

## CIRCULATION OF CORTICAL AND THALAMIC NEURONAL ACTIVITY IN WAKEFULNESS AND IN SLEEP \*

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It is well known that the development of rhythmic waves in the cortex and in the thalamus is accompanied by a highly organized circulation of neuronal impulses, which can be detected by means of recordings obtained simultaneously, with several microelectrodes (Verzeano 1956, 1963, 1972, 1973; Verzeano et al. 1965, 1970; Andersen and Andersson 1968). The successive passages of the circulating activity through the neuronal networks are closely and consistently associated with the periodicity of the rhythmic waves. This association maintains its consistency as the rhythmicity changes while the animal passes from a state of wakefulness to that of slow wave sleep or to sleep induced by barbiturates (Verzeano and Negishi 1960, 1961; Verzeano et al. 1965, 1970).

Recent investigations conducted in restrained as well as unrestrained animals have ascertained, by the application of autocorrelation and cross-correlation techniques, that, in the state of wakefulness, the circulation of neuronal activity in the cerebral cortex, is maintained with consistent regularity over sufficiently long periods (as long as several hours), to be implicated in physiological processes which require time before they can be accomplished, such as the transport, processing, and storage of sensory information (Rinaldi et al. 1976).

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Still to be ascertained is how consistent the circulation of neuronal activity is in slow wave sleep, and whether it occurs at all in paradoxical sleep, a state in which thalamic and cortical rhythmicity are believed to be greatly disrupted.

In an attempt to resolve these questions a series of experiments have been conducted, in unanesthetized, unrestrained animals, in which the circulation of neuronal activity has been studied, in the cortex as well as in the thalamus, in the states of wakefulness, slow wave sleep and paradoxical sleep.

The examination of the results by means of autocorrelation, cross correlation and spectral analysis, indicates that the circulation of neuronal activity develops, for long periods, in all three states and that in wakefulness and in paradoxical sleep it is frequently infiltrated by rhythmic activity in the 4–8 c/sec frequency range (the theta range).

### Methods

Experiments were conducted in six unrestrained, unanesthetized cats. Arrays of microelectrodes made of platinum-iridium wire, sharpened electrolytically to diameters of 0.5–2  $\mu\text{m}$  and insulated with glass (Wolbarsht et al. 1960) were stereotaxically implanted in the brain of these animals, under barbiturate anesthesia. The technique of implantation of arrays of microelectrodes was previously described (Verzeano 1970). Electrodes for recording the occipital electro-

encephalogram (EEG), the electromyogram (EMG) from the neck muscles, and the electrooculogram (EOG) were implanted at the same time. The animal was allowed to recover for 5 days before any recording sessions were conducted.

During each experimental session, the activity of neurons and gross waves in the brain was recorded through the microelectrode channels, while the EEG, EMG, and EOG were simultaneously recorded and monitored on a 'Grass' polygraph, in order to determine the state of wakefulness or the specific state of sleep — slow wave or paradoxical — at any particular period.

Attentive wakefulness was defined as a state in which the animal sat or reclined with his eyes open and attentive, the EEG exhibited low voltage fast activity, the EMG showed a high level of activity and the EOG indicated occasional eye movements; slow wave sleep was defined as a state in which the animal reclined quietly with his eyes closed, the EEG exhibited a very regular spindle activity (11–14 c/sec.), the EMG remained active but at a lower level than in the waking state and the EOG indicated the absence of eye movements; paradoxical sleep was defined as a state in which the animal reclined, usually in a curled position, the EEG exhibited low voltage fast activity with complete absence of spindles, the EMG showed complete disappearance of the muscle tone, and the EOG indicated the appearance of rapid eye movements.

To these criteria were added the characteristics of the gross waves indicated by an electrode tip of 0.2 mm diameter implanted along with the array of microelectrodes and in their immediate vicinity (0.5 mm away), either in the cortex or in the thalamus.

Each microelectrode recorded gross waves as well as action potentials of neurons, which were magnified by means of amplifiers with an input impedance of over 200 M $\Omega$  and a frequency response of 1 Hz–10 kHz, and recorded on magnetic tape for subsequent analysis. The gross waves were separated from

the action potentials by appropriate filter circuits, for the purpose of crosscorrelation studies between the two, or between various groups of action potentials. In most cases each microelectrode was sufficiently large to detect the activity of several neurons or groups of neurons and, accordingly, recorded action potentials of different amplitudes (Verzeano et al. 1965, 1970; Rinaldi et al. 1976).

The groups of neurons whose activities were correlated were determined in the following way: (a) the action potentials recorded by *each* microelectrode were separated by means of amplitude discriminators into two ranges, one range containing the high amplitudes and another containing the low amplitudes, with a sufficient gap between them, to insure that the two ranges represented the activities of two different groups of neurons of different size or different type (Verzeano 1970; Grover and Buchwald 1970; Tyler et al. 1971; Verzeano and Mahnke 1972; Rinaldi et al. 1976). Correlating these two ranges of action potentials provided the means for studying the relations between the activities of large and small neurons within the territory surveyed by one microelectrode; (b) the distance between the tips of the microelectrodes in the implanted array was large enough to insure that each microelectrode surveyed a different territory. Correlating the action potentials recorded by different microelectrodes provided the means for studying the relations between the activities of groups of neurons located in neighboring but different territories. Thus, one array of three microelectrodes could clearly and unequivocally detect the activities of at least six groups of neurons: three groups generating action potentials of high amplitudes and three groups generating action potentials of low amplitudes (Fig. 1). The activity of single neurons was detected either by selecting, through the discriminators, the action potentials whose constant amplitude was markedly and consistently higher than all other amplitudes present in the record, or by using microelectrodes of small diameters which would

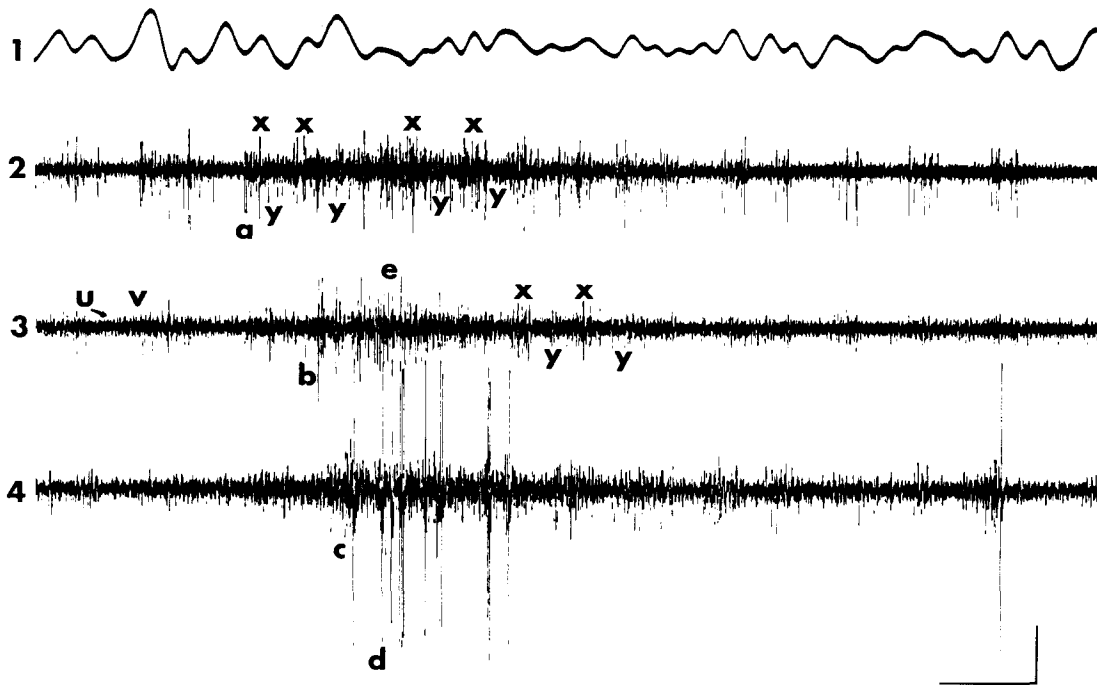


Fig. 1. Gross waves (1) and neuronal activity (2, 3, 4) in the association cortex of the waking unrestrained, unanesthetized cat, recorded by means of an array of microelectrodes displayed antero-posteriorly along a straight line. Distances between microelectrodes:  $308 \mu\text{m}$  between 2 and 3;  $168 \mu\text{m}$  between 3 and 4. The anterior microelectrode (2) was  $208 \mu\text{m}$  deeper than the other two. Note: activity appearing in sequence at the tips of the microelectrodes (at a, b, c); the intervals (x-y) between alternating clusters of action potentials of higher and lower amplitudes; simultaneous discharge of two clusters or action potentials recorded by the middle and posterior microelectrodes (at d and e); short period of silence (u-v). The gross wave (1) was recorded by the anterior microelectrode. Calibration: 100 msec,  $200 \mu\text{V}$ .

detect the activity of isolated neurons only. The gross waves were recorded either by one of the microelectrodes in the array or by the gross electrode ( $0.2 \text{ mm}$  in diameter) located  $0.5 \text{ mm}$  from the center of the array.

Autocorrelations were performed on gross waves and trains of action potentials in order to determine the consistency of their periodicity; cross correlations were performed between gross waves and trains of action potentials or between trains of action potentials generated by different neurons or groups of neurons in order to determine the consistency of their time and phase relations. Correlations of action potentials were made by two methods. With the first method, the trains of pulses provided by the amplitude discriminator and representing trains and

clusters of action potentials produced by groups of neurons were translated, by means of integrators, into waves whose amplitude was proportional to the frequency of neuronal discharge. By autocorrelating or cross correlating these waves it was possible to study the periodicity of clusters of action potentials generated by one group of neurons or the time and phase relations between clusters of action potentials generated by different groups of neurons; by cross correlating them with the gross waves it was possible to study the time and phase relations between clusters of action potentials and gross waves. With the second method, the pulses provided by the amplitude discriminator were correlated directly, without integration, by using an averaging process, similar to that which is

used in computing post-stimulus histograms; however, instead of a stimulus pulse, the computer was triggered by an action potential. Thus, should a correlation exist between two trains of action potentials, triggering with the action potentials of one train and averaging the other with respect to time, a high probability of occurrence should appear at the time at which the action potentials of the second train follow those of the first train. The great advantage of this method, in addition to its simplicity, is that correlations are not limited to two channels containing one train of action potentials each; they can be extended to any number of channels that the computer can handle, by triggering with the action potentials of one train and averaging all the others in time, on as many channels as needed. The method can also be applied to correlations between action potentials and gross waves, by triggering with the former and averaging the latter or vice versa (Rinaldi et al. 1976). In addition, by triggering the computer with the

action potentials of one train and averaging both trains, the rhythmicity of discharge in both groups of neurons, if it exists, can be easily determined (see Fig. 6).

All computations were made by means of a DEC PDP11 computer. The location of the points from which recordings were obtained was ascertained by serial section of the brain and histological preparation.

## Results

### *Circulation of activity in different states*

The recordings obtained from unrestrained, unanesthetized animals show that the circulation of neuronal activity develops in all three states: wakefulness, slow wave sleep and paradoxical sleep. This is illustrated in Figs. 1, 2, and 3 which show recordings obtained from the associational cortex by means of an array of three microelectrodes (lines 2, 3, 4) whose position in the cortex remains fixed while the

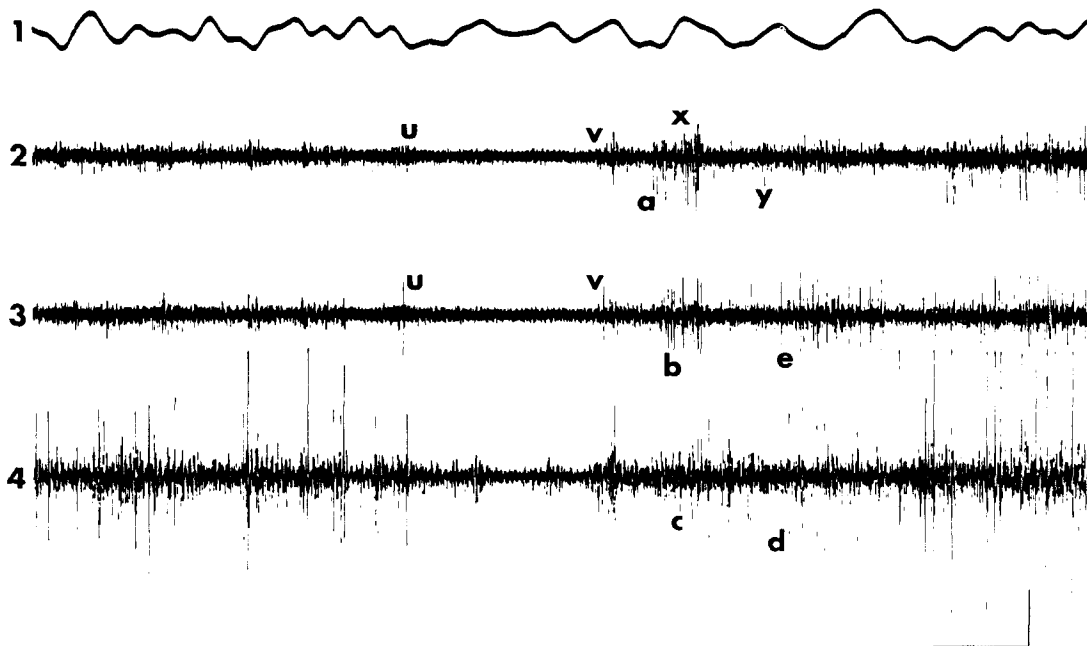


Fig. 2. Recordings in slow wave sleep from the same animal in the same experiment as that illustrated in Fig. 1, with the same array of microelectrodes, at the same location. Note: activity arriving in sequence at the tips of microelectrodes (at a, b, c); longer intervals between alternating clusters of action potentials of higher and lower amplitudes (x-y); longer periods of silence (u-v). All markings and calibrations identical to Fig. 1.

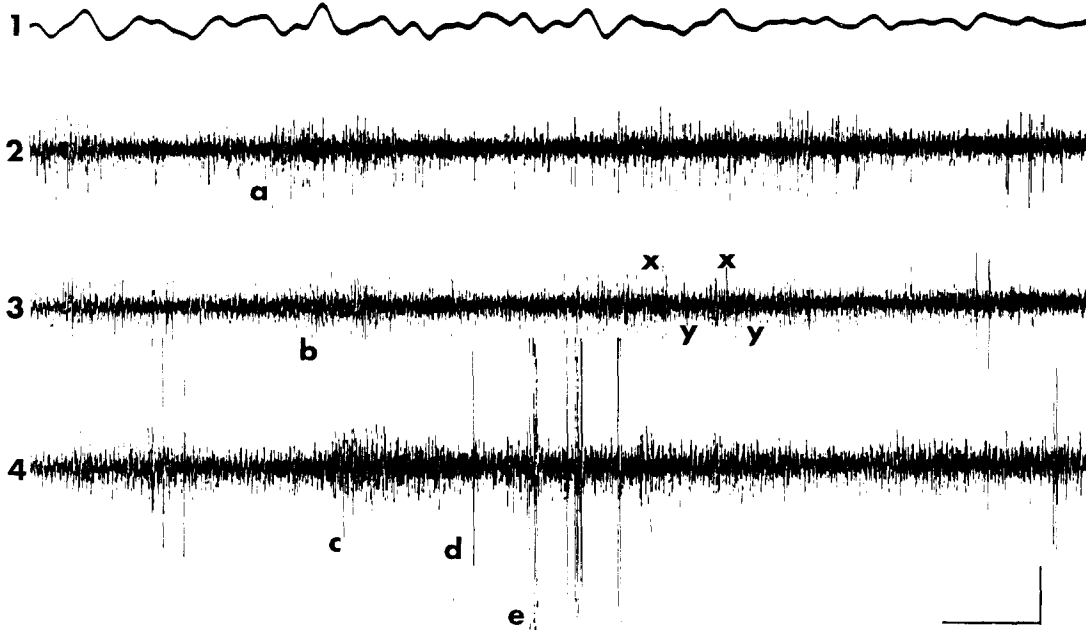


Fig. 3. Recordings in paradoxical sleep from the same animal, in the same experiment as that illustrated in Figs. 1 and 2, with the same array of microelectrodes, at the same location. Note: activity appearing in sequence at the tips of the microelectrodes (at a, b, c); intervals x—y shorter than in Figs. 1 and 2; all markings and calibrations as in Figs. 1 and 2.

animal changes states from wakefulness (Fig. 1) to slow wave sleep (Fig. 2) and to paradoxical sleep (Fig. 3). Examples of the arrival of the activity at the tip of each microelectrode, in sequence, are shown in each figure, at a, b and c. Occasionally the activity can be seen to involve, sequentially, several groups of neurons, within the neuronal network surveyed by a single microelectrode (c, d and e in Figs. 2 and 3). In each one of the tracings, recorded by each microelectrode, clusters of action potentials of higher amplitudes alternate at equal intervals with clusters of action potentials of lower amplitudes (at x and y). This is seen in all three states, with the difference, however, that the intervals between the alternating groups are shorter in wakefulness and in paradoxical sleep than they are in slow wave sleep.

Similar recordings showing a similar sequential appearance of activity at the tips of the microelectrodes in the array, and similar relations between alternating clusters of

action potentials of high and low amplitudes are seen in the thalamus, in wakefulness, slow wave sleep and paradoxical sleep.

Occasionally, both in the cortex and in the thalamus, the series of clusters of action potentials are interrupted by periods of silence, which are of the longest duration in slow wave sleep (Figs. 1 and 2, at U—V).

*Rhythmicity of gross waves and clusters of action potentials and phase relations between them in the different states*

As the animal passes from one state to another and as the rhythmicity of the gross waves changes accordingly, so does the rhythmicity of the clusters of action potentials and the phase relations between them and the gross waves. This is illustrated in Figs. 4 and 5. In both figures, A, B, and C represent results obtained in wakefulness, slow wave sleep and paradoxical sleep, respectively. In all of these states, line 1 shows the autocorrelation which evaluates the rhythmicity of

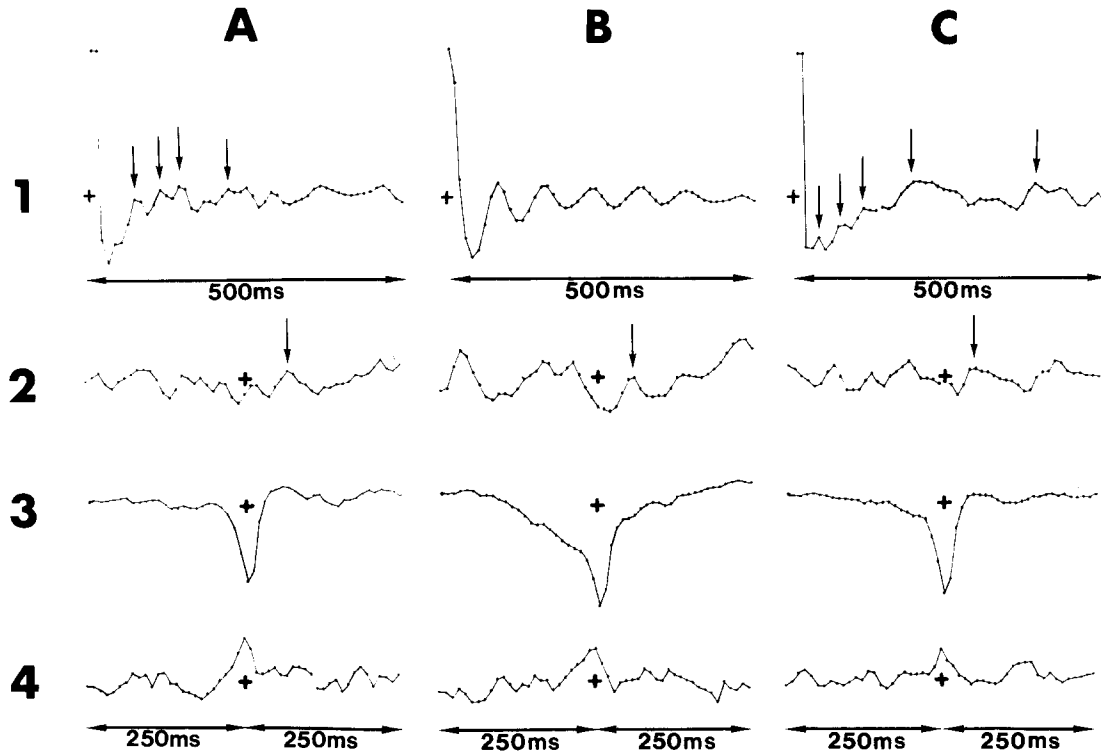


Fig. 4. Consistency of rhythmicity and of time and phase relations in the activity of the neuronal networks in the visual cortex of the unrestrained, unanesthetized cat, in the states of wakefulness (A), slow wave sleep (B) and paradoxical sleep (C). 1: autocorrelations of gross waves; 2: crosscorrelations between gross waves and clusters of action potentials of amplitudes higher than  $80 \mu\text{V}$ ; 3: crosscorrelations between clusters of action potentials of amplitudes higher than  $80 \mu\text{V}$  and clusters of action potentials of amplitudes of  $20\text{--}30 \mu\text{V}$ , recorded by a single microelectrode; 4: crosscorrelations between clusters of action potentials of amplitudes higher than  $80 \mu\text{V}$  recorded by one microelectrode and clusters of action potentials in the same amplitude range recorded by another microelectrode located  $330 \mu\text{m}$  away and posterior to the first. The gross waves correlated on lines 1 and 2 were recorded by a gross electrode located between the two microelectrodes and  $0.5 \text{ mm}$  above them. The arrows in the autocorrelograms of line 1 indicate the presence of two superimposed frequencies: 25 and 12.5 c/sec in A; 25 c/sec and 5.2 c/sec in C (theta range). The arrows in the crosscorrelograms of line 2 indicate the time by which the waves lead the clusters of action potentials. All correlograms were computed from recordings of 90 sec duration.

the gross waves recorded by the gross electrode in the array, and line 2 shows the cross correlogram between them and the clusters of action potentials of high amplitude, recorded by one of the microelectrodes in the same array.

In the cortex (Fig. 4, line 1) autocorrelograms of the gross waves show two rhythmicities (25 c/sec and 12.5 c/sec) in wakefulness, a single rhythmicity (12.5 c/sec) in slow wave sleep, and again two rhythmicities (25 c/sec and 5.2 c/sec) in paradoxical sleep; the

crosscorrelograms between the gross waves and the clusters of action potentials (Fig. 4, line 2) show that, in all states, there is some correlation between the occurrence of the two, with variable phase relations between them: the clusters of action potentials lead the gross waves by 64 msec in wakefulness and in slow wave sleep and by 45 msec in paradoxical sleep.

As the same array of microelectrodes and gross electrode is lowered from the cortex into the thalamus, in the same animal and the

sequence of sleep states develops again, similar changes in rhythmicity and in phase relations are found (Fig. 5, lines 1 and 2). The rhythmicity of the gross waves changes from 25 c/sec in wakefulness to 12.5 c/sec in slow wave sleep and to a double rhythmicity, 25 c/sec and 4.8 c/sec, in paradoxical sleep. The clusters of action potentials lead the gross waves by 80 msec in wakefulness and slow wave sleep and by 135 msec in paradoxical sleep.

*Time and phase relations between the activities of different groups of neurons*

When the alternating clusters of high and

low amplitude action potentials recorded either in the cortex or in the thalamus by a single microelectrode are integrated and cross-correlated, it is found that this alternation at regular intervals appears as a phase displacement of 180 degrees between the clusters (Figs. 4 and 5, line 3). When the clusters of action potentials of high amplitudes recorded by one microelectrode are cross correlated with similar clusters of action potentials of high amplitudes recorded by another microelectrode located 300–500  $\mu\text{m}$  away, it appears that these clusters are fully in phase (Figs. 4 and 5, line 4). The same phase relations between the activities of such clusters

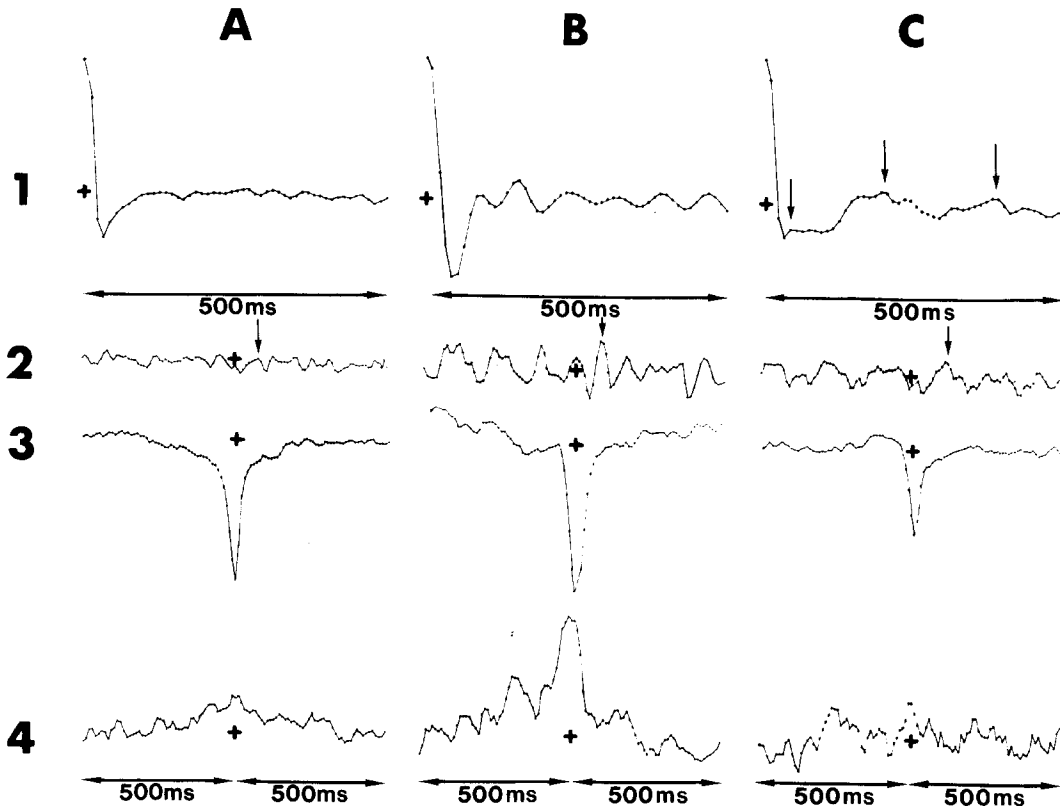


Fig. 5. Consistency of rhythmicity and of time and phase relations in the activity of neuronal networks in the thalamus (n. lateralis posterior) of the unanesthetized, unrestrained cat in the states of wakefulness (A), slow wave sleep (B), and paradoxical sleep (C). All computations were done on recordings obtained with the same electrode array from the same animal, in the same experiment as that illustrated in Fig. 4. The amplitude ranges of the clusters of action potentials crosscorrelated on line 3 were: higher than 80  $\mu\text{V}$  and 25 to 35  $\mu\text{V}$ . All designations of columns and lines are the same as in Fig. 4. Arrows in C, line 1, indicate the presence of two superimposed frequencies: 25 c/sec and 5.2 c/sec (theta range). All correlograms were computed from recordings of 90 sec duration.

of neurons obtain in all the states of wakefulness and sleep studied in this series of experiments.

*Time and phase relations between action potentials within the clusters*

When cross-correlations between trains of

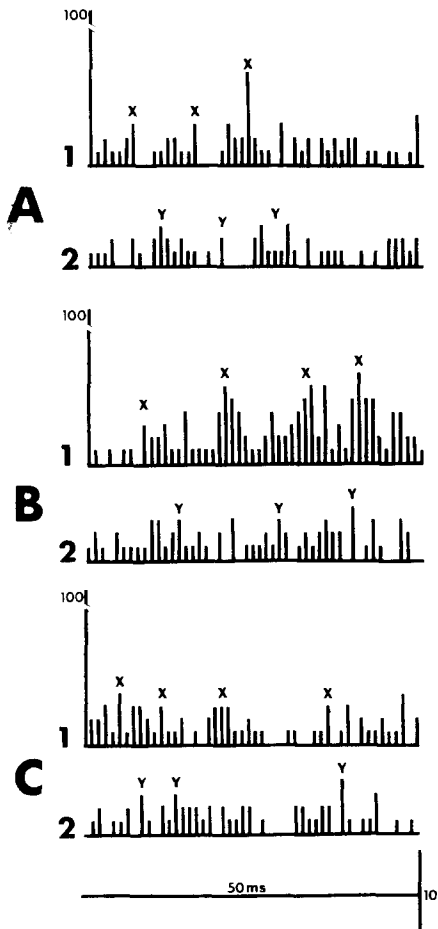


Fig. 6. Crosscorrelations between two trains of individual action potentials recorded by two microelectrodes, from the cortex of the cat in the states of wakefulness (A), slow wave sleep (B), and paradoxical sleep (C). The computer is triggered by the action potentials of the train on line 1 and 'post-trigger' histograms are computed for both trains. Rhythmicity of discharge is shown at x, x, x, ... y, y, y, etc., correlation between the two trains is shown at x-y. Distance between the microelectrodes 330  $\mu$ m. Amplitude range of action potentials in either train: 80  $\mu$ V and over. Number of sweeps: 100; duration of sweep: 50 msec; bin size: 1 msec.

individual action potentials recorded by two different microelectrodes are obtained, it is found that, both in the cortex and in the thalamus, and in all three states, the action potentials are generated, rhythmically, at intervals of 6 to 9 msec. (Fig. 6A,B and C at X), and that the highest probabilities of discharge in one train alternate with those of the other train at intervals of approximately half that duration (Fig. 6 at X, Y).

*Consistency of findings in different animals*

The results described above were found in all six animals. In some animals, however, during certain periods of wakefulness or paradoxical sleep, rhythmicities in the range of 5-8 c/sec appeared in the gross wave tracings as well as in the sequence of clusters of action potentials. In these cases, the clusters of action potentials led the gross waves by about 40 msec (Fig. 7A and C, lines 1, 2 and 3); phase relations between clusters of action potentials of high and low amplitudes recorded by a single microelectrode or between clusters of action potentials of high amplitudes recorded by two different microelectrodes remained the same as in all other states and rhythmicities (Fig. 7A and C).

**Discussion**

It has been known for a long time that the circulation of neuronal activity associated with the rhythmic waves of the cortex and of the thalamus occurs both in wakefulness and in slow wave sleep and that, as the rhythmicity of the waves changes from one state to the other, so does the periodicity of the circulation (Verzeano and Negishi 1960, 1961). The present findings indicate that the circulation of neuronal activity occurs not only in wakefulness and in slow wave sleep but in paradoxical sleep as well, and that, in any of these states it is not a transient phenomenon, but goes on and remains consistent for long periods. In addition, they provide new information on the time and phase relations



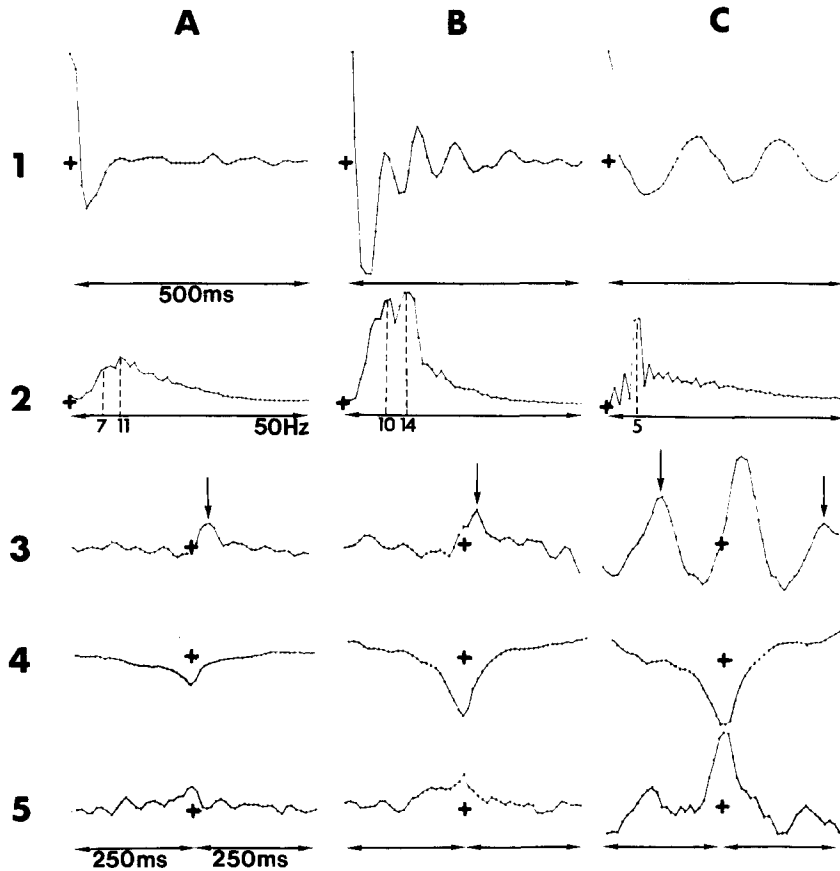


Fig. 7. Appearance of dominating theta activity in the neocortex of the unrestrained, unanesthetized cat. A: wakefulness; B: slow wave sleep; C: paradoxical sleep. Line 1: autocorrelation of gross waves; line 2: spectral distribution (power spectrum) of gross waves; line 3: crosscorrelations of gross waves and clusters of action potentials of amplitudes higher than  $70 \mu\text{V}$  recorded by the same microelectrode; line 4: crosscorrelations between clusters of action potentials of amplitudes higher than  $70 \mu\text{V}$  and clusters of action potentials of amplitudes of 20 to  $30 \mu\text{V}$ , recorded by the same microelectrode; line 5: cross correlations between clusters of action potentials of amplitudes higher than  $70 \mu\text{V}$  recorded by one microelectrode and clusters of action potentials of the same amplitudes recorded by another microelectrode located  $300 \mu\text{m}$  away and posterior to the first. The gross waves correlated on lines 1 and 2 were recorded by the anterior microelectrode in the array. Note the broad spectral distribution of the waves in wakefulness, showing peaks at 7 c/sec and 11 c/sec and the narrow spectral distribution in paradoxical sleep, at 5 c/sec; note the high degree of correlation between gross waves and clusters of action potentials occurring at times which correspond to the theta range (arrows, at C 3).

between the discharge of different neurons and groups of neurons, which leads to a clearer picture of the mechanisms which are at the basis of the circulation of activity.

Another remarkable finding in this series of investigations is that the periodicities in the range of the theta rhythm may appear, both in the cortex and in thalamus and that, when they are present, they are based on the circulation of neuronal activity which occurs with-

in the neuronal networks from which they are recorded. This finding has important bearings on the role of the circulation of neuronal activity in the processing and storage of information.

#### *The circulation of activity*

The time and phase relations between the discharge of different groups of neurons, as determined by the investigations described in

this report give strong support to the hypothesis advanced by Verzeano (1972; 1977) according to which the circulation of neuronal activity is based on positive and negative feedback activities developing over intrathalamic, intracortical and corticothalamic feedback loops.

The time and phase relations demonstrated in these experiments give strong support to this hypothesis: the very short intervals between action potentials (such as x—y—x in Fig. 6) may be related to activity within very short feedback loops, including only two or three neurons; longer intervals between bursts of high amplitude and low amplitude action potentials (such as x—y in Figs. 1, 2 and 3) occurring with a phase difference of  $180^\circ$  (Figs. 4, 5 and 7) may be related to activity within longer loops including a larger number of neurons and interneurons, operating within the territory surveyed by a single microelectrode; intervals between bursts of action potentials recorded by different microelectrodes in the array (such as a—e in Figs. 1 and 2) may be related to much longer feedback loops which would include neurons and interneurons located within different cortical layers (or between different thalamic nuclei); cross correlating such sequences of bursts of action potentials (d—e in Figs. 1 and 2) over long periods, would result in the type of crosscorrelograms shown in Figs. 4 and 5, line 4, and Fig. 7, line 5.

The transition from wakefulness to sleep or from one state of sleep to another, involves changes in the action of synaptic transmitters (Jouvet 1969; Verzeano and Mahnke 1972; Rinaldi et al. 1975) and in the interplay of excitatory and inhibitory interactions, in such a way that some groups of neurons may be left out of and other may be taken into the pathways over which the activity circulates. This would result in changes in the length of the intervals between the successive discharge of neurons or groups of neurons such as those which have been shown to occur in these experiments.

#### *The cortical and thalamic theta rhythm*

It has been shown some years ago that during the appearance of the theta rhythm, the hippocampal output may influence the neocortex (Parmeggiani 1967) and that this influence may be mediated by the thalamus (Parmeggiani and Rapisarda 1969). The results presented in this report confirm the presence of the theta rhythm, both in the thalamus and in the cortex, during wakefulness or paradoxical sleep, and demonstrate that when it does occur, it is due to changes induced in the circulation of neuronal activity in the thalamic and cortical networks themselves as indicated by the high degree of relation between the neuronal action potentials and the gross waves of the theta rhythm, and not to the effects of volume conduction from other structures as some authors have suggested.

These findings have an important bearing on the concepts which deal with the process of memory consolidation. It has been suggested that the circulating neuronal activity may serve as a carrier which, modulated by incoming sensory information, may transport the neural representation of the events to be stored, over the networks in which it would ultimately be retained (Verzeano et al. 1970; Verzeano 1977). It is well known that consolidation may occur in wakefulness. It has been shown that during this process a theta rhythm may appear in the cortex and in the thalamus. (Elazar and Adey 1967; Landfield et al. 1972). It has also been shown that consolidation may occur during paradoxical sleep (Bloch 1975). During this time a theta rhythm may also appear in the cortex and in the thalamus. The findings presented in this report indicate that the theta rhythm which appears in the cortex and in the thalamus in wakefulness or in paradoxical sleep is closely correlated with the circulation of neuronal activity and that its development may, actually, be based on it. These facts strongly support the hypothesis which suggests that the circulation of neuronal activity is implicated in the consolidation process.

## Summary

The present study has attempted to determine, by quantitative methods, the changes which occur in the circulation of neuronal activity, in the cerebral cortex and in the thalamus, in the transition from wakefulness to slow wave sleep and to paradoxical sleep.

Gross waves and neuronal activity have been recorded by means of arrays of extracellular microelectrodes from the cortex and the thalamus of unrestrained, unanesthetized cats. Autocorrelations have been performed on trains of rhythmic gross waves. Cross correlations have been performed between waves and neuronal activity and between trains of action potentials generated by different groups of neurons.

It has been found that: (1) the circulation of activity develops and remains consistent for long periods in all states of wakefulness or sleep; (2) as the rhythmicity of the gross waves changes in the transition from one state to another, so do the characteristics of the circulation; however, the time and phase relations between the activities of the groups of neurons involved in circulation, maintain a high degree of correlation in all the states of wakefulness or sleep and (3) in the states of wakefulness and paradoxical sleep the cortical and thalamic activities are, frequently, infiltrated by rhythmicities of the theta range; when this occurs, the time and phase relations between the gross waves and the circulating neuronal activity show that the infiltrating theta rhythm develops within the cortex or the thalamus and is based on the activity of local networks.

## Résumé

*Circulation de l'activité neuronique corticale et thalamique au cours de la veille et du sommeil*

L'étude actuelle cherche à déterminer, par des méthodes quantitatives, les modifications qui surviennent dans la circulation de l'activité neuronique, dans le cortex cérébral et dans

le thalamus, au cours de la transition de la veille au sommeil à ondes lentes et au sommeil paradoxal.

Les ondes EEG de l'activité neuronique sont enregistrées au moyen de faisceaux de microélectrodes extracellulaires dans le cortex et le thalamus, chez des chats non contenus et non anesthésiés. Des autocorrelations sont réalisées sur des trains d'ondes rythmiques. Des cross-corrélations ont également été réalisées entre les ondes EEG et l'activité neuronale et entre des trains de potentiels d'action provenant de divers groupes de neurones.

Il a été observé que: (1) La circulation d'activité se développe et demeure constante pendant de longues périodes à tous les stades de la veille ou du sommeil; (2) Quand la rhythmicité des grandes ondes change au cours de la transition d'un stade à l'autre, les caractéristiques de la circulation changent également; cependant les relations de temps et de phase entre les activités des groupes de neurones impliqués dans cette circulation conservent un degré élevé de corrélation dans tous les états de sommeil et de veille et (3) Dans les états de veille et de sommeil paradoxal les activités corticales et thalamiques sont fréquemment infiltrées d'activités rythmiques de la bande thêta; quand ceci survient, les relations temporelles et de phases entre les ondes EEG et l'activité neuronale circulante montrent que le rythme thêta infiltrant se développe à l'intérieur du cortex ou du thalamus et qu'il prend sa source dans l'activité de réseaux locaux.

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