contralateral stimulation at the inferior colliculus.

of confidence. The correlations range from .89 for left inferior colliculus--right inferior colliculus to .96 for left cochlear nucleus--right cochlear nucleus. The magnitude of these correlations, once again, suggest that all four auditory sites were exhibiting very similar discharge patterns to the acoustic stimulus.

CHAPTER V

DISCUSSION AND SUMMARY

For several years it has been a common observation in our laboratory that large multiple unit spike bursts could be evoked in subcortical auditory nuclei by stimulation with sound. At the level of the cochlear nucleus and inferior colliculus this has been such a consistent observation that it was thought that the spike bursts represented a sensory coding mechanism.

The study of sensory coding in the central nervous system has been almost the exclusive domain of researchers using single unit recording techniques. Several theoretical articles have recently appeared (Erickson, 1968; Pfaff, 1969; Uttall, 1969) which propose that the study of the overall activity of a large population of neurons may contribute information about sensory coding which is not provided by single neuron studies. Although there are a vast number of neurons in the central nervous system, the number of cells in the classical sensory pathways is small in comparison to the large number of stimuli which may be perceived as different from each other. The proponents of the "overall activity" view of stimulus coding maintain that there are simply not enough neurons in the primary sensory pathways so that every stimulus can be represented by a separate neuron. If this view is correct, an experimental technique monitoring the overall response of a neuronal pool should prove useful in the study of sensory coding mechanisms. The present study has used the multiple unit recording technique to investigate "overall" patterns of neuronal discharges at subcortical auditory nuclei. It has been demonstrated that with this technique the maximum recording distance from the electrode tip is approximately 1.0 mm (Halas and Beardsley, 1968). The multiple unit responses thus provide an overall measure of discharge characteristics of the cellular units composing this pool.

Measures of spike discharge frequencies were obtained from four adult cats. In all cases, stimuli consisted of recorded male and female voices presenting the words "one" through "ten". Neuronal recordings were made during the stimulus presentations. Data was collected from four sites: left and right cochlear nuclei and left and right inferior colliculi. Because of the length of each experiment, it was necessary to anesthetize the cats. Qualitative observations made in the laboratory indicated that the multiple unit recordings at these two levels of the auditory pathway did not differ in conscious or anesthetized animals. The literature tends to confirm this view (e.g., Warden and Marsh, 1968).

The dependent variable was the number of neural spike discharges counted during each 500 milisecond of recording time. No attempt was made in this experiment to monitor the amplitude of these multiple unit neuronal responses. The basic hypothesis of the experiment was that the large multiple unit spike burst to aural stimulation represented a stimulus coding mechanism. It was thought that our recording technique would provide a useful method of investigating this phenomenon. It was predicted that an analysis of discharge frequencies would reveal that the subcortical auditory nuclei discharge differentially to the different stimuli. If a coding mechanism was in fact operating, it was also thought that different voices presenting the same stimuli would evoke very similar patterns of activity both within and between anatomical sites tested. The following effects were discussed in the data analysis: laterality of stimulation; stimuli; voice presenting the stimuli; and anatomical sites both within and between cats. The results presented were representative selections made from the total pool of data collected in the experiment.

At the level of the cochlear nuclei in all cats, the results clearly indicated that ipsilateral stimulation evoked a sustained multiple unit spike burst while contralateral stimulation had no observable effect on the on-going neuronal activity. These results were not unexpected, since there are no known direct afferent anatomical connections between the cochlear nucleus and the contralateral ear. This finding was valuable, however, since it provided an indirect check on several aspects of the experimental methodology. Throughout the course of the experiment it was assumed that the large multiple unit spike bursts observed at the auditory nuclei were evoked by presentation of sound. Had we observed large spike bursts at the cochlear nucleus under conditions of contralateral stimulation, this assumption would have been much less tenable. Failure to elicit a spike burst at the cochlear nucleus with contralateral stimulation also confirmed the fact that the earpieces were placed securely enough in the external auditory meatus to prevent the passage of sound through the air from one ear to the other.

The results of the experiment also clearly confirmed the importance of laterality of stimulation at the inferior colliculi level of the auditory pathway. The classic literature suggests that in the central auditory pathway above the level of the cochlear nucleus, projection is generally bilateral with perhaps a slight preference for the contralateral side. Hind (1963) using single unit studies at the inferior colliculus, found units which were not responsive to ipsilateral stimulation. He reported that these cells often fired more to binaural stimulation than to contralateral stimulation alone. The multiple unit recordings made at the inferior colliculus in this experiment corresponded with these results. Only rarely did ipsilateral stimulation at the inferior collicular level cause any detectable change in the on-going level of neuronal discharge. Contralateral stimulation at the inferior colliculi sites was consistent in evoking a sustained spike burst. There was also evidence that bilateral stimulation yielded greater spike counts than contralateral stimulation alone. With the same stimulus word, however, the average inter-response similarity between different voices was not significantly affected by bilateral as opposed to only contralateral stimulation.

Although it was not as conclusive as hoped, the experiment did provide evidence that at both the cochlear nucleus and the inferior colliculus different stimulus words did generate different over-all patterns of multiple unit spike discharges. The most outstanding examples of this finding occurred with the stimulus words "five", "six", and "seven" at both anatomical sites. These stimulus words generated neuronal discharge configurations which clearly differed from each other. This finding suggests that a sensory coding mechanism was operating. This coding mechanism probably reflects a frequency-following type of mechanism. Although no formal attempt was made in the experiment to relate the frequencies of the stimulus words with the neuronal discharge frequencies, spectrographs of the voices (Walker, Halas, and Oring, 1970) have indicated that with most of the voices the fundamental frequency ranged from approximately 700 to 1800 Hz. Spectrographs of female voices presenting the word "three", for example, showed a fundamental frequency of about 1200-1400 Hz. Figure 6 presented the neuronal response at the cochlear nucleus in cat Pg to this stimuli. The maximum average response observed in this situation was 40.8 spike discharges. This figure would correspond to a discharge rate of 1440 spikes per second--a number not far removed from the basic frequency range of the eliciting sound. Although the evidence is not conclusive, it appears that the neuronal coding mechanism tapped in this experiment was probably a volleying or frequency-following type of response.

Some of the strongest evidence obtained in the experiment for a central coding mechanism came from a comparison of neuronal responses obtained within the same site during stimulation with different voices. The sequential data presented for the left dorsal cochlear nucleus of cat Pg, for example, yielded an average Pearson-product-moment correlation across all ten stimuli of .66 for female voices and .88 for male voices (both under ipsilateral stimulation). These statistics suggest that there was a moderate to high degree of association of "pattern similarity" at this site between neural responses evoked by the ten stimulus words regardless of which same-sex voice presented the stimuli. In other words, the stimuli themselves, seemed to be generally more important in determining the pattern of neuronal discharge than the voice presenting the stimulus. A "common sense" interpretation supports this finding. We perceive a word as identical even though it is presented by several different persons with widely differing vocal characteristics. If the coding mechanism tapped in this study represented a perfect frequency reproductive system (at least within a low frequency range) and all factors were held constant except for speakers, that magnitude of our average intercorrelations which deviated from unity would represent the different frequency ranges of the voices utilized in the experiment. If the responses generated by different speakers were identical, it would be difficult to conceptualize how the brain could perceive differences between voices.

The average correlations reported in the sequential presentation of the right inferior colliculus in cat Pg correspond in magnitude to those obtained at the cochlear nucleus in the same cat. Under conditions of contralateral stimulation, the average neuronal association for female voices was .54 and .80 for male evoked responses. Once again, a moderate to high degree of pattern similarity was found for evoked activity generated by same-sex speakers. Although the average correlations between neuronal responses at the inferior colliculus were somewhat lower than those obtained at the cochlear nucleus, the difference was not statistically significant.

The results thus far have indicated that a multiple unit spike discharge mechanism may participate in stimulus coding of low frequency auditory stimuli. Different stimuli generated different spike patterns within the same cat at both the cochlear nucleus and the inferior colliculus. Same-sex voices presenting identical stimuli also were found to generate neuronal responses having a moderate to high degree of similarity to each other. This discharge phenomenon was found to occur consistently in all of the experimental animals at both the dorsal cochlear nucleus and the inferior colliculus. At the cochlear nuclei level, the intercorrelation between neuronal discharge patterns ranged from .53 (N=18, P .05) to .97 (N=18, p .01). Of the sample of 24 intercorrelations reported for comparison between cats at the level of the cochlear nucleus, 11 (45 percent) had a magnitude of .90 or larger and six correlations (25 percent) fell between .80 and .89. This finding proved to be rather dramatic since such a high degree of similarity between responses recorded across subjects was not expected. The results indicated that at the dorsal cochlear nucleus a very similar discharge pattern was being recorded in all of the experimental animals.

The similarity of neuronal response between cats was maintained at the inferior collicular level, but the intercorrelations between cats was of a somewhat smaller magnitude than was observed at the cochlear nucleus. The range of the 24 correlations at the inferior colliculus was from a low of .53 (N=18, p .05) to a high of .96 (N=18, p .01). Fifty percent of these correlations were .80 or above. These data suggested that although there was high similarity between responses in some stimulus situations, the general similarity between cats at the inferior colliculus may be lower than at the cochlear nucleus. However, the extent of similarity at this level remained statistically significant ranging from moderate to very high correspondence between cats.

The results of this experiment comparing neuronal responses between the cochlear nucleus and inferior colliculus (within subject) strongly suggested that very similar neuronal discharge patterns were observed at both sites. When average intercorrelations between responses evoked by same-sex voices were compared in cat Pg between left dorsal cochlear nucleus and right inferior colliculus, it was found that the significant comparisons (e.g., where laterality of stimulation evoked a spike burst) tended not to be statistically different between the two anatomical sites. In other words, at both the dorsal cochlear nucleus and the inferior colliculus in cat Pg the similarity of neuronal responses generated by same-sex voices was high. The neurological coding mechanism representing the stimulus word did not appear to break down at this higher level of the auditory pathway.

The intercorrelations for between site comparisons (within subject) which were presented also indicated a high degree of response similarity between the cochlear nucleus and the inferior colliculus. These correlations ranged from .57 (N=18, p .05) to .96 (N=18, p .01). Of the correlations for between site comparison, 61 percent had a magnitude of .90 or larger. This finding also strongly suggested that within the same cat, both cochlear nuclei and inferior colliculi sites were responding in very similar manners to the stimuli.

At this point it has been demonstrated that multiple unit neuronal recording techniques can be useful in the investigation of sensory coding mechanisms within the central nervous system. The technique yields neuronal data reflecting the activity of a population of neurons about the electrode tip. The "average" activity of these neural elements reflected differing patterns of discharge as a function of low frequency aural stimulation. It would be interesting to speculate about the discharge characteristics of each individual cellular unit that was sampled in this experiment. The possibility seems fairly large statistically (considering the great number of neurons that must have been involved) that many cells were either completely unresponsive to the frequency ranges of the stimuli or presented discharge patterns that differed greatly from the obtained multiple unit discharge patterns. Assuming that this phenomenon occurred, the interpretation given to stimulus coding phenomena at the immediate anatomical area could be vastly different from conclusions drawn from recording techniques sampling the over-all activity of larger population of neurons. This line of reasoning certainly does not imply that the results of single unit research have not contributed a great bulk of valuable knowledge about how the nervous system works. It is meant, rather, to suggest that multi-unit research can also contribute unique findings which are not directly detectable from the "behavior" of individual neurons.

The experiment has also demonstrated that the multiple unit spike bursts observed at the cochlear nucleus and inferior colliculus seem to have a functional significance. Different stimulus words tended to generate discharge patterns which differed from each other. Different voices presenting identical stimuli also generated responses having a moderate to very high similarity to each other. The spike discharge patterns were highly similar at both cochlear nucleus and inferior colliculus in all experimental animals. There was also a very close association between anatomical sites within each cat. These findings lend strong support to the basic hypothesis of this experiment: the spike bursts observed during aural stimulation represent a neuronal encoding mechanism. The failure of the dorsal cochlear nucleus to respond to contralateral stimulation provided the experiment with a "built in" control condition. In all cases, the neuronal discharge patterns at the cochlear nucleus with contralateral stimulation were flat. The intercorrelations between these neuronal responses during stimulation with different voices generally were small and indicated only random association between patterns.

The neuronal responses reported in this experiment appear similar, if not identical, to the frequency-following response reported by Worden and Marsh (1968). These authors describe a form of acoustically elicited response recorded from gross electrodes in the subcortical auditory pathway. Like the cochlear microphonic potential, the FFR is said to reproduce the sine wave of the sound stimulus. Worden and Marsh were able to record a distinct cochlear microphonic response from each site presenting the FFR. This finding was replicated in the present experiment. At each anatomical site which yielded a multiple unit spike burst, a strong microphonic response was also observed.

Worden and Marsh report that the FFR never reproduces the eliciting sound as accurately as does the microphonic response. It was also reported that the FFR amplitude was greatest at the onset of the stimulus with up to a 75 percent decrease in amplitude after the first 10 msec. of the neuronal response. The amplitude data collected in this experiment have yet to be analyzed, however, many hours of visual inspection of the multiple unit spike bursts failed to reveal any amplitude decrement. The large sample of photographs made of the spike bursts also failed to demonstrate the sizable amplitude decrease reported by Worden and Marsh.

Like the FFR, the multiple unit spike burst appeared with a threshold-like abruptness. Unlike the cochlear microphonic which tends to reproduce the graded onset of the stimulus, the multiple unit burst exhibited the characteristics of neuronal activity.

The results of this study deviate in several important ways from the data reported for the FFR. Our results have indicated that there was minimal variation in comparing recordings across electrodes both within the same neural structure or between the cochlear nucleus and inferior colliculus. Worden and Marsh, on the other hand, found extensive variation in the response even within the same neural structure. It is difficult to explain this discrepancy since the anatomical sites and recording techniques used by Worden and Marsh were similar to those employed in this experiment. These workers did employ a pure tone as a stimulus, but this difference in stimuli would not seem to account for the different results. There would seem to be no inherent reason why a low frequency pure tone would generate more neuronal variability than the low frequency complex vocal stimuli used in this experiment.

Another difference obtained in this study involved the anatomical level exhibiting the multiple unit spike discharges to aural stimulation. Worden and Marsh report that negative findings were obtained above the afferent side of the inferior colliculus bordering the lateral lemniscus. Although histological verifications are not yet avilable, the experimenters have reason to believe that the inferior collicular sites represented in the experiment were located in the corpus of the inferior colliculus higher and more dorsally than the border of the lateral lemniscus. This conclusion will, however, have to remain tentative pending the results of the histological verification.

The results have contributed evidence that the original hypothesis of the existence of a neuronal coding mechanism was confirmed. This phenomenon appeared to be a prominent feature of the neuronal response to low frequency complex stimuli through the level of the inferior colliculus. Low frequency sounds which are coded at the cochlear nerve by frequency of nerve fiber discharge appear to be encoded in the same way by groups of neurons at the dorsal cochlear nucleus and the inferior colliculus. No observations of this mechanism were made in the auditory pathway higher than the collicular level. The fact that the encoding mechanism occurs only below the level of the thalamus may be suggestive that pitch discrimination may be essentially completed before the neuronal discharges proceed to the medial geniculate body of the thalamus.

APPENDIX

TABLE 8

PEARSON PRODUCT MOMENT CORRELATIONS AMONG NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES IN CAT PG

Left Dorsal Cochlear Nucleus, Female Voices									
	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
1	.84	.74	.93	.19	-.12	-.37	.91	.81	.94
2	.83	.70	.90	.06	-.08	.11	.82	.76	.93
3	.87	.65	.83	.19	.49	.41	.67	.72	.94
4	.95	.68	.58	.18	.55	.40	.95	.72	.61
5	.78	.34	.71	.49	.69	.63	.81	.44	.74
6	.54	.16	.75	.52	-.29	-.06	.14	.15	.87
7	.28	.15	.27	.28	-.37	-.08	.30	.18	.22
8	.65	.54	.85	-.23	.57	-.54	.66	.45	.82
9	.85	.58	.70	.24	.15	.13	.85	.80	.86
10	.88	.57	.68	.63	.07	.36	.86	.64	.79
Left Dorsal Cochlear Nucleus, Male Voices									
1	.91	.96	.93	.52	.63	.56	.92	.98	.94
2	.93	.92	.93	.13	.74	.10	.94	.90	.94
3	.99	.97	.98	.48	.69	.72	.97	.97	.97
4	.94	.96	.88	.32	.71	.49	.97	.90	.83
5	.96	.86	.84	.30	.91	.34	.95	.90	.83
6	.40	.75	.34	.11	.66	.15	.29	.82	.32
7	.72	.79	.55	.33	.66	.48	.76	.83	.65
8	.81	.90	.90	.76	.69	.69	.82	.90	.90
9	.87	.93	.86	.58	.57	.63	.89	.94	.88
10	.93	.82	.91	.74	.29	.23	.94	.82	.91
Right Dorsal Cochlear Nucleus, Female Voices									
1	.85	.71	.90	.45	.26	.65	.88	.75	.91
2	.61	.73	.84	.07	.52	.21	.71	.75	.80
3	.61	.78	.90	.37	.42	.78	.86	.72	.79
4	.88	.86	.81	.73	.46	.35	.91	.81	.72
5	.81	.68	.79	.57	.41	.44	.79	.44	.64
6	.44	.18	.82	.23	.45	.32	.57	.11	.57
7	.28	-.08	.26	.13	.03	.41	.28	.06	.37
8	.57	.61	.85	.66	.72	.51	.65	.79	.81
9	.55	.59	.17	.16	.01	.51	.66	.46	.43
10	.69	.53	.21	.64	.63	.62	.74	.44	.62

TABLE 8--Continued

	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Right Dorsal Cochlear Nucleus, Male Voices									
1	.87	.95	.90	.77	.74	.79	.82	.92	.95
2	.93	.93	.95	.72	.80	.82	.96	.95	.93
3	.84	.87	.92	.82	.83	.81	.92	.83	.84
4	.96	.90	.87	.78	.87	.56	.91	.85	.73
5	.88	.90	.74	.44	.81	.48	.94	.81	.89
6	.54	.71	.60	.31	.69	.50	.31	.76	.48
7	.55	.86	.42	.74	.85	.73	.62	.85	.62
8	.84	.88	.86	.68	.93	.85	.78	.90	.89
9	.72	.78	.78	.83	.74	.76	.87	.94	.89
10	.82	.93	.70	.89	.87	.86	.86	.93	.80
Left Inferior Colliculus, Female Voices									
1	.01	.48	.57	.72	.76	.90	.84	.80	.78
2	.73	.26	-.02	.80	.74	.61	.71	.42	.33
3	.04	-.43	-.10	.55	.71	.67	.67	.64	.92
4	.61	.84	.45	.87	.84	.84	.62	.84	.52
5	.56	.49	.69	.67	.54	.92	.64	.58	.85
6	.34	.12	-.02	.02	[a]	.80	.23	.04	.83
7	.30	-.06	.13	.36	.43	.27	.32	.16	.22
8	.34	.12	.37	.50	.53	.77	.58	.61	.85
9	.70	-.17	.29	.76	.67	.79	.85	.67	.69
10	.12	.23	-.44	.82	.64	.79	.77	.63	.69
Left Inferior Colliculus, Male Voices									
1	.62	.58	.37	.69	.89	.89	.06	.10	.85
2	.18	.44	-.06	.91	.90	.89	.85	.86	.89
3	.04	.74	.17	.84	.85	.89	.81	.95	.81
4	-.03	.27	-.34	.85	.88	.80	.58	.84	.79
5	.29	.85	.25	.64	.74	.76	.85	.70	.69
6	-.27	.48	-.07	.12	.68	.12	.12	.41	.22
7	.48	.44	.24	.52	.59	.38	.50	.59	.51
8	.34	-.56	-.18	.67	.78	.65	.58	.76	.82
9	.53	.44	.59	.82	.86	.79	.19	.75	.25
10	.25	.63	.40	.87	.86	.82	.82	.70	.86

[a] Erratic data used to compute correlation.

TABLE 8--Continued

Word	Ipsilateral			Contralateral			Bilateral		
	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Right Inferior Colliculus, Female Voices									
1	.14	-.40	.24	.35	.68	.51	.65	.54	.94
2	-.10	.16	.26	.85	.79	.82	.81	.89	.83
3	.36	.74	.05	.61	.57	.90	.61	.56	.92
4	-.02	.23	.02	.78	.68	.63	.76	.61	.47
5	.30	.35	.27	.64	.54	.82	[a]	[a]	[a]
6	.47	.28	.53	.00	.16	.86	.50	.26	.61
7	.04	-.9	.35	.03	.21	-.23	[a]	.23	[a]
8	.43	.56	.09	.48	.33	.74	.65	.25	.77
9	.62	.46	.26	.56	.28	.77	.75	.36	.60
10	.06	.41	.12	.75	.57	.77	.76	.47	.63
Right Inferior Colliculus, Male Voices									
1	.02	-.31	-.41	.94	.95	.94	.92	.96	.93
2	.60	.40	.22	.96	.85	.86	.95	.86	.86
3	.65	.68	.77	.95	.93	.87	.96	.95	.93
4	.09	.18	.40	.89	.81	.73	.90	.84	.76
5	.05	.60	.27	.91	.84	.81	.91	.85	.81
6	.39	.64	.74	.08	.68	[a]	.09	.66	.19
7	.27	.37	.61	.47	.68	.42	.46	.58	.23
8	.70	-.36	-.51	.54	.77	.78	.52	.79	.74
9	.32	.40	.61	.68	.84	.65	.71	.78	.68
10	.64	.78	.76	.89	.95	.86	.90	.96	.84

[a] Erratic data used to compute correlation.

TABLE 9

PEARSON PRODUCT MOMENT CORRELATIONS AMONG NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES IN CAT LZ

	Ipsilateral			Contralateral			Bilateral		
Word	Voices 1-2	Voices 1-3	Voices 2-3	Voices 1-2	Voices 1-3	Voices 2-3	Voices 1-2	Voices 1-3	Voices 2-3
Right Dorsal Cochlear Nucleus, Female Voices									
1	.78	.65	.91	.79	.76	.92	.83	.67	.89
2	.63	.83	.78	.77	.60	.29	.78	.74	.84
3	.91	.93	.97	.88	.90	.83	.92	.60	.76
4	.75	.81	.86	.35	.83	.53	.80	.86	.85
5	.74	.44	.60	.76	.64	.76	.72	.31	.51
6	.78	.22	.14	.64	-.08	.42	.82	.16	.15
7	.70	-.06	-.16	.46	.20	-.03	.44	[a]	[a]
8	.74	.75	.87	.90	.02	.11	[a]	.72	[a]
9	.56	-.50	-.34	.49	.23	.43	.61	[a]	[a]
10	.76	.77	.57	.58	.45	.72	.79	.64	.48
Right Dorsal Cochlear Nucleus, Male Voices									
1.	.84	.95	.92	.78	.86	.92	.88	.91	.95
2	[a]	.95	[a]	.91	.86	.83	.98	.95	.93
3	.88	.87	.96	.22	.34	.94	.90	.89	.97
4	.95	.90	.89	.92	.89	.86	.96	.86	.85
5	.96	.91	.91	.93	.91	.85	.93	.90	.84
6	.54	.57	.73	.25	.03	.55	.61	.61	.67
7	.79	.76	.66	.73	.64	.55	.72	.84	.65
8	.74	.88	.89	.69	.88	.82	.70	.86	.86
9	.83	.95	.82	.83	.92	.85	.88	.95	.90
10	.93	.91	.85	.83	.91	.83	.91	.97	.86
Left Inferior Colliculus, Female Voices									
1	-.02	.18	.91	.84	.68	.89	.86	.77	.92
2	.65	.66	.89	.62	.51	.53	.69	.65	.86
3	.77	.77	.91	.85	.94	.83	.93	.85	.86
4	.36	.78	.59	.56	.68	.83	.62	.79	.77
5	.90	.75	.84	.82	.15	.30	.85	.73	.81
6	.74	.36	.35	.73	.32	.26	.49	.06	.22
7	.71	-.19	-.28	.50	-.10	-.14	.55	-.37	-.36
8	.78	-.61	-.58	.85	.72	.79	.87	.64	.54
9	.55	.24	-.14	.30	.47	.25	.38	.20	.16
10	.24	.26	.72	.50	-.03	.33	.59	.43	.60

[a] Erratic data used to compute correlations.

TABLE 9--Continued

Left Inferior Colliculus, Male Voices

Word	Ipsilateral Voices 1-2	Ipsilateral Voices 1-3	Ipsilateral Voices 2-3	Contralateral Voices 1-2	Contralateral Voices 1-3	Contralateral Voices 2-3	Bilateral Voices 1-2	Bilateral Voices 1-3	Bilateral Voices 2-3
1	.86	.93	.92	.80	.91	.85	.83	.79	.87
2	.89	.82	.81	.89	.80	.71	.52	.55	.95
3	.42	.85	.79	.79	.84	.94	.18	.29	.92
4	.94	.90	.86	.93	.86	.90	.94	.84	.79
5	.88	.86	.91	.89	.87	.87	.83	.84	.92
6	.31	.64	.60	.41	.45	.47	.21	.31	.75
7	.82	.70	.54	.53	.65	.29	.66	.84	.52
8	.67	.88	.84	.66	.84	.77	.57	.85	.72
9	.85	.90	.83	.83	.81	.82	.85	.91	.85
10	.89	.86	.79	.82	.88	.82	.86	.88	.72

TABLE 10

PEARSON PRODUCT MOMENT CORRELATIONS AMONG NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES IN CAT LG

	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Right Dorsal Cochlear Nucleus, Female Voices									
1	.83	.81	.96	.75	.65	.79	[a]	.58	[a]
2	.60	.70	.56	.23	.65	.57	.73	.72	.78
3	.80	.88	.80	.79	.83	.85	[a]	.86	[a]
4	[a]	.47	.28	.41	.23	.04	[a]	.60	[a]
5	.83	.58	.75	.85	.03	.30	.79	.37	[a]
6	.84	[a]	[a]	.78	.14	.09	.50	[a]	[a]
7	.35	[a]	[a]	.17	-.16	-.06	.76	[a]	[a]
8	.37	.84	.23	.37	.47	.57	.78	.75	.64
9	.68	.45	.74	.55	.15	.67	.39	.57	.75
10	[a]	.44	.65	.70	.43	.20	[a]	[a]	.69
Right Dorsal Cochlear Nucleus, Male Voices									
1	.62	.65	.72	.76	.87	.85	.84	.91	.88
2	.49	.14	.56	.53	.74	.86	.93	.81	.79
3	.47	[a]	[a]	.81	.62	.90	.87	.71	.93
4	.78	.82	.69	.91	.72	.54	.92	.90	.77
5	.71	.84	.63	.92	.74	.78	.94	.87	.87
6	.60	.52	.66	.49	[a]	[a]	.49	.45	.60
7	.55	.44	.26	[a]	.71	[a]	.61	.67	.70
8	.60	.84	.84	.59	.70	.93	.65	.79	.88
9	.76	.91	.89	.88	.97	.87	.85	.97	.82
10	.55	.52	.77	.75	.93	.74	.82	.89	.75
Left Inferior Colliculus, Female Voices									
1	.16	.11	.32	.55	.72	.75	.50	.60	.55
2	-.37	-.24	-.16	.64	.26	.06	.41	.37	.31
3	.19	.51	.30	.31	.55	.55	[a]	.59	[a]
4	-.34	-.08	.36	.20	.22	.35	.19	.41	.26
5	.00	.24	-.30	.55	.70	.45	.49	.54	.59
6	.03	.06	.06	.43	.26	.55	.43	.18	.49
7	.07	.27	-.15	-.20	.25	-.14	[a]	[a]	[a]
8	-.22	.30	.01	.56	.72	.38	[a]	.66	.30
9	.51	-.29	-.02	.38	.48	.46	.42	.75	.71
10	.04	-.40	.08	.51	.53	.58	[a]	.19	.44

[a] Erratic data used to compute correlations.

TABLE 10--Continued

Left Inferior Colliculus, Male Voices

Word	Ipsilateral			Contralateral			Bilateral		
	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
1	.09	.32	.11	.61	.64	.29	.59	.77	.57
2	.32	-.18	.21	.18	.10	.71	[a]	[a]	.80
3	.60	.24	.12	-.15	-.20	.65	.81	.74	.81
4	.29	.30	.02	.62	.61	.65	.81	.73	.72
5	.13	.42	.15	.69	.78	.74	.83	.77	.77
6	.08	.19	.23	.17	.32	.66	.65	.31	.52
7	.14	.26	.45	.53	.57	.60	.48	.40	.21
8	.49	.19	.56	.34	.66	.45	.56	.83	.76
9	.26	.07	-.10	.76	.77	.87	.69	.77	.55
10	.31	.14	.53	.62	.72	.25	.61	.62	.27

[a] Erratic data used to compute correlations.

TABLE 11

PEARSON PRODUCT MOMENT CORRELATIONS AMONG NEURONAL RESPONSES EVOKED BY SAME-SEX VOICES IN CAT RP

	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Left Dorsal Cochlear Nucleus, Female Voices									
1	.29	.31	.94	.18	-.06	.59	.62	.47	.88
2	[a]	[a]	.89	-.03	.00	.12	.85	.86	.90
3	[a]	[a]	.65	.25	.63	.73	.92	.78	.70
4	.48	.82	.48	-.05	.18	.10	.48	.80	.31
5	.82	.38	.61	-.08	-.10	.30	.83	.41	.50
6	.49	[a]	[a]	[a]	[a]	[a]	.30	.20	.09
7	.67	[a]	[a]	.13	.53	.32	.79	.23	.11
8	.65	.40	.51	.34	.41	-.11	.89	.47	.43
9	.69	[a]	[a]	.46	.24	.43	.95	.06	.10
10	.86	.80	.89	-.17	.52	.18	.56	.56	.91
Left Dorsal Cochlear Nucleus, Male Voices									
1	-.28	.94	-.35	.88	.82	.86	.85	.95	.88
2	.04	.90	-.14	.71	.79	.73	.83	.93	.89
3	.89	.90	.96	.70	.76	.81	[a]	[a]	.96
4	.81	.91	.70	.34	.78	.46	[a]	.78	[a]
5	.97	.88	.93	.67	.79	.76	.93	.88	.82
6	.37	.64	.34	.69	.66	.44	[a]	.77	[a]
7	.67	.82	.70	.40	.75	.60	.66	.82	.70
8	.51	.74	.80	.87	.87	.87	.47	.68	.81
9	.91	.93	.84	.58	.67	.67	.91	.98	.87
10	.91	.93	.94	.63	.18	.51	.81	.94	.91
Right Dorsal Cochlear Nucleus, Female Voices									
1	.82	.71	.86	.16	.11	-.03	.78	[a]	[a]
2	.72	.55	.81	.31	.15	.43	.80	[a]	[a]
3	.91	.85	.89	.00	.16	-.09	.81	.38	.52
4	.40	.68	.19	-.15	-.10	-.56	.85	[a]	[a]
5	.88	.41	.63	-.33	.30	.08	.75	.36	.65
6	.79	.22	.24	-.12	-.07	.43	.23	.22	.88
7	.64	[a]	[a]	.31	.04	.06	.34	[a]	[a]
8	.69	.63	.57	-.25	-.27	.07	.75	.50	.63
9	.93	.50	.64	[a]	[a]	.42	.91	.62	.76
10	.37	.58	.80	[a]	[a]	.36	.70	.59	.65

[a] Erratic data used to compute correlation.

TABLE 11--Continued

	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
Right Dorsal Cochlear Nucleus, Male Voices									
1	[a]	[a]	.81	[a]	[a]	[a]	.92	.95	.94
2	[a]	[a]	.87	.29	-.30	-.09	.92	.88	.94
3	[a]	[a]	.86	.25	.00	-.12	.88	.74	.90
4	[a]	[a]	.80	[a]	.17	[a]	.92	.76	.86
5	.95	.88	.89	.52	.41	.68	.90	.85	.91
6	.64	.44	.67	.01	.07	.17	.55	.55	.56
7	.77	.74	.70	.15	.09	.78	.64	.73	.61
8	.62	.86	.78	-.18	.26	.24	.74	.71	.63
9	.84	.83	.80	-.64	.39	-.32	.82	.91	.88
10	.89	.79	.86	.16	-.04	-.45	.89	.94	.89
Left Inferior Colliculus, Female Voices									
1	.05	.06	.11	.88	.64	.68	.90	.53	.70
2	-.18	-.34	.01	.05	.16	.65	.46	.22	.40
3	-.07	.09	.14	.50	.15	.05	.66	.18	.27
4	.32	-.13	.57	.85	.87	.89	.72	.80	.76
5	.25	-.31	-.52	.55	.50	.56	.54	.45	.59
6	-.01	-.14	-.48	.31	.09	.63	.59	.21	.57
7	.04	-.26	.09	.23	.37	-.04	-.01	.39	.16
8	.19	.79	.23	.16	.15	.35	.03	-.07	.60
9	.00	-.10	.26	.77	.68	.79	.67	.58	.68
10	-.13	.28	-.27	.57	.44	.40	.52	.59	.52
Left Inferior Colliculus, Male Voices									
1	.35	-.36	-.53	.76	.71	.93	.72	.83	.84
2	.12	.31	.31	.79	.65	.88	.76	.50	.73
3	.17	.53	.02	.82	.85	.53	.76	.74	.48
4	-.05	.28	.30	-.30	.86	-.35	.81	.86	.71
5	.16	-.30	-.29	.87	.75	.79	.74	.79	.79
6	-.05	.32	.18	.43	.22	.62	.48	.27	.51
7	.27	.69	.24	.39	.38	.29	.27	.40	.16
8	-.02	.00	.60	.40	.50	.67	.30	.57	.54
9	.47	.74	.76	.48	.79	.27	.25	.73	.25
10	.32	.02	.09	.67	.75	.81	.49	.65	.69

[a] Erratic data used to compute correlation.

TABLE 11--Continued

Right Inferior Colliculus, Female Voices

	Ipsilateral			Contralateral			Bilateral		
Word	Voices			Voices			Voices		
	1-2	1-3	2-3	1-2	1-3	2-3	1-2	1-3	2-3
1	.13	-.10	.12	.90	.69	.85	.89	.71	.89
2	-.23	.12	-.48	.68	.43	.61	.62	.45	.68
3	.35	-.29	.02	.88	.44	.64	.59	.14	.68
4	-.33	-.03	.18	.82	.68	.46	.68	.74	.37
5	.04	-.05	.09	.68	.35	.65	.67	.48	.64
6	.40	-.20	.27	.37	.46	.69	.21	.41	.77
7	-.16	-.33	.13	-.20	.11	-.20	-.18	.15	-.26
8	.08	-.07	.00	.37	.27	.62	.41	.22	.60
9	.01	.16	.07	.92	.26	.34	.88	.13	.28
10	.19	-.17	-.23	.77	.42	.70	.71	.44	.65
Right Inferior Colliculus, Male Voices									
1	.08	.00	.03	.83	.92	.85	.86	.84	.82
2	-.06	-.01	.16	.84	.72	.88	.83	.73	.87
3	.28	-.25	.16	.96	.86	.85	.92	.94	.93
4	.44	-.62	-.37	.70	.91	.58	.79	.90	.64
5	.00	.15	.08	.33	.75	.25	.87	.81	.84
6	.13	.25	.21	.21	.20	.48	.29	.18	.12
7	.13	.48	.33	.40	.64	.02	.33	.55	.10
8	-.07	.42	.35	.11	.60	.71	.33	.56	.77
9	-.08	-.08	.32	.35	.83	.45	.40	.80	.49
10	.27	.35	-.16	.74	.94	.82	.77	.95	.70

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