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PHASIC ACTIVITY IN THE AUDITORY PAHTWAY DURING PARADOXICAL SLEEP OR INDUCED BY RESERPINE

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ABSTRACT

Phasic activity, frequently called ponto-geniculo-occipital (PGO) activity, is commonly recorded from different areas of the brain during paradoxical sleep or following reserpine administration. In this study, phasic activity was recorded from the auditory cortex, the medial geniculate body, and the dorsal and ventral cochlear nuclei of chronically implanted cats under both of these conditions. The results suggest that the activity from the auditory structures might be part of a more complex functional organization which includes the visual and oculomotor systems already described by other authors. Due to the broad distribution of phasic activity found over the brain, it is proposed that the term *paradoxical sleep phasic activity* replace that of *PGO activity*.

RESUMEN

Durante la fase paradójica de sueño o después de la administración de reserpina, se registra comúnmente una actividad fásica en diferentes estructuras del sistema nervioso .De acuerdo con estudios anteriores, esta actividad ha sido llamada frecuentemente actividad ponto-genículo-occipital (PGO). En este trabajo experimental se registró la actividad fásica en gatos crónicamente implantados en la corteza auditiva, cuerpo geniculado medial y en los núcleos cocleares dorsal y ventral en las condiciones anteriormente mencionadas. En virtud de la amplia distrihución cerebral presentada por la actividad fásica, se propuso el término *actividad fásica del sueño paradójico* en lugar de *actividad PGO*. Los datos aquí presentados sugieren que la actividad fásica de las estructuras auditivas pudieran ser parte de una organización funcional más compleja incluyendo los sistemas visual y oculomotor descritos previamente por otros autores.

INTRODUCTION

Periodic phasic activity consisting of high voltage waves has been observed during paradoxical sleep. This phenomenon has been extensively studied and is considered to be one of the principal phasic events which occur during sleep. The activity was first described in the pontine reticular formation (Jouvet and Michel, 1959), and later in the lateral geniculate body (Mikiten *et al.*, 1961) and occipital cortex (Mouret *et al.*, 1963). Due to this anatomical distribution, it was called ponto-geniculo-occipital (PGO) activity. However, considerable circumstantial evidence has accumulated following these initial reports indicating the presence of morphologically and physiologically similar activity in other areas of the central nervous system (CNS), such as the parietal-occipital cortex and the superior colliculus (Calvet *et al.*, 1964; Syka *et al.*, 1973); the nuclei of cranial nerves III, VI and VII (Brooks and Bizzi, 1963; Costin and Hafemann, 1970; Cespuglio *et al.*, 1976); the inferior colliculus, auditory cortex and medial geniculate body (Roffwage *et al.*, 1973); and the cerebellar cortex (Pellet *et al.*, 1974).

PGO activity is also found in physiological conditions other than paradoxical sleep. It has been observed that various substances which act upon brain monoamines can elicit this activity, thus giving rise to a pharmacological model which has permitted some detailed studies to be made. Reserpine, which is frequently used, is capable of inducing the continuous appearance of phasic activity following a latency of 60-90 minutes after administration (Delorme *et al.*, 1965; Jeannerod, 1965; Brooks and Gershon 1971, 1972), although the animals remain awake.

In this study, in has been recorded phasic activity during paradoxical sleep and after reserpine injection in structures of the auditory pathway, some of which have not been previously analyzed.

MATERIALS AND METHODS

Healthy chonically implanted adult cats were used in all experiments Stainless steel bipolar electrodes were stereo-taxically implanted in the medial geniculate nucleus and in the dorsal and ventral cochlear nuclei under nembutal anesthesia. Electrodes in the form of stainless steel needles were placed on the surface of the auditory cortex, and others with clamps were inserted in the posterior cervical muscles for electromyogram recordings. During implantation of the electrodes, auditory stimulation was used so that their placement in regions where maximum amplitude responses, monitored with a Tektronix double beam oscilloscope, model 565, was assured. At the end of the experimental phase, several animals were sacrificed and their brains perfused with formalin in order to histologically confirm the position of the electrodes.

The recording sessions were begun a minimum of five days after surgery. Unanesthetized animals with complete liberty of movement were placed in a soundproof chamber and connected to a Grass model 7 polygraph. Recordings were made for several days during different stages of wakefulness and sleep. One group of observations was obtained during paradoxical sleep and another following an intraperitoneal injection of reserpine (0.5 mg/kg).

RESULTS

Medial Geniculate Body and Auditory Cerebral Cortex

The phasic activity recorded in these structures was quite variable; no explanation was discovered for this finding. In some animals, phasic activity could be clearly distinguished from the basal rhythm. In others, despite a lower amplitude, a phasic phenomenon different from the basal electropysiological pattern was also discerned. However, phasic activity could not be detected in a relatively high proportion of animals (10 out of 18).

In the cats in which it was observed, rhythmic activity appeared periodically during the paradoxical phase of normal sleep (Fig. 1) and after pharmacological induction with reserpine as well (Fig. 2). The latter effect was present continually after a minimum latency of 90 minutes while the animals were fully awake, and persisted several hours as has been described in the visual pathway.

Morphologically, phasic activity in the medial geniculate body consisted of either one or two components; in the latter case, the first was generally greater thant the second. The pattern of activity in the auditory cortex was more complex, since mono- and biphasic waves were found together with those made up of a larger number of components.

Cochlear Nuclei

In contrast to the findings in the auditory structures mentioned above, the electrodes located in the dorsal and ventral cochlear nuclei registered phasic activity in nearly 100% of the animal both during paradoxical sleep (Fig. 3) and after reserpine administration (Fig. 4). This activity was occasionally present in the form of isolated spikes, but more frequently they were grouped in fusiform discharges. Although some spikes were monophasic, the majority were biphasic with an amplitude varying from 50-200 μV, meaured peak to peak.

DISCUSSION

Due to the discovery of a much broader distribution of phasic activity in CNS structures than was iniatially described, it appears that the use of the term "ponto-geniculo-occipital activity" is no longer justified except on historical grounds. A more general expression such as *paradoxical sleep phasic activity* is more appropriate and of greater accuracy. This term would include those phasic modifications which cannot be registered by means of macroelectrodes, but which fine electrodes have revealed to exist. They follow a temporal sequence similar to the larger "PGO" waves (Mukhametov *et al.*, 1970; Hobson and McCarley, 1972). In this regard, Roffwarg *et al.*, (1973) have shown that phasic activity can be recorded at the level of the auditory cortex and medial geniculated body in some animals but not in others during paradoxical sleep. These variable results might be due to the diameter of the electrodes used.

The phasic activity we have recorded in different structures of the auditory pathway is similar to that found in the visual pathway, in that it occurs periodically during paradoxical sleep as well as in situations apart from normal sleep, such as following pharmacological induction with reserpine while the animals are awake.

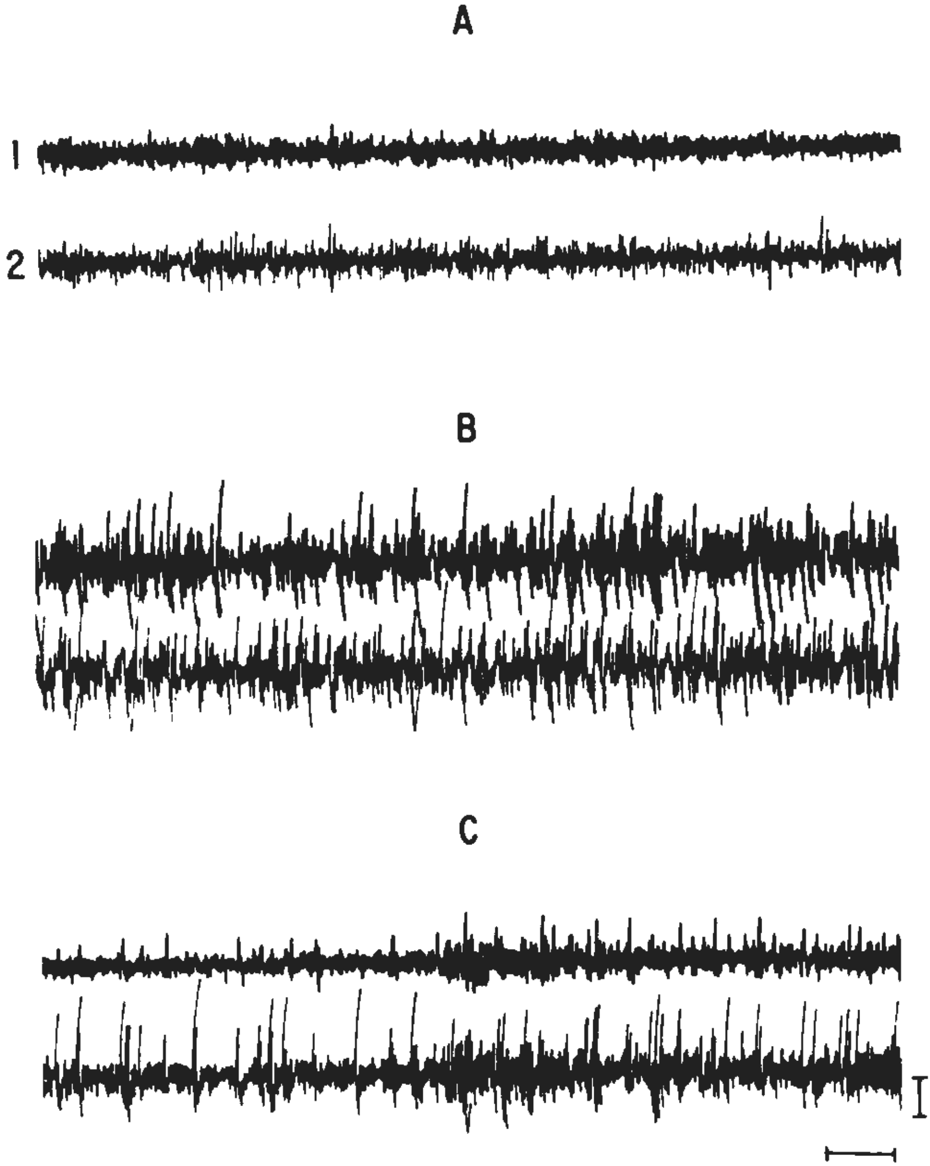

Fig. 1. Phasic activity in the auditory cortex (1) and medial geniculated body (2) during paradoxical sleep. A. Wakefulness. Rapid low amplitude activity characteristic of this states can be observed. B. Slow wave sleep. Slow high voltage waves are present. C. Paradoxical sleep. Phasic activity which can be distinguished from the basal rhythm can be seen. Calibration: 50 μV; 5 sec.

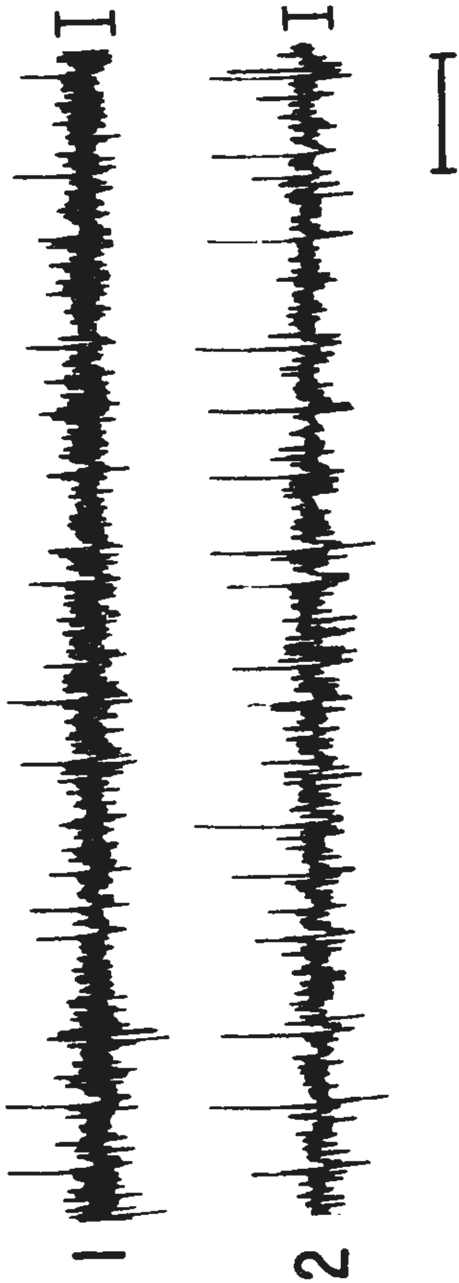

Fig. 2. Reserpine-induced phasic activity in the auditory cortex (1) and medial geniculate body (2). See text for description. Calibration: 50 μV; 5 sec.

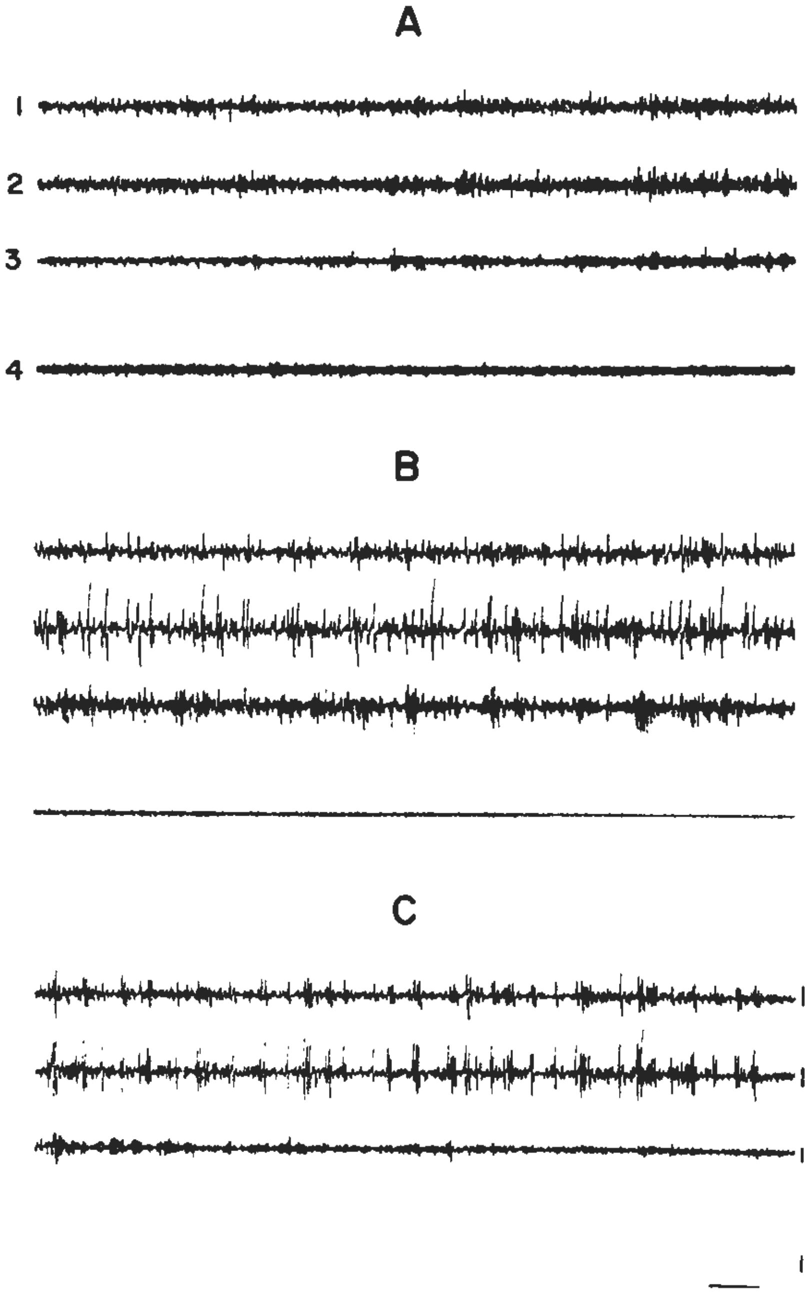

Fig. 3. Phasic activity in the cochlear nuclei during paradoxical sleep. Right dorsal cochlear nucleus (1); left dorsal cochlear nucleus (2): auditory cortex (3): electromyogram (4). A. Wakefulness. Rapid low voltage waves and muscular activity can be observed. B. Transition from slow wave sleep to paradoxical sleep. Phasic activity begins to appear. C. Paradoxical sleep. Phasic activity is well established in the cochlear nuclei of this animal, but is hardly present in the auditory cortex. Calibration: 50 μV; 5 sec.

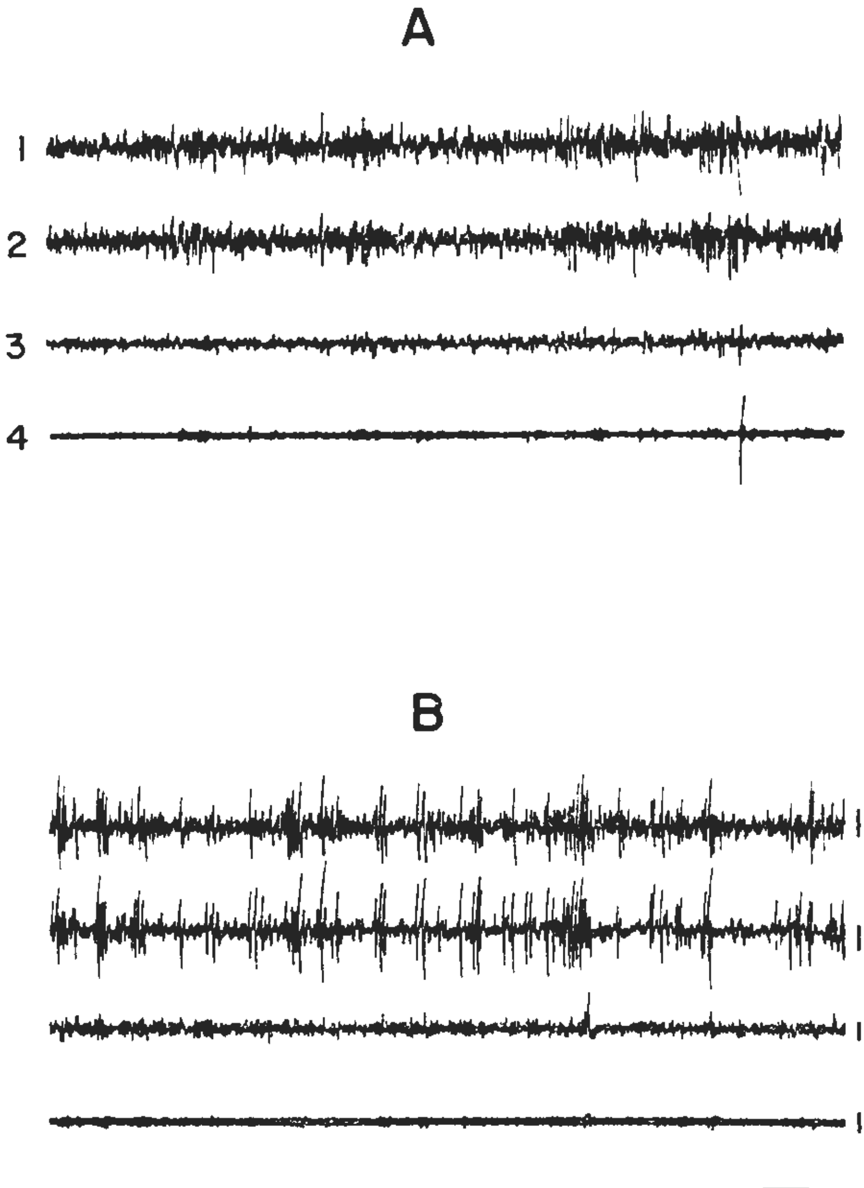

Fig. 4. Reserpine-induced phasic activity in the cochlear nuclei. Right dorsal cochlear nucleus (1); left dorsal cochlear nucleus (2); auditory cortex (3); electromyogram (4). A. Prior to reserpine administration. B. Following reserpine injection (0.5 mg/kg i.p.) Phasic activity during muscular activation which is an electrophysiological indication of wakefulness is present. Calibration: 50 μV; 5 sec.

These results lead to the conclusion that the activity registered in these two pathways is virtually identical, forming part of a single system which probably originates in common anatomical sites situated at the level of the brainstem. Such an arrangement has previously been described for the phasic activity in the lateral geniculate body, visual cortex (Laurent *et al.*, 1972, 1974), and oculomotor nuclei (Cespuglio *et al.*, 1976).

Further experiments which could prove or disprove this hypothesis remain to be done, together with the delineation of the projection pathways from their point of origin to the different structures which make up the auditory pathway.

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