FROM ATTENTIVENESS TO SLEEP.
A TOPOGRAPHICAL ANALYSIS OF LOCALIZED
"SYNCHRONIZED" ACTIVITIES ON THE CORTEX OF NORMAL
CAT AND MONKEY

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Abstract. In normal implanted cats, squirrel monkeys and baboons, various types of localized rhythms can be identified in somatic area I and in the visual zone. Their relation to levels of attentiveness, alertness or drowsiness, and their possible correspondence to human EEG activities, wicket or $\mu$ rhythms and occipital alpha rhythms is considered. Subcortical recordings tend to show that these rhythms correspond to distinct thalamo-cortical systems, involving different thalamic nuclei.

INTRODUCTION

Given the large amount of experimental studies performed on sleep phenomenology and sleep mechanisms in the last 25 years, the major features of both slow and paradoxical sleep are now fairly well known; no doubt other studies in the near future will further increase our knowledge in this field. In contrast to this abundance, the transient, often very short-lasting stages leading from alertness to sleep through various degrees of drowsiness have been much less explored or at least not as extensively as sleep phenomena themselves.

It is not that these phases were ignored. A certain number of studies were indeed directed toward identifying the variety of mechanisms of "sleep induction", for instance those of Akert, Bremer, Hess, Magoun, and more recently those of Dell, Jouvet, Moruzzi and others. Our own
interest has been directed to the electrophysiological (mostly electro-
cortical) phenomenology of these transitory stages, an aspect often ne-
glected. The reason is mainly because the recording technology most
frequently used by others included very low recording speed and rela-
tively few implanted electrodes on the chronic animal and because the
detailed aspects of this evolution are not (as far as our own experience
is concerned) observable in the acute preparation (paralyzed or encé-
phale isolé) ¹.

Our purpose here in undertaking these topographical studies in the
cat and monkey was threefold:

1. To try to identify the various groups of localized rhythms and
their evolution during sleep induction: some of these have already been
observed by some groups of authors but often with no precise localiza-
tion. This inventory is far from being achieved. The general concept
underlying the kind of investigation thus performed progressively em-
phasized rhythms being subject to localization, somewhat like sensory
responses.

2. To establish as far as possible a parallel with rhythms observed
in the human EEG. Analogies have often been proposed in the literature
between “spindles” in cats or other species and the human alpha
rhythm but, as will be seen below, these do not hold. We tried to take
advantage of studying several species, assuming that comparison of the
cat and monkey might give indications as to the “phylogeny” of these
rhythms and render more feasible comparisons with the human EEG.

3. To determine behavioral correlates of these various rhythms.
As our exploration developed, we realized more and more that up to
a given extent the local rhythmic systems appeared in rather distinct
situations of the normal animal; although these were not always easily
characterized, a rough delimitation proved possible in terms of orienta-
tion reaction, selective or diffuse attentive behavior, relaxation and fin-
ally drowsiness.

Our study is based on experiments with cats and with two species
of monkeys (Baboon: Papio papio; Squirrel monkey: Saimiri sciureus).
Electrophysiological explorations were carried out using various me-
thodologies. Electrocorticograms (ECoG) were recorded with a large
number of electrodes (monopolar or bipolar transcortical) implanted at
various cortical sites but close enough together to permit a systematic
spatial “scanning” of the activities over restricted zones. Thalamic
“macrecordings” were made using multilead wire electrodes implant-

¹ The technology recently developed by Puizilloux et al. (14) with painless fixat-
ion of encéphale isolé cats might perhaps provide new possibilities for exploring
these transitional stages.
ed according to given stereotaxic coordinates. The animal was either left free in the experimental room (cat and Saimiri) or simply sitting in a restraining chair (Baboon). In other experiments the animals were first prepared for painless stereotaxic fixation using horizontal brass tubes cemented to the skull. Once fixated, the head was automatically brought to the adequate Horsley-Clarke coordinate system, thus allowing deep electrode exploration exactly as in the acute preparation.

In all cases the experimental animal had been previously accustomed to the recording situation and become familiar with the operator. Indeed, cats and squirrel monkeys usually became quite tame and familiarized. On the other hand, baboons had to remain seated in their chair and never showed perfect adaptation or cooperation, as is well known to those working with this species.

RESULTS

Table I summarizes some salient points of our findings. It also includes some comparisons with data from the literature. As may be seen, a first distinction is made between various categories of localized activities and the well known patterns which develop during “slow” sleep, i.e., slow waves and spindles. In contrast to some common belief, slow wave sleep patterns are quite distinct from the various phenomena to be described below. Considering the latter, a distinction is also made between rhythms developing in the anterior part of the cortex (frontal and central areas) and those displayed by more posterior (occipital and posterior parietal) cortical regions.

Anterior rhythm systems

Our as yet most detailed investigation concerns the anterior rhythms which could be localized in somatic area I of the cat (postcruciate gyrus) and the monkeys studied (postcentral gyrus). More precisely, three rhythmic systems were thus identified, with distinct morphologies and temporal characteristics and corresponding to three distinct behavioral situations. We shall designate these systems as: (i) rhythms of hypervigilance (RHV); (ii) rhythms of quiet wakefulness (RVI); (iii) anterior rhythms of drowsiness (RAA). The principal features of these somatic rhythms together with the behavioral conditions of their appearance are indicated on Table I. As will be seen below, experimental arguments also point to the existence of distinct thalamic sites corresponding to each of these systems.

2 Using here the French terminology employed in our previous publications (16-18).
Comparison between rhythms recorded in animals (cat and monkey) and man. Middle row: slow wave sleep: increasing levels of alterness are indicated upward from mid-row for anterior cortical areas and downward for posterior areas. C, cat; M, monkey. For terminology (left column) see text.

<table>
<thead>
<tr>
<th>Terminology</th>
<th>Characteristic frequencies (c/sec)</th>
<th>Cortical focus</th>
<th>Thalamic site</th>
<th>Behavioral correlates and sensory reaction</th>
<th>Animal data</th>
<th>Human data</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Anterior</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>RHV</td>
<td>C: 36 M: 18</td>
<td>C and M: SI of upper limb</td>
<td>Posterior nucleus</td>
<td>Animal hypervigilant and immobile (watching prey)</td>
<td>Animal data</td>
<td>Human data</td>
</tr>
<tr>
<td>RVI</td>
<td>C: 14 M: 8</td>
<td>SI</td>
<td>VB nucleus</td>
<td>Animal quiet, immobile</td>
<td>“sensori-motor rhythms” (19)</td>
<td>“μ” or “wicket rhythm”</td>
</tr>
<tr>
<td>RAA</td>
<td>C: 4-18 M: 4-13</td>
<td>SI + SII</td>
<td>CM-Pf</td>
<td>Animal immobile, drowsy</td>
<td>All classical descriptions of slow wave sleep; two types of spindles (see 7)</td>
<td>Stages II III IV</td>
</tr>
<tr>
<td><strong>Spindles + slow waves</strong></td>
<td></td>
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</tr>
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<td></td>
<td>C: fast spindles 12-18</td>
<td>Motor cortex</td>
<td>GL, Pulvinar, Lateralis posterior</td>
<td>Eyes closed, eyelids lowered; attention to various non-visual stimuli</td>
<td>Post reinforcement rhythms” (19)</td>
<td>Alpha rhythm (12, 20)</td>
</tr>
<tr>
<td></td>
<td>slow spindles 8-11</td>
<td>visual cortex</td>
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<td></td>
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<td></td>
<td>slow waves 2-3</td>
<td>no precise localization</td>
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<td>M: undetermined</td>
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<td><strong>Posterior</strong></td>
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<td>RAP alpha fast</td>
<td>C: 4-6 C: 8-13 M: 8-13 C: 12-18</td>
<td>C: anterior marginal and suprasylvian M: visual with limits unknown</td>
<td>GL, Pulvinar, Lateralis posterior</td>
<td>Eyes closed, eyelids lowered; attention to various non-visual stimuli</td>
<td>Post reinforcement rhythms” (19)</td>
<td>Alpha rhythm (12, 20)</td>
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Notes: Abolished by body movement, not by visual stimulus; sleeping; sleeping; sleeping.
Three cortical rhythms in area SI

Hypervigilance (RHV). A cat exploring an unknown environment or a monkey who perceives a strange sound or noise may undergo phases of immobility. They are as a rule accompanied by the development of sequences (lasting 1 to 5 sec) of rhythms with a relatively high frequency. This frequency depends on the subject but is surprisingly stable for any given subject. It ranges from 20 to 40/sec in the cat and from 12 to 18/sec in the monkey. RHVs are blocked by the least body movement (but not by isolated eye movements).

Fig. 1. Rhythms in somatic area I of cat (left) and baboon (right). From top to bottom: RHV during episode of intense vigilance; RVI in quiet wakefulness; anterior drowsiness rhythms (RAAs). For cat only: (left), “slow” sleep with spindles (F) and slow waves (OL). Localizations of foci are indicated by corresponding symbols on brain schemes. Figures indicate dominant frequency in each case.
Quiet wakefulness (RVI). When an animal remains in a familiar environment, showing neither any signs of particular attention or curiosity nor mobility, ECoG rhythms develop in somatic area I, which are morphologically distinct from the preceding ones. These RVIs appear in sequences of fairly variable durations (1 to 20 sec); their fre-
quency now ranges from 12 to 18/sec in the cat ($f = 14$/sec) and from 8 to 12/sec in the monkey ($f = 10$/sec). Like RHVs, RVIs are also suppressed by body movements (and not by eye movements).

**Drowsiness rhythms** (RAA). When the animal goes from wakefulness into sleep, it undergoes transitional stages, with alternating phases of movements (cleaning, licking, changing posture) and of immobility. Under these conditions, groups of rhythms develop in somatic area I, with variable duration; their frequencies now range between 4 and 19/sec in the cat, 4 and 10/sec in the baboon. In other words, RAAs are on the average slower than the activities described above.

Samples of these various ECoG patterns are given in Fig. 1 and 2. All three rhythmic activities thus described, RHVs, RVIs and RAAs, are essentially localized in somatic area I and more specifically in the anterior limb area. This could be shown through controlling the topographical distribution of the evoked potential in each particular subject (put under barbiturate anesthesia for that purpose).

For each wave system, a "focus" was defined as being the cortical area where its probability of occurrence was highest; very often a certain extension around this focus towards other neighbouring zones could be observed.

When the animal fell into typical sleep (with all known behavioral correlates), RAAs disappeared and were replaced by spindles alternating with slow waves. The spatio-temporal characteristics of sleep spindles are distinct from those of the previously described rhythms. In fact two categories of spindles have sometimes been distinguished: a particular category of "fast-spindles" was identified in the cat by Creutzfeldt and Jung (7) in the motor cortex; elsewhere on the convexity, sleep spindles are of lower frequency but with no particular focalization. Actually these "slow spindles" extend over the entire suprasylvian and marginal gyrus, with even some spread toward the sensorimotor sector where they coexist with fast spindles.

**In search of thalamic correlates of the anterior cortical rhythms**

(Fig. 3, 4, 5)

Macroelectrode stereotaxic explorations were performed in order to localize thalamic sites presumably displaying rhythms similar to the identified cortical activities.

Our investigations in this field are at their beginning, so data to be presented herein can only be considered partial; let us review them briefly.

1. RHV-like rhythms could be detected at a thalamic level which
A. ROUGEUL-BUSER, J. J. BOUYER AND P. BUSER

Fig. 3. Cortical RHVs (top trace) and corresponding rhythms in lateral posterior area of the thalamus (bottom trace) in cat.

Fig. 4. Cortical RVIs (top traces) and corresponding rhythms in VB nucleus of the thalamus (bottom traces) during quiet vigilant states in cat (left) and baboon (right). Dominant frequencies indicated in each case.

was identified by its topographical anatomy as belonging to the posterior group (nucleus posterior and nucleus suprigeniculatus).

2. Rhythms coinciding with RVIs could be found in another thalamic area, namely the ventrobasal group (VB), the somesthetic relay nucleus. This localization could even be further specified, thalamic RVI-like rhythms being found in a restricted VB zone corresponding to the arm or anterior leg projection area. This result was first obtained in the cat and later on confirmed in the monkey.

In the cat, a bilateral coagulation was performed on several subjects of this VB area. Consequently, it was observed that RVI had disappeared on the cortex and instead, RHV and RAA could still be recorded.
3. During the onset of drowsiness, conditions appeared more complex, in that rhythmic activities could still be recorded in the VB complex in concomitant with the development of RAAs. In addition, however, a new category of rhythms was identified with a frequency close to that of RAAs in an entirely distinct area, namely, its postero-median division, encompassing n. centre median and parafascicularis.

**Posterior rhythm systems**

Our knowledge of the posterior rhythms is less elaborated at this time. In various situations of immobility we could record rhythmic patterns with various characteristics on the marginal and suprasylvian cortices in the cat, and from the occipital region in the monkey, although their localization could not as yet be defined with the desired precision.

The frequencies in the posterior zones enable us distinction of at least three categories in the cat: fast rhythms (12–18/sec), “alpha-like” frequencies (8–13/sec) and slow drowsiness rhythms, termed posterior (RAP) as opposed to those located more anteriorly (RAA). All three are abolished by opening of the eyes and/or visual stimulation; on the other hand, they
are unaffected by limb and head movements, provided that these are sufficiently moderate to provoke no, or only slight, changes in eye position.

The behavioral conditions which accompany the development of these posterior rhythms, however, remain less well known. It seems as if their concomitants correspond to more complex conditions than do anterior rhythms.

Fig. 6. Behavioral correlates of anterior (upper trace, som) and/or posterior (vis) rhythms in cat during drowsy state: 1, drowsy, motionless; 2, eyes closed, extends limb; 3, eyes open, motionless; 4, eyes open, extends limb.
Fast posterior rhythms appear when the animal displays behavioral signs of attention to various non-visual stimuli (noise, smell); complete immobility does not seem to be a prerequisite for their appearance. The circumstances for development of the slow posterior patterns (RAPs) are also complex: they appear mainly when the animal passes into drowsiness by closing its eyes; they also appear soon after the operator lowers the animal’s eyelids with hand. Here too, complete immobility is not necessary (Fig. 6).

Thalamic macroelectrode explorations were also performed. Our findings in this field remain rather general though rhythms with various frequencies accompanying the posterior rhythms could be recorded from a thalamic area comprising lateral geniculate nucleus, n. lateralis posterior, and pulvinar, as would be expected from recent findings in dogs (13) but with as yet no further specification.

**DISCUSSION**

This exploration of the morphological characteristics and behavioral correlates of localized rhythms, requires further experimentation. Whereas the anterior part of the cortex is fairly definitely characterized by its synchronized activities, the posterior areas, as well as the medial aspect of the cortex, remain to be studied in detail. It is expected that a greater number of such localized systems will be identified in the future.

Various aspects of the findings deserve discussion.

1. Many other workers in the past have described localized rhythms and their behavioral correlates. Some are indicated in Table I. Anterior rhythms were thus clearly identified by Sterman and Wyrwicka (19) as “sensorimotor rhythms” and some posterior rhythms as “post-reinforcement rhythms” (Sterman, ibid). Posterior rhythms in the “alpha range” were also isolated by Lanoir and Cordeau (12) in the cat and by Storm Van Leeuwen et al. (20) and Lopes da Silva et al. (12a) in the dog. In the great majority of such animal studies, however, only few recording electrodes had been implanted and thus no systematic topographical investigations could be performed (nor sought for, in fact).

One of the indications of our data is, we think, that the rhythms thereby isolated are quite distinct from sleep spindles, a distinction which is far from being commonly accepted. Using only a few electrodes most often leads to a kind of “binary” distinction between a “waking desynchronized state” and a “synchronized state” with no gradation between immobility as such, drowsiness and sleep.
2. In acute preparations available data on synchronized rhythms are generally even more schematic; as a result, to establish a correlation with our observations remains very difficult. Although these rhythms were used more more as rough indicators of the state of alterness of the preparation, some studies of the “spindle” distribution have been performed on various occasions. In cat, spontaneous spindles are generally most conspicuous on the suprasylvian gyrus. In a study of the “evoked” spindles, i.e., spindles elicited through single electrical stimulation of either caudate nucleus or thalamus, Horvath and Buser (4, 10) for instance, distinguished an “anterior” spindle system located in the sensorimotor cortex from a “posterior” system with its maximum in the middle suprasylvian gyrus. No clear relationship can be drawn, ever, between these data on flaxedil-paralyzed animals and our present findings.

3. Another type of acute preparation which has been known for a long time to display amounts of “spindles” is the animal under barbiturates. Following the older observations on “dial bursts”, recent studies (1) have focused attention on the spindles. In our opinion, these barbiturate induced rhythms are clearly distinct from the activities studied here under more physiological conditions. We do not mean, however, that the fundamental mechanisms underlying the two groups of rhythms are different: indeed we have no indication favorable or unfavorable to the “inhibitory interneuron hypothesis”, as proposed by Andersen, Eccles and Sears (2) and later on developed by Andersen and Andersson (1). Instead, we mean that under the influence of barbiturates systems may begin to spindle which do not “normally” display rhythmic activity and, hence, that a spindle distribution established under anesthesia is of little interest in determining a functional topography of the synchronized activities. On the other hand, our findings coincide with the previous authors’ assumption that one given spindle system may be localized in a restricted cortical zone, with very little lateral spread.

4. Going a little further, we come to the human EEG. Relatively little data exists, regarding the rhythms initially described by Jasper and Penfield (11), Gastaut et al. (8), Chatrian et al. (6) under the term of “wicket” or “μ rhythm”. As is well known, these rhythms predominate in the central region, and they react mainly to movement (in contrast to the posterior alpha activities). They were recently studied in some detail in children (5) and the data obtained fits our own animal findings. Finally, one assumption from the present data is that the frequently proposed parallel between animal spindles and human alpha rhythm is essentially erroneous. The correspondence — if any — may
exist with some of the posterior drowsiness activities as indicated in Table I.

5. Beyond topographical homologies and differences, the functional significance of these localized rhythms with restricted cortical spread deserves a final brief comment. We have tried to show that localized synchronization of one type or another can be correlated with rather distinct behavioral situations. Synchronized rhythms with anterior localization develop only when the animal is immobile, but this immobility may underlie various possible degrees of alertness: hypervigilance of the orientation reaction, quiet vigilance, drowsiness and the "going to sleep" procedure. Our knowledge of the behavioral situations accompanying the development of the posterior rhythms is yet less complete. As was indicated, immobility or closure of the eyes represent favorable conditions, but as strict a distinction between the levels of alertness could not be drawn as in the case of the perisigmoid activities.

Significant changes in size and shape of human averaged evoked potentials were repeatedly observed in relation to selective attention (see, e.g., 9, 13, 18, 21). On the other hand animal studies using a similar methodology have been less successful in trying to find such psychophysiological correlates. It is tempting to conclude from our findings that the localized rhythms — and conversely the localized activations — reveal changes in levels of specific attention to one or other sensory domain (somatic vs. visual). It is not unreasonable to suggest that the development of synchrony in a given sensory channel is incompatible with the normal transfer and elaboration processes within that pathway and that inattentiveness to a sensory modality is indeed accompanied by, and concomitant with, the development of synchronized patterns in that same channel. In spite of the still very impractical way of formulating this hypothesis we believe that overall variations in the excitability states of localized neuronal pools, leading to either "synchrony" or "disynchrony" might be another electrophysiological index of higher nervous elaboration in that pool (besides the evoked potential, which represents the response of this receptive system to a "step" or to a "pulse" function).

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