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The concept of Consciousness at the Laurentides meeting in 1953

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ABSTRACT

The "Laurentian symposium" organised by Dr. J.F. Delafresnay in 23-28 August 1953 gathered twenty outstanding participants together. The main topic of the meeting was to demonstrate that recent physiological data on the reticular formation (RF) opened new fields of research related to the study of "consciousness".

The lecture by Magoun and Moruzzi presented cortical arousal due to RF. They explained that a lesion in RF induced a comatose state. The neurosurgeon W. Penfield summarized the results accumulated with brain surgeries. He explained any portion of the cerebral cortex may be removed without producing unconsciousness. By contrast, any injury of the brain stem induced a state of unconsciousness. However, the psychologists of the meeting, Hebb and Lashley did not understand the interest of physiologists for the concept of consciousness, they considered not well defined and mostly discussed by philosophers.

It seems obvious that, after 1980 and today, the concept of consciousness is a key problem in neuroscience. It is now discussed regularly by neuroscientists. Although very incomplete approaches were available, due to technical limitations, the Laurentides meeting appeared quite crucial and the first, following behaviorism, to consider consciousness as a scientific enquiry.

Key words

Consciousness • Reticular formation (FR) • Centrencephalon • Arousal • EEGs recordings • Non specific thalamic projections

Introduction

Promoted by the Council for International Organisations of Medical Sciences, the Laurentides meeting organised in 1953, August, 23rd-28th, corresponded to the third international congress on EEG and to the nineteenth International Physiological Congress. It was proposed at the Unesco House in Paris by Dr. J.F. Delafresnay, by Henri Gastaut (1915-1995) and mainly by Herbert Henri Jasper (1906-1999). It aimed to show the new field of enquiry opened by the recent works on the reticular formation (RF). As Jasper wrote in his introduction: "Discovery of the remarkable functional properties of the extensive core of grey matter lying adjacent to the principal afferent and efferent pathways in the brain stem and diencephalon has stimulated new conceptions of the integrative action of the brain as a whole".

Giuseppe Moruzzi (1910-1986) whom we honour today, played a key role in the exploration of RF. He visited the laboratory of Horace Winchell Magoun (1907-1991) after the war. At that time, several experiments demonstrated that the stimulation of the central core of RF, at different levels from the medulla oblongata to the thalamus, controlled both the cortical as well as the spinal parts, through facilitatory and inhibitory pathways (Morison and

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Dempsey, 1942). Magoun and Rhines (1946) have described an inhibitory control of the spinal muscular tone by the reticular formation in the bulbar region, suppressed when the brain stem is sectioned. Along with Magoun, Moruzzi found, in a narcosed cat or in the "*encéphale isolé*" of Frederic Bremer (1892-1982, see Bremer, 1935), that a 300 Hz stimulation of the mesencephalic RF induced an arousal reaction defined by an EEG, with rapid waves and a cessation of the alpha rhythm (Moruzzi and Magoun, 1949). Such a discovery changed how the central nervous system (CNS) was viewed. Several meetings have given a great emphasis to this peculiar part of the nervous system. In opposition to the main nervous pathways involved in sensory and motor functions, this central structure was the object of considerable speculations and hypotheses. This explains the subject of the Laurentides meeting.

The "Laurentian symposium" gathered only twenty participants together, Magoun and Moruzzi of course, Jasper, Gastaut and Bremer, already mentioned, but also two Nobel Prizes, Edgar D. Adrian (1889-1977) and Walter R. Hess (1881-1973), as well as the best scientists working on issues dealing with the cortex, Wilder Penfield (1891-1976) Alfred Fessard (1900-1980), Donald O. Hebb (1904-1985), Karl S. Lashley (1890-1958), W.J.H. Nauta (1916-1994), R. Jung (1911-1986), William Grey Walter (1910-1977) or Mary A.B. Brazier (1904-1995) (see Fig. 1).

Fig. 1. - Photo of the Laurentides meeting with the main participants (in Meulders et al., 2010). First row (from left to right): Karl Lashley, Wilder Penfield, Edgar Adrian, Mary Brazier, Herbert Jasper, Frederic Bremer, Horace Magoun and Green. Second row: Henri Gastaut… Alfred Fessard… Jerzy Olszewski, William Grey Walter, Richard Jung, Donald Hebb. Last row: Ajmone-Marsan, Livingston, Giuseppe Moruzzi… Walle Nauta, Pierre Buser, J.F. Delafresnaye…

The papers of the neurophysiologists were written in advance and they were circulated between all members of the symposium. This organisation of the meeting was unusual, with very few participants and the technical assistance taken in charge by young scientists. For example, Drs Green, Livingston, Courtois and Ajmone-Marsan noted discussions and transcribed them, also compiling the index. Dr. Ingvar was the projectionist. Dr. Buser who supervised the discussion, mentioned in his autobiography (Buser, 2001) that when he came to the US. to work in the laboratory of Magoun, he was invited at that meeting: "The climax of this first New World experience occured when I was lucky enough […] to be invited to attend the symposium […] I discovered many of the key players in the new push given to studies on the mammalian brain […] I remember this meeting as one of the most illuminating events in my scientific life".

Discussions were favoured, many questions were asked after each talk and the general discussion was quite long, covering thirty-four pages of the book published later (Delafresnaye, 1956 [first publication 1954]). The concept of consciousness was chosen for the subject of the meeting, but appeared a difficult term to use for several participants. According to them, consciousness had several meanings and if the term were associated with arousal in opposition to sleep, it could be associated with very complex psychical functions and appeared too vague to some scientists. The fact that the term was employed in the heading of the meeting demonstrated that the results obtained with RF had changed some common ideas. Today the concept of "consciousness" is very popular and extensively studied in neuroscience. At the Laurentides meeting, it was the first time that physiologists discussed this concept officially. Only philosophers and psychologists had used it before. Historically such meeting represents a new trend of research, and in the same time, it corresponds to the end of behaviorism (Watson, 1913) where the brain was described as a black box.

In this article, we will only present the talks directly dealing with the concept of consciousness. Hence, we will not focus on the majority of the presentations, although of great interest, like those of Fessard on "nervous integration", Bremer or Hess on sleep, or Gastaut or Grey Walter on EEG recordings.

Anatomy and physiology of the reticular formation (RF)

Usually, anatomical studies of a CNS region is done before physiological experiments. For RF, it was not the case. Cajal mentionned the specific central region of RF and named it "*région de la calotte*" corresponding to an intermediate stage of the brain stem (Ramon y Cajal, 1972). He described the extensive multiple branchings of its neurons, as they ascended and descended through the middle of the brain stem. However, he did not characterize the different parts of the RF. As W.J.H. Nauta wrote, the anatomy of RF was just a starting point. In his lecture on anatomical studies, with D.G. Whitlock, he presented the connections in the cat between the "non-specific" thalamic projection system and cortical area. Thalamic lesions were done by focal coagulations and the animals was sacrificed after 7 days. The study of the degenerations were done with serial sections and a histological technique derived from Bielschowsky.

Jerzy Olszewski presented the anatomy of the medulla, pons and midbrain of the human RF. However his first remarks concerned his disagreement with the term RF: "1. Anatomically the RF is a poorly defined structure. 2. The anatomical and physiological conceptions of RF do not correspond with each other. 3. The RF is not a morphological unit, but is composed of many nuclei of very different structures". In the lower brain stem, Olszewski was able to identify ninety-eight nuclei. He delineated particularly well forty-eight and he described only twenty nuclei. He explained the evolution of the cytoarchitecture by serial sections stained with the Nissl method.

Today, we know anatomists could not understand the anatomy of this region corresponding to the locations of several neurotransmitter pathways. In this region, no more than ten years later, Falk and Hillarp (1916-1965) were able to visualize the functional map of different neurotransmitters (Falk et al., 1962).

The physiology of RF was first presented by Magoun who gaves a summary of the studies on the ascending system. In the rabbit, cat and monkey, he analysed different stimulations of the brain stem and of the non-specific thalamic nuclei inducing wakefulness with a desynchronisation of the EEG. He compared the RF cortical responses with those obtained by a stimulation of a given sensory afferent. He described the ascending reticular activating

system in the brain stem that received collaterals from afferent paths and projects to the associational areas of the hemisphere.

After such experiments, nervous ablations were conducted in these same regions. The effect was spectacular: a lesion in the brain stem induced a comatose state (French and Magoun, 1952). In these cases, the EEG were chronically hypersynchronous and did not induce a response of a peripheral stimulus. Magoun discussed the possible role of RF in filtering sensory afferents. He also discussed if the anaesthetic agents were acting in priority at the level of the RF. After his talk, he had several questions on the different parameters of stimulations necessary to induce cortical arousal, with a comparison between the diffuse thalamic stimulations and those from the brain stem.

The presentation of Moruzzi also devoted to the RF brain stem was quite impressive. In his experiments, he recorded RF single units and analysed their discharges in relation with the activity of others CNS structures. He studied their physiological properties using floating nichrom or stainless steel microelectrodes in (12 and 37 μm). He used a decerebrate cat to see the effect of RF actions on the spinal cord or the *encéphale isolé* from Bremer (1935), to analyse the relations with cortex. Microelectrode stimulations of the medio-ventral bulbo-reticular formation in the decerebrate cat inhibit the decerebrate rigidity ipsilateraly and increases it contralaterally. RF units can have different spontaneous patterns, a low frequency discharge (down to 2-5/s), a continuous high frequency discharge (50-100/s) and show bursts of one second above a background of low frequency discharges.

These units of the medio-ventral RF are part of the inhibitory control of postural tonus. They are in close relation with the cerebellum. "Surface positive polarization of the anterior lobe has a striking effect on the spike discharge of the medial bulboreticular neurones". Cerebellar polarization induced a generalized EEG arousal in the "*encéphale isolé*" preparation. In order to see the connections between bulbar RF and the cortex, the motor cortex was strychninized. When single electrical shocks were applied to the motor cortex, both facilitation and inhibition were obtained in the discharges of the different RF units. The stimulation of the cerebellum inhibited units of the bulbo reticular region. These different effects were abolished by midbrain lesions destroying the RF.

Moruzzi compared cortical wakefulness induced by RF stimulation or by sensory stimulation. He found that both responses were very similar. He confirmed the role of filter played by bulbar RF. Often a spontaneous discharge of a bulbo-reticular unit is increased by sensory volleys and inhibited by cerebellar polarization. These experiments showed that the lower RF was correlated with the arousal reaction and with the maintenance of wakefulness. These two presentations synthesized results on the RF arousal and its relation with consciousness, giving the planning and the general framework of the meeting.

The centrencephalon: neural basis of consciousness

Neurosurgeon Penfield firmly stated that RF is the locus of consciousness. For him, this idea emerged from his observations during brain surgeries and after the discussions he had with his patients under surgery. He used them as very useful experimenters, asking them questions during different types of electrical stimulations of different cortical areas. He explained: "When a motor area of the cortex is stimulated, conscious patients do not believe that they have willed action. They recognize invariably that movement occurs independent of, or in spite of, their own volition". Penfield remarked more importantly: "Any portion of the cerebral cortex may be removed without producing unconsciousness. On the other hand, injury to the brain stem does result in unconsciousness and epileptic seizures produced by discharge in certain parts of the brain stem are characterized by invariable loss of consciousness […] the indispensable substratum of consciousness lies outside the cerebral cortex and probably in the diencephalons […]".

The crucial region was located "in the intralaminar systems of the thalamus, the reticular formation of the brain stem and the non-specific projection systems which have widespread connections with the cortex of both sides […]". Such connection between cortex and brain stem defined the centrencephalic system. The temporal lobe has a particular role essential in memory and in the processus of consciousness that he summarized as follow: "The hypothesis is suggested that sensory information is integrated within the centrencephalic system. A selected portion of this information is then somehow

projected outwards to the temporal cortex by that portion of the system which is in functional connection with the temporal cortex of both sides. As it is thus projected, a comparison is made with past similar experiences, thanks to the records of the past that are held there, and judgement with regard to familiarity and significance is made". He proposed that the centrencephalic system favours a close coordination between both hemispheres. This implies that "there is evidence that one temporal lobe is to speak the carbon copy of the other".

In his talk, Jasper reviewed some studies trying to explain functional properties of the thalamic reticular system comparing at the cortical level, the action of the ascending sensory system with thalamic RF stimulation. First, he dissociated the specific and unspecific thalamic projections. Referring to Lorente de No (1943) and to Chang (1952), he proposed that axo-dendritic synapses from the unspecific afferent fibres must have different functions in the cortex than the axo-somatic synapses originated from specific afferents. Then Jasper studied the form and the distribution of electrical responses at different depths of sensory motor cortex in the cat while stimulating specific or unspecific thalamic nuclei. The unspecific system has a different synaptic distributions through the cortex and a close relationship with the spontaneous rhythms, such as the alpha rhythm.

Jasper found that the central thalamo-cortical system is much more elaborated than it was thought: "Finally, our observations upon the finer structure of both the descending and ascending reticular systems in diencephalon and brain stem have convinced us that it is highly organized system whose function is not adequately described as simple overall inhibition and facilitation, or general awakening or arousal of the nervous system as a whole, though this is one aspect of its mass action". The discussion mainly concerned the details of the unspecific thalamocortical projection system.

Oppositions to consciousness at the Laurentides meeting and general discussion

Three eminent scientists appeared in opposition to such an hypothesis, Adrian, Lashley and Hebb. If Adrian hesitated in linking RF with consciousness, the situation of the two psychologists of the meeting was clearly against that concept. Hebb started his contribution with this remark: "It has not been easy to see what, exactly, should be my task in this symposium", and later: "I propose to you accordingly that the existence of something called consciousness is a venerable hypothesis: not a datum, not directly observable, but an inference from other facts. I propose that your conviction that you are aware of your are awareness […] may be illusion […]". The style is not only virulent, but ironical! He then considered that an analysis of behaviour could be useful for the "curious" proposal of the conference! He explained his interest of behavioural concepts concrete and precise: "I would like to make it clear that I am not saying that consciousness is behaviour. I am only saying that behaviour is our main source of information. Because processes that go on in the cerebrum may cause movement does not mean that they always cause movements which are observable. Consciousness is a complex inference from what movement is eventually observed, of the speech organs or otherwise".

He discussed the evolution of consciousness along the evolutionary scale and considered consciousness as the higher state of behaviour. He dissociated a series of stimulus-responses with central actions facilitated both sensorily and centrally. He considered "thought" to be composed of an internal stream facilitated by series of sensory informations. Later, Hebb discussed the importance and the role of speech, and he defined "intelligence".

In the general discussion, he confirmed his great difficulty in understanding the role of centrencephalon: "Dr. Penfield stressed earlier that we should think of consciousness as a function. I would think that we must be relatively modest in our attempts to attack the problem. We should not try to devise a theory that will be completely adequate to account for all of what we know, feel, and do. We should try to account for those aspects of the problem we might have some chance of accounting for […]". For Hebb, this question was not only without interest, but it could not lead to any real and serious explanation of biological functioning.

Famous psychologist and behaviourist, Lashley, proposed to talk about brain mechanisms and dynamical processes involved in perception. He was quite surprised that physiologists were interested in consciousness, while psychologists refused to analyze

such concept: "What role if any can the reticular system play in these complicated dynamic functions of perception?", and later, "it seems to me that a system, as diffuse and poorly organized for limited, patterned activity as the reticular system appears to be, is unlikely to contribute anything more than a general, undifferientiated facilitation in these processes".
He even asked the question about the real role of the centrencephalic system. Why such an interest? He stated: "I conceive of the cortex itself, primarily as a continuous network, and except in its extent, I see no fundamental difference in constitution between the cortex as a whole and the centrencephalic system as a whole. They both are networks of cells within which patterns of activity can spread. I see no advantage in ascribing to the more limited system functions which seem to be at the highest level of complexity of which the brain is capable". Lashley insisted on considering the brain stem structures to be less important to elaborate complexities: "Further, the evidence for this centrencephalic system seems to point to a diffuse function. It is the pattern of neural activity which is the determining thing in producing behaviour or conscious state".
Lashley ends his contribution on the dynamic processes in perception: "the reticular system may contribute to the general level of activity of cerebral fields, but there is no evidence that it exerts a such localized and selective function as appears in the dominance of specific perceptual processes, nor does it provide the structural diversity necessary for such control".

The last part of the meeting was devoted to the general discussion directed by Jasper. Each participant now had a clear opinion. The divergent positions even obviously expressed a certain effort to find a synthetic position through a compromise:
Penfield concluded his comments by insisting on the interest of the concept: "Consciousness exists because of neuronal activity, and as the accompaniment of that activity, the pattern of which must be ever various. It is misleading to say that its seat is here or that it is there. But I suspect that one essential feature in all awareness is a centrencephalo-temporal back-and-forth passage of nerve impulses".
Jasper presented a diagram to illustrate a summary of experimental findings of thalamocortical and cortico-thalamic relationships. It explained the particular projections which may act independently of one another. An elaborative system seem to exist, composed of the sensory and the para-sensory system with their projections to portions of the brain stem RF. Gastaut proposed another diagram, that he used in teaching for his students, with thalamo-cortical connections on the diffuse cortical projections.
Perhaps the scientific conclusion was in the following sentence of Jung, when he said: "Consciousness represents certainly some selective process. It uses only integrated and simplified results which are worked out at lower levels. Only the end-results seem to come to consciousness. Everything else is preliminary. What we investigate as neurophysiologists are these preliminaries. Who 'reads' the 'Whole' as Dr Adrian says, nobody knows [...]".
Jasper closed the discussion encouraging the participants to continue by their future works the new proposal they have discussed: "Just what comes of this meeting depends upon us in our future work and upon the influence we may have upon the young men working with us".
The following years have firmly established the RF structuration (Rossi and Zanchetti, 1957; Moruzzi et al., 1963).

Consciousness and neuroscience: 50 years of discussions

We are now more than fifty years later, and ideas have changed. A new synthetic discipline has emerged from the various disciplines studying the brain. Neuroscience started around the sixties. At the Laurentides meeting, behaviorist Lashley considered the concept of consciousness strange, "bizarre", but mainly "over". He was wrong. Not only the subject never has been abandoned, but around the eighties it became a respectable and legitimate subject! The development of cognitive sciences and theoretical approaches on network functioning have led to a materialist analysis of the concept. We will here select some works demonstrating the actual interest in this concept.
American philosopher John Roger Searle (2000), in complete opposition to behaviorism, tried to relate consciousness with intentionality. He considered consciousness is a real subjective experience, caused by physical processes of the states of the brain. D. Dennett (1991) defined "qualia" as corresponding

to integrative entities developed by each individual and related to his consciousness. This vision is also largely discussed by Llinas (2002). With their concept of dynamic core, Edelman and Tononi (2000) consider that the background of consciousness is due to the operations of complex networks involved in reentry processes. Antonio Damasio (2010) analyzing the "self", explained that it is a combination of emotions and feelings in close relations with cognitive processes, like sensory integration and decisions of actions. Consciousness is due to primitive action even in the low region of the brain. He spoke about the brain stem and mentioned the name of Penfield. However a question was raised in the 1980s by B. Libet (1916-2007), that has been quite controversial. In a pioneering experiment, he suggested that when a subject is doing a voluntary movement, 500 ms before an electrical event, a readiness potential is recorded in the cortex (Libet et al., 1983). It seemed then that decisions made by a subject are first being made at a subconscious level, and only after it becomes a conscious decision. With new brain scanning technology, Soon et al. (2008) confirmed that the delay of cortex response could reach 10 seconds before a subject is conscious of his decision. This suggested that most of the brain activities are unconscious (Haynes, 2009; Jeannerod, 2010). This explained why concepts presented by Sigmund Freud (1856-1939) are now re-analyzed by neuroscientists. Dehaene and Naccache (2001) by their brain imaging experiments on "unconsciousness" have given some important contributions to the subject.

If we want to refer to the functional anatomy presented in 1953 at the Laurentides with the role devoted to the centrencephalon, this idea is still valid. If the role of this unique structure was not confirmed with the experiments done on the split brain (Doty, 1975), the concept of a particular relation between thalamus and cortex has been favoured within recent works. In particular, the ionic activation of different thalamocortical waves has been studied by Steriade and his group (Bazhenov et al., 2002), and the hypothesis of consciousness as proposed by the group of Llinas, can be viewed in the straight line of the 1953 discussion (Llinas et al., 1998). In his hypothesis, consciousness is associated with some internal thalamo-cortical rhythms. Such activity is supported by resonance between thalamic and cortical structures at gamma band frequencies, often between 20 and 50 Hz (around 40 Hz). Llinas proposed that such activity is due to two neuronal systems. One is induced by specific sensory and motor nuclei that project to the layer IV of the cortex. Cortical oscillations are produced by direct activation and feedforward inhibition of particular 40 Hz inhibitory interneurons. These oscillations re-enter the thalamus through collaterals from layer VI pyramidal neurons that inhibited the thalamus via reticular nucleus. The second system involves the thalamus intralaminar non-specific nuclei, presented in great detail at the Laurentides. It projects to cortical layers I and VI and to other reticular nucleus. Pyramidal neurons of layer V returned the oscillation to the intralaminar nuclei and all the system oscillate at the gamma band frequency being capable of recursive activation. Such central vision of an oscillating coherent system linked with attention or learning or even with consciousness has been discussed by Singer (1993). The realization of the Laurentian symposium appeared as a pioneering initiative!

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