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Attention in cat revisited. A critical review of a set of brain explorations in fully alert animals

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ABSTRACT

Introduction. The greater majority of animal studies based on the ongoing electrocortical activity have been devoted to correlates of sleep-wakefulness, with their characteristic rhythms with a large cortical distribution. By contrast, "focal" rhythmic activities, with limited cortical extent were surprisingly not so often explored so far in animals. During the past 50 years, we precisely adopted this strategy to analyze attention in cat and shall herein try to summarize and critically examine some of our data obtained over the years.

Methods. All experiments were carried out on adult animals implanted with cortical electrodes, and in some cases also with subcortical macroelectrodes stereotaxically introduced to reach the requested levels[1]*. Cats were daily introduced into an experimental space (about 2 m^2) which contained both a rectangular perspex box and a vertical opaque wall with a small hole at its base (see Fig. 1). Within the space, the cat would face one of two possible experimental situations, alternatively day after day. In situation 1, a living mouse was left free behind the wall and the cat used to remain quasi-immobile close to it, apparently waiting for a possible appearance of the mouse at the hole. In situation 2, the living mouse was instead placed into the closed perspex box and the cat, again free in the space, used to stay or sit close to the box, watching the mouse. The surprising fact was that in both situations, the cat would generally maintain its particular attitude, almost motionless either waiting or watching, for more than 30 mn. As indicated by the electrooculogram (EOG), the animals made very few eye movements during these attention episodes. More recently, in order to know more about the ECoG during a saccade, we changed our protocol, now placing the animal into a cylindric space where it could observe a moving vertical bar suddenly appearing and then stopping. All brain activities and the EOG were dispatched through a flexible lead to the amplification and processing devices with auto- and cross-correlation analyses and, more recently, through a frequency-time display (wavelet transform). Except for the initial surgery of electrode implantations; our cats were never submitted to any general anesthesia during the experimentation period.*

Results. In a first set of data we shall describe cortical activities recorded during attentional states. Most of them were obtained during immobile attention, others during the protocol with attentional shifts. Thalamic recordings and brain stem modulations of the attentive states will follow.

Key words

Cat • Attention • Expectancy • Electro-cortical mu and beta rhythms •
Thalamic concomitants • Mesencephalic control

Cortical activities

Motionless attentive states

Our major finding was that expecting and attending differed by their ECoG correlates. *Expecting the mouse* to appear at the hole elicited very characteristic trains of rhythms at 12 to 14 Hz confined to a specific site of the anterior cortex, the post-cruciate S1 somato-sensory receiving area. Based on previously described human "sensori-motor" or "rolandic" or "wicket" rhythms in connection with movement or arrest of movements (Jasper and Penfield, 1949;

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Arlette Rougeul-Buser died in early 2010. This paper summarizes our common scientific work since late 60th.

Gastaut, 1952; Chatrian et al., 1959; Pfurtcheller et al., 1994), we called these activities "mu rhythms" (Rougeul-Buser et al., 1983). Fig. 1 (left frame) shows these mu rhythms and also the "waterfall display" of successive autocorrelograms, indicating the persistence of the mu activity during almost 90 mn. At the same moment (not shown) rhythms at a frequency range of 7 to 14 Hz in other words an alpha-like activity was recorded from the primary visual cortex (anterior part of area 18 and area 17) (Chatila et al., 1992, 1993). *Attending the mouse* in its perspex box was this time accompanied by trains of rhythms at a much higher frequency, between 25 and 40 Hz (Bouyer et al., 1981) with a different localization, dominating on two cortical sites, the posterior parietal area (roughly, Brodmann area 5) and the motor precruciate cortex. This is shown on Fig. 1 (right frame). Again, notice the waterfall display with dominance of fast # 40 Hz during the 90 mn of parietal recording. We called these activities "beta", since similar rhythms had initially been recorded from the fronto-parietal human scalp area by Jasper and Penfield (1949) and later on by many others (see e.g. Pfurtscheller, 1993)[2]. We also recorded 40 Hz rhythms in the visual area, as we shall see now.

Expectancy, attentional shift and focused attention

To illustrate those more precisely, we used this time our second experimental set up, where all types of attention could occur, expectancy and focused attention with no eye movements and, in between, an eye saccade presumably underlying an attentional

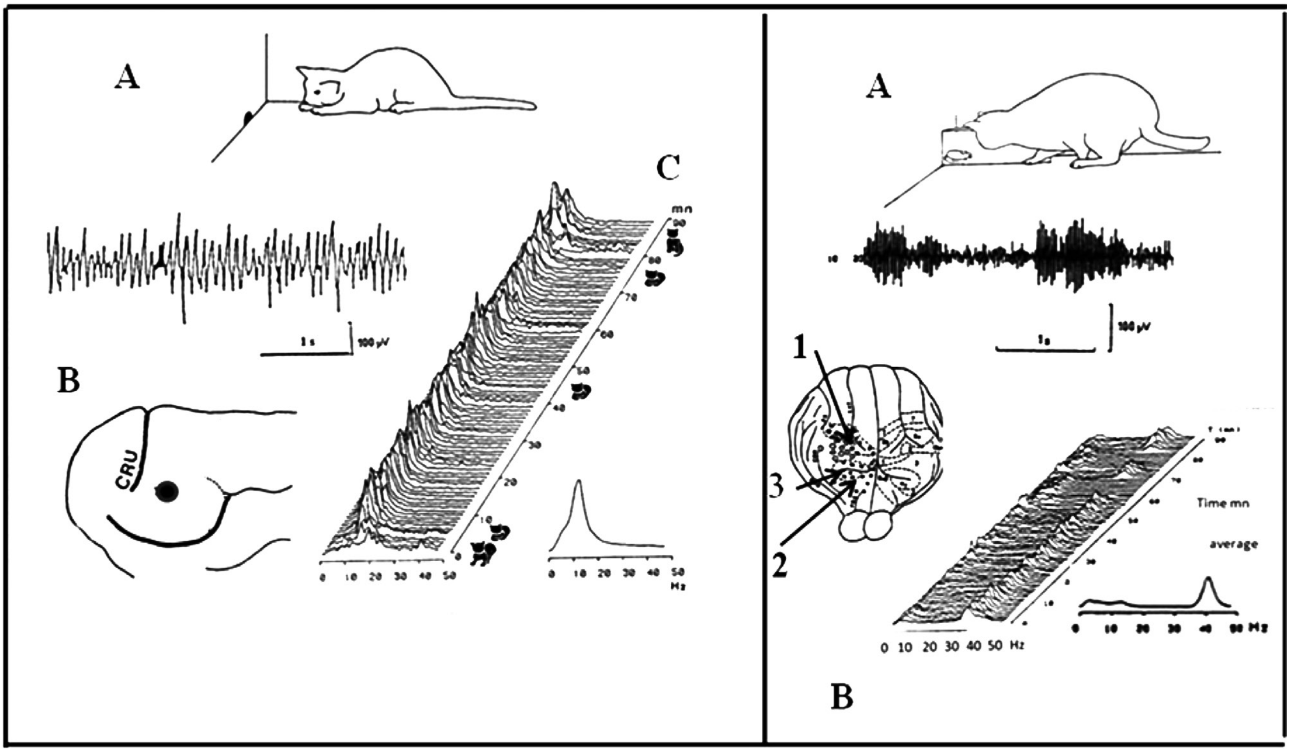

Fig. 1. - Two "attentional" situations in cat.
At left, *expectancy*. On top [A] the experimental situation, with the cat "waiting for the mouse to appear". The animal was implanted with multiple electrodes (not shown). [A] then shows a sample of a record taken from the postcruciate S1 area (black dot on [B], showing the anterior part of the left cortex with the cruciate sulcus (CRU). [C] shows the frequency distribution between 0 and 50 Hz evaluated on each successive 1 mn record during 90 minutes (Fourier autocorrelogram). At bottom right, average autocorrelogram over the total recording time.
At right, *selective attention*, On top [A] again, experimental situation of cat now watching the living mouse. Below, samples of a record taken in situation [A] from the anterior cortex. As [B], same processing as at left, with successive 1 min epochs of Fourier analysis over a total duration of 90 min. At bottom right, average frequency distribution over the 90 minutes. At left, cortex visible from its anterior aspect, with, at its left side, i.e. on the right hemisphere, active (black) sites on parietal area 5 (arrow 1) and on motor cortex (arrow 2) Arrow 3 indicates cruciate sulcus.

shift at appearance of the moving bar (Buser and Rougeul, 2005). Fig. 2 depicts a typical record from the visual cortex, the ECoG now being analyzed with the wavelet transform program. At first the animal faced an "uninteresting" space with no specific target and developed some alpha-like activities presumably associated with expectancy. The major finding followed, rather unexpected, when two sequences at "very high" frequency (80 to 130 Hz) suddenly appeared in relation to a saccade, as indicated by the EOG. A first short 80 Hz burst developed before the saccade, and a second, more important in power, occurred during it. It is only after these eye movements that beta rhythms appeared, when the animal then was in a state of motionless focused attention. We were thus having a complete picture of the various activities accompanying three behavioural situations. Such high ECoG frequencies were seldom observed yet (see however Munk and Neuenschwander, 2000). On the other hand, 20 Hz activities were also described in the visual cortex of cats "attending to visual stimuli" (Wrŏbel et al., 1994), probably corresponding to some forms of our beta rhythms.

Thalamic concomitants of mu and beta rhythms

While analyzing the cortical concomitants of motionless attention, we also searched for possible thalamic corresponding activities. These studies were carried out on cats additionally implanted with thalamic bipolar macroelectrodes (diameter # 0.6 mm), stereotaxically introduced during the initial surgery at given chosen thalamic sites. This of course required a rather high number of animals to explore a variety of thalamic nuclei, evidently chosen according to what was known about their cortical projections. These thalamic explorations were only systematically achieved for two classes of rhythms, somatic mus and parietal betas.

Thalamic site for mu rhythms

We evidently explored *nucleus ventralis posterior* (VP) and its vicinities. Macroelectrode recordings clearly confirmed that the VP area developed rhythms simultaneous with the cortical post-cruciate S1 mus. Fig. 3 (upper frame) well illustrates this correspondence between cortex and VP nucleus activities, with a number of active (black dots) and inactive (white dots) thalamic sites. We then performed unit explorations of the VP area. In these cases, the animal had no thalamic macroelectrode, but was prepared with one or several small holes in its skull, and with a painless stereotaxic fixation[3]. Brief and light air puffs were used to stimulate the skin and thus detect the thalamic VP unit responses. The cat was this time not submitted to the usual attention test but, carefully following its cortical activity, we were nevertheless able to select transient mu episodes that sufficed to establish the wished correspondences (Bouyer et al., 1982). The data were in brief as follows: i) as expected a large number of cells responded to an air puff on their corresponding receptive area (forepaw or wrist); ii) none of these cells displayed rhythmicity during the mu train (which were not interrupted by the weak skin stimuli); iii) only a small proportion of cells changed their firing rate during mus; iv) none of them behaved as typical thalamo-cortical relay cells carrying tactile messages to the cortex; v) during mus, these particular cells became either "rhythmic", discharging at the frequency of the cortical mu, or displayed a "sustained" change (acceleration or silence); vi) they were characterized as being either long axon thalamo-cortical or not, in this case being perhaps interneurons. Delagrange et al. (1987) further confirmed that no tactile relay cell participated in the VP rhythmicity, and suggested that the "rhythm cells" were of a limited number, perhaps belonging to a particular "rhythmogenic" network within the nucleus.

Thalamic site for posterior fast rhythms

Essentially guided by anatomical data (Avendaño et al., 1985), we explored the thalamic posterior group POm which is known to project onto area 5a. A clear coherence was established between POm and parietal beta rhythms (Bouyer et al., 1981). In single unit studies (Canu et al., 1994), thalamic cells were found with clear correlation with the parietal beta waves (Fig. 3, lower frame), but here again, they were only a few cells. These were localized in the POm or its immediate vicinity and displayed either a one spike-to one wave relationship or a diminution or even an arrest of their discharges throughout each beta episode.

While recording from the POm, it happened that the cat suddenly developed a sleep episode. Clearly

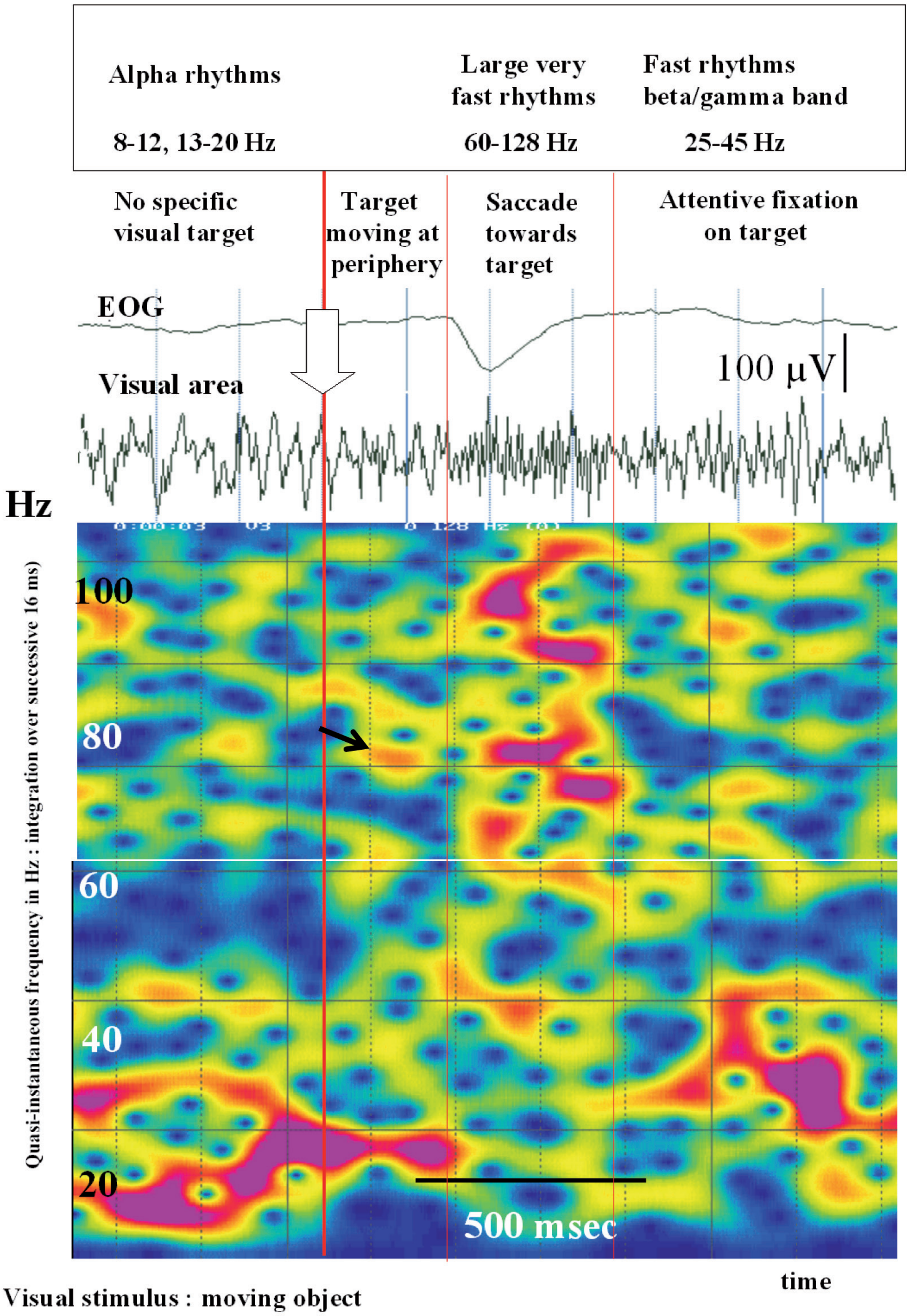

Fig. 2. - Very fast rhythms recorded from the visual cortex before, during and after an ocular saccade. Top to bottom: EOG, electro-oculogram; visual area ECoG; time-frequency (wavelet) analysis of the ECoG, with time as abscissae (see 500 ms bar), frequency in Hz as ordinates and power density in conventional colours from blue (low) to red (high) values. First section at left, no target in the cat's visual field, presumably expectancy with, irregular 8 to 20 Hz waves. At arrow and vertical red line, appearance of the bar in the extreme right peripheral field. Before any eye movement, presence of slight very high frequency rhythms (80 Hz) superimposed on the persisting alpha waves, and indicated on wavelet display by a small arrow. At next vertical red line, saccade toward the moving bar began, as indicated on the EOG. During the saccade, presence of very high frequency activity (60 to ca 130 Hz). After the saccade, the animal developed focused attention with beta rhythms up to 40 Hz. Notice on wavelet display the succession of three dominating frequencies during the three episodes as specified above, some "expecting" with alpha before saccade, very high frequency during saccade and focused attention with beta thereafter (Buser and Rougeul Buser, 2005, slightly modified).

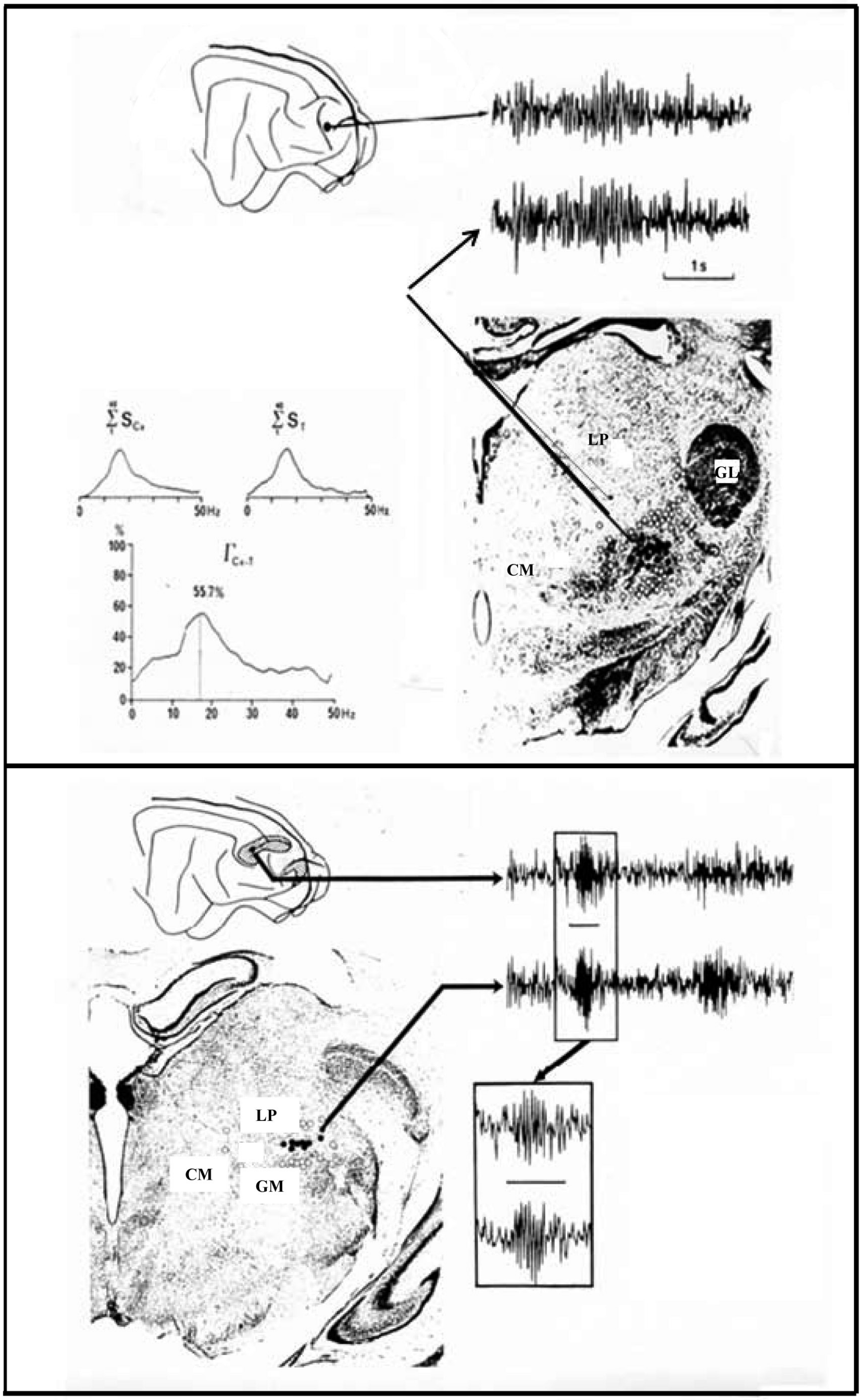

Fig. 3. - Simultaneous cortical and thalamic field potential recordings of mu activity (upper picture) and beta activity (lower one).

Upper frame: recordings from right S1 cortex and from *nucleus ventralis posterior* (VP). Thalamic recordings of the field potential with macroelectrodes. Active sites as black dots, silent ones as open dots. Notice simultaneous activity on cortex and in thalamus. At bottom left, autocorrelograms taken from cortex (upper left curve $\Sigma\ S_{cx}$) and thalamus (upper right curve $\Sigma\ S_t$). Lower curve, cross-correlogram $\Gamma_{cx\text{-}t}$ between cortex and thalamus. Frequency as abscissa, 0 to 50 Hz.

Lower frame: recordings from right parietal cortex and from thalamic *nucleus posterior medialis* POm, Notice simultaneous bursts on cortex and in thalamus.

In both frames, thalamic nuclei: GM, medial geniculate; LP, n. *lateralis posterior*, GL, lateral geniculate; CM, centre median.

then, no POM cell was found to fire in correlation with the sleep spindles, while this type of cell firing was encountered when recording from the neighboring *nucleus reticularis thalami* (RET), a site considered strategic for sleep spindles. Moreover no RET cell was found to participate in a mu or beta episode. To sum up, thalamic rhythmic cells in VP and POm nuclei may probably belong to two distinct oscillatory systems having in common a given participation in the animal's active life (to "stand still and to display a certain class of cognitive activity"), at variance with RET cells involved in drowsiness or sleep (Canu et al., 1992).

A quick view at modulatory brainstem mechanisms

That attentive states can be modulated by bioamines has long been repeatedly demonstrated in animal and man. It was therefore interesting to explore whether the discovered thalamo-cortical focal rhythms systems were undergoing some influence from structures known to be involved in these aminergic controls. For this purpose we used as dependent variables our two indicators, the animal's behaviours and their concomitant focal rhythms to test the possible effects of noadrenaline and dopamine.

Noradrenergic control of expectancy and mu rhythms

Two informations on a possible noradrenergic control of the mu system were obtained by Delagrange et al. (1993). First, lesions were practiced in the locus coeruleus (LC), known as containing noradrenergic cell groups. Bilateral lesions of the anterior 3/4 of the nucleus (containing the A6 noradrenergic cell group) resulted in a considerable increase and even dominance of mu rhythms and expectancy-like behaviour, without affecting the sleep-waking cycle. These findings suggested that part at least of the LC exerts a regulatory-inhibitory effect on structures involved in the production and persistence of an expectancy-like posture and its accompanying mu activity. Delagrange et al. (1989) then administered DSP4[4] to normal cats. They observed that the prevailing attitude of the animals after treatment was now again an almost permanent "expectancy-like watching", with a large if not exclusive dominance of only one ECoG pattern, namely mu-like activity. These changes were again interpreted as due to a release of the mu system from a noradrenergic modulatory regulation, in accordance with the above LC data.

Dopaminergic control of beta and focused attention

A second set of observations concerned another probable control of the attentional systems, this time through dopamine. One of its possible strategic sites was the ventral mesencephalic tegmental area (VMT) with its dopamine releasing neurons. This was precisely shown by Montaron et al. (1982): after bilateral VMT electrolytic lesions, attentive immobility was no longer observed, the control experimental situation now eliciting locomotor hyperactivity, the cat being unable to fixate its attention even on the mouse, and beta activity now being completely absent. Correspondingly, the same group (Montaron et al., 1984) could find, in the VMT of normal animals, units that briskly increased their firing rate (from ca 10/s to 50/s) just before the appearance of a cortical beta train and ceased their high rate around the end of the train. These data were strongly indicative that the VMT exerts a kind of "positive regulatory modulation" of focused attention and the accompanying beta thalamo-cortical system. Moreover a variety of complementary pharmacological observations confirmed that this VMT control was dopaminergic. From the literature, we knew however that the routes to the thalamocortical systems were complex and indirect. Among the likely intermediate structures, *nucleus accumbens* was a possible candidate (Sesack and Grace, 2010). Precisely, in 1986, Bouyer et al., found that its bilateral lesions also strongly perturbed the beta attentional system, but this time inducing perseveration in tests requiring focused attention, difficulty to shift to other targets, moderate hypokinesia, and a significant increase in beta rhythms. Later on Montaron and Fabre-Thorpe (1996) confirmed part of these latter results, but could notice that the cat's aptitude for visuo-motor activity was on the contrary improved. Taken together, these data tend to illustrate the complex modulatory role of *nucleus accumbens*, usually seen as an interface between limbic and motor structures, acting here not only on motor performance, but also on focused attention.

Obviously, many more investigations would have been necessary to understand all aspects of these complex controls, in view of the large amount of information now available on the aminergic modulations of attention. In particular, it is clear that the role of *locus coeruleus* has been amply documented mainly in rats and monkeys with other, more analytical approaches (Aston-Jonnes et al., 1999; Sara, 2009). The fact that loosing the noradrenergic control mainly exagerates the "waiting system", remains we think an interesting finding. This observation does not contradict the fact that "phasic activation of noradrenergic neurons of the *locus coeruleus* in time with cognitive shifts could permit rapid behavioral adaptation to changing environmental imperatives" (Bouret and Sara, 2005). It also remains to be determined to what extent the noradrenergic systems can play a role in some attentional clinical disorders (Biederman and Spencer, 1999). This precisely because the major clinical point concerning dopamine is its importance in the treatment of ADHD (attention-deficit hyperactivity disorder), mostly prominent in children. As yet the most efficient drug is Ritalin (Méthylphénidate) which is known to stimulate the dopaminergic system. It was therefore interesting to notice that our VMT-lesioned animals displayed a "sort of ADHD" syndrome. One should also retain some other data on the importance of the A10 dopaminergic cell group in cognitive functions in rats.

Discussion

In this long series of studies on the visually "attentive" cat, we did not initially concentrate our exploration on the visual pathways themselves, which are indeed involved in visual attention. Somewhat by chance, we selected behavioural situations which, as we now judge them, belonged in fact to classes of visuo-motor performances, probably combining a cognitive (visual perception) and a "volitional" ("active" immobility) component. It is perhaps to this choice of complex behavioural situations, but quasi-normal for a cat, that we owe most of our data. To terminate, let us briefly underline a few general points. From the beginning, we fundamentally believed that the chosen paradigms concerned states of "attention", but we soon felt that this option was refutable, since many psychologists would not accept our (disputable) tendency toward anthropomorphic judgment and terminology. We nevertheless persisted, this because years after years, our data showed relative coherence. Our most persistent problem was that the findings were mainly phenomenological and not really explanatory, showing correlations but no causal links (like so many other electrophysiological studies on brain mechanisms!), We did not suggest any mechanism or follow one of the attractive hypotheses about cortical processing based on the observed "synchronizations" of neuronal activities underlying the rhythms, often inspired by the Gestalt or similar classes of theories (Eckhorm et al., 1988; Engel et al., 1991a,b; Gray et al., 1989, 1992; Fregnac et al., 1994; Tallon-Baudry and Bertrand, 1999; and many others). We did not at all refute these views, that might have benefitted our results but we did on purpose not go beyond correlations. Our only tentative in this line was to search for coherences between rhythms simultaneously developing in different cortical areas, in order to detect possible signs of interareal interactions, so often postulated by brain theorists. Our results were all negative. We can instead only report one interesting observation, namely that when comparing (at an adequate recording speed) the instants of onset of a given beta rhythmic episode, "simultaneously" occurring on the posterior parietal, the motor cortex and eventually the visual cortex, there always existed a slight but significant precession of the parietal over the two other cortical trains. This observation could well be in accordance with the often claimed parietal dominant command in visuo-motor performances (Edelman and Mountcastle, 1982; Corbetta, 1998; Shuman et al., 2002). Finally, at the time when we were obliged to interrupt our experimental work, we were perfectly aware that our findings were immensely incomplete!

Summary

This paper summarizes studies performed on alert cats placed in conditions prompting two possible types of immobile attentive behaviour to the surrounding space, either expecting a visible event to occur, or displaying focused attention upon a visible target. Two distinct classes of electro-cortical rhythmic activities were thus identified, depending on the situation, low frequency (10-14 Hz) "mu" rhythms

on the somatic cortex and "alpha" rhythms on visual areas during expectancy and much faster rhythms (about 25-40 Hz), that we designated beta, during focused attention, mainly on the posterior parietal and motor and visual cortices. Two different thalamic sites were then isolated corresponding to two classes of rhythms (*nucleus ventralis posterior* for somatic mus, *nucleus postero-medialis* for parietal beta). Deep aminergic modulatory (noradrenergic and dopaminergic) systems were also identified, acting on both behaviour and concomitant rhythms Another class of attention was also described, namely attentional shifts, accompanied by short bursts of "very-fast" rhythms around and even above 100 Hz. Our discussion critically examines some of these data in the light of other group's findings and hypotheses**.**

This paper was written in honour of Professor Moruzzi. We admired his scientific intuition, his wide expertise and his sheer humanity.

Notes

[1] All our cats were housed, manipulated and operated (for implantations as well as for unit explorations) in accordance with the international directives concerning the preparation and maintenance of higher mammals during neurophysiological experiments.

[2] The nomenclature has been subject to discussions, in the later period, when other "fast rhythms " were also recorded in animals in the visual areas in fairly distinct conditions and designated "gamma" (Engel et al., 1989). See also discussion.

[3] Stereotaxy was achieved through fixation holes managed in the plastic electrode head holder. Of course no ear-bars were used.

[4] N-(2-chloroethyl)-N-ethyl-2-bromobenzylamine (DSP4), a neurotoxic agent known to destroy noradrenergic endings in the CNS. The administration dose was 10mg/kg i.p.

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References

Aston-Jones G., Rajkowski J., Cohen J. Role of locus coeruleus in attention and behavioral flexibility. *Biol. Psychiatry*, **46**: 1309-1320, 1999.

Avendaño C., Russell E., Reinoso-Suarez F. Thalamic projections to areas 5a and 5b of the parietal cortex in the cat: a retrograde horseradish peroxydase study. *J. Neurophys.*, **5**: 1446-1470, 1985.

Biederman J. and Spencer T. Attention-deficit/hyperactivity disorder (ADHD) as a noradrenergic disorder. *Biol. Psychiatry*, **46**: 1234-1242, 1999.

Bouret S. and Sara S.J. Network reset: a simplified overarching theory of locus coeruleus noradrenaline function. *Trends Neurosci.*, **28**: 574-582, 2005.

Bouyer J.J., Montaron M.F., Fabre-Thorpe M., Rougeul A. Compulsive attentive behavior after lesion of the ventral striatum in the cat: a behavioral and electrophysiological study. *Exp. Neurol.*, **92**: 698-712, 1986.

Bouyer J.J., Rougeul A., Buser P. Somatosensory rhythms in the awake cat: a single unit exploration of their thalamic concomitant in nucleus ventralis posterior and vicinity. *Arch. Ital. Biol.*, **120**: 95-110, 1982.

Bouyer J.J., Montaron M.F., Rougeul A. Fast fronto-parietal rhythms during combined focused attentive behaviour and immobility in cat: cortical and thalamic localizations. *Electroenceph. Clin. Neurophys.*, **51**: 244-252, 1981.

Buser P. and Rougeul-Buser A. Visual attention in behaving cats: Attention shifts and sustained attention episodes are accompanied by distinct electrocortical activities. *Behav. Brain Res.*, **164**: 42-55, 2005.

Canu M.H. and Rougeul A. Nucleus reticularis thalami participates in sleep spindles, not in beta rhythms concomitant with attention in cat. *C.R. Acad. Sci. Serie III, Sciences de la vie*, **315**: 513-520, 1992.

Canu M.H., Buser P., Rougeul A. Relationship between posterior thalamic nucleus unita activity and parietal cortical rhythms (beta) in the waking cat. *Neuroscience*, **60**: 679-88, 1994.

Castelo-Branco M., Neuenschwander S., Singer W. Synchronization of visual responses between the cortex, lateral geniculate nucleus and retina in the anesthetised cat. *J. Neurosci.*, **18**: 6395-6410, 1998.

Chatila M., Milleret C., Buser P., Rougeul A. A 10 Hz "Alpha-like" rhythm in the visual cortex of the waking cat. *Electroenceph. Clin. Neurophysiol.*, **83**: 217-222, 1992.

Chatila M., Milleret C., Rougeul A., Buser P. Alpha rhythm in the cat thalamus. *C.R. Acad. Sci. Paris. Serie III, Sciences de la vie*, **316**: 51-58, 1993.

Chatrian G., Petersen M., Lazarte J. The blocking of the rolandic "wicket" rhythm and some central changes related to movement. *Electroenceph. Clin. Neurophysiol.*, **11**: 497-510, 1959.

Corbetta M. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent or overlapping neural systems ? *Proc. Natl. Acad. Sci. USA*, **95**: 831-838, 1998.

Delagrange P. Unit activity of neurons of the posterior ventral nucleus of the thalamus for various waking stages in the normal cat. *C.R. Acad. Sci. III*, **305**: 149-155, 1987.

Delagrange P., Tadjer D., Bouyer J.J., Rougeul A., Conrath M. Effect of DSP4, a neurotoxic agent, on attentive behaviour and related electrocortical activity in cat. *Behav. Brain Res.*, **33**: 33-43, 1989.

Delagrange P., Canu M.H., Rougeul A., Buser P., Bouyer J.J. Effects of locus coeruleus lesions on vigilance and attentive behaviour in cat. *Behav. Brain Res.*, **53**: 155-165, 1993.

Eckhorn R., Bauer R., Jordan W., Brosch M., Kruse W., Munk M., Reitboek H.J. Coherent oscillations: a mechanism of feature linking In the visual cortex. *Biol. Cybernet.*, **60**: 121-130, 1988.

Edelman G.M. and Mountcastle V.B. *Mindful Brain*. Cambridge, MA, MIT Press, 1982.

Engel A.K., König P., Gray C.M., Singer W. Stimulus-dependent neuronal oscillations in the cat visual cortex: intercolumnar interaction as determined by cross-correlation analysis. *Eur. J. Neurosci.*, **2**: 588-606, 1991a.

Engel A.K., Kreiter A.K., König P., Singer W. Synchronization of oscillatory neuronal responses between striate and extrastriate visual cortical areas in the cat. *Proc. Natl. Acad. Sci. USA*, **88**: 6048-6052, 1991b.

Frégnac Y., Bringuier V., Baranyi A. Oscillatory neuronal activity in visual cortex: a critical evaluation. In: Buzsaki et al. (Eds.) *Temporal coding in the brain*, Berlin, Springer Vg, 81-102, 1994.

Gastaut H. Etude électrocorticographique de la réactivité des rythmes rolandiques. *Rev. Neurol. (Paris)*, **87**: 176-182, 1952.

Gray C.M., König P., Engel A. Singer W. Oscillatory responses in cat visual cortex exhibit intercolumnar synchronization which reflects global stimulus properties. *Nature*, **338**: 334-337, 1989.

Gray C.M., Engel A., König P., Singer W. Synchronization of oscillatory neuronal responses in cat striate cortex: temporal properties. *Vis. Neurosci.*, **8**: 337-347, 1992.

Jasper H.H. and Penfield W. Electrocorticograms in man: effect of voluntary movement upon the electrical activity of the precentral gyrus. *Arch. Psych. Nervenkr.*, **182**: 162-174, 1949.

Montaron M.F., Bouyer J.J., Rougeul A., Buser P. Ventral mesencephalic tegmentum (VMT) controls electrocortical beta rhythms and associated attentive behaviour in the cat. *Behav. Brain Res.*, **6**: 1209-1145, 1982.

Montaron M.F., Bouyer J.J., Rougeul A., Buser P. Activité unitaire dans l'aire tegmentale ventrale et état d'attention focale chez le chat normal éveillé. *C.R. Acad. Sci. Paris III*, **298**: 229-236, 1984.

Montaron M.F. and Fabre-Thorpe M. Effect of lesioning the nucleus accumbens on attentive preparation and performance of a reaching movement in the cat. *Behav. Brain Res.*, **79**: 31-40, 1996.

Munk M.H. and Neuenschwander S. High-frequency oscillations (20-130 Hz) and their role in visual processing. *J. Clin. Neurophysiol.*, **17**: 341-360, 2000.

Pfurtscheller G., Neuper C., Kalcher J. 40-Hz oscillations during motor behavior in man. *Neurosci. Lett.*, **164**: 179-182, 1993.

Pfurtscheller G. and Neuper C. Event-related synchronization of mu rhythm in the EEG over the cortical hand area in man. *Neurosci. Lett.*, **174**: 93-96, 1994.

Rougeul-Buser A., Bouyer J.J., Montaron M.F., Buser P. Patterns of activities in the ventro-basal thalamus and somatic cortex S1 during behavioral immobility in the awake cat: focal waking rhythms. *Exp. Brain Res.*, suppl **7**: 67-87, 1983.

Sara S.J. The locus coeruleus and noradrenergic modulation of cognition. *Nat. Rev. Neurosci.*, **10**: 211-223, 2009.

Sesack S.R. and Grace Cortico A.A. Basal ganglia reward network: microcircuitry. *Neuropsychopharmacology*, **35**: 27-47, 2010.

Shuman G.L., d'Avossa G., Tansy A., Corbetta M. Two attentional processes in the parietal lobe. *Cereb. Cortex*, **12**: 1124-1131, 2002.

Simon H., Scatton B., Le Moal M. Dopaminergic A10 neurons are involved in cognitive functions. *Nature*, **286**: 150-151, 1980.

Tallon-Baudry C. and Bertrand O. Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn. Sci.*, **3**: 151-182, 1999.

Wrŏbel A., Bekisz M., Kublik E., Waleszczyk W. 20 Hz bursting beta activity in the cortico-thalamic system of visually attending cats. *Acta Neurobiol. Exp.*, **54**: 95-107, 1994.