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Neurosciences

Time, from psychology to neurophysiology. A historical view

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Abstract

Two aspects of psychology and physiology of time are dealt with in this paper: the way time perception was increasingly studied during the 19th century by scientists, including many physicists, and the way the temporal properties of the nervous system were discovered and explored by physiologists. The neurophysiological correlation between both aspects still remains to be explained. The relationship between time consciousness and consciousness mechanisms was often guessed by philosophers and looked for by scientists. It remains a major subject of investigation in neuroscience as well as a philosophical puzzle. ***To cite this article: C. Debru, C. R. Biologies ••• (••••).***

Résumé

? ? ? Deux aspects de la psychologie et de la physiologie du temps sont décrits ici : la manière dont la perception du temps fut de plus en plus étudiée au cours du XIX^{e} siècle par les scientifiques, y compris de nombreux physiciens, et la manière dont les propriétés temporelles du système nerveux ont été découvertes et explorées par les physiologistes. La corrélation neurophysiologique entre les deux aspects reste à expliquer. La relation entre conscience du temps et mécanismes de la conscience, qui a été souvent soupçonnée par les philosophes et recherchée par les scientifiques, reste un sujet majeur en neurosciences aussi bien qu'une énigme philosophique. ***Pour citer cet article : C. Debru, C. R. Biologies ••• (••••).***

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1. Introduction: the Kantian background

In the *Critique of Pure Reason* (1781), Immanuel Kant conceived time as an a priori, intuitive form of human sensibility. Together with space, time was conceived as a special structure of the receptive, passive framework of human knowledge, and distinguished from the conceptual structure, which belongs to the human understanding, endowed with a spontaneous character. Space and time were conceived as subjective properties, a precondition for many later scientific developments in psychology and physiology, which Kant himself could foresee and tried to prevent. Indeed, in the Introduction of the *First Metaphysical Principles of Natural Science* (1786), Kant argues that no empirical theory of the soul can receive the status and rank of a

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true science, because a true science has a mathematical character which in the particular case of psychology could apply only to a very limited extent. Indeed, mathematics in psychology could not go much farther than the statement of the continuity principle.

2. Herbart's mathematical psychology

Kant's idea of science as a necessarily mathematical knowledge created an obstacle for the development of scientific psychology, which began to be overcome when Johann Friedrich Herbart developed the idea of psychology as a science founded on experience, on metaphysics and on mathematics (*Psychologie als Wissenschaft, neu gegründet auf Erfahrung, Metaphysik und Mathematik*, 1824–1825). Psychology in Herbart's sense is essentially a mechanics (statics and dynamics) of representations. Herbart named inhibition (*Hemmung*) the effect of the arrival of new representations on preexisting ones in consciousness. He defined space and time as notions of series, which paved the way for a mathematical psychology. In this respect, he paid attention to the problem of determining precisely the amount of time that may be grasped immediately by the mind and may thus be considered as a kind of psychological unit. In order to determine this amount of time, Herbart relied on musical phenomena. He reflected on the way the duration of a musical pause is estimated, and tried to solve this problem by considering what happens in the mind during a pause. In the absence of any new musical stimulus, the representation of the preexisting stimulus keeps going for a certain time while other kinds of representations occupy the mind. There exists a kind of equilibrium between all these different representations that, according to Herbart, is typical of the mind's representative activity during the pause. Now Herbart asks a profound question: how is the constancy of time measurement in thought produced? The answer is given by taking into account the intensity variation of the representations in time, which is supposed to correspond to the inhibition phenomenon as a function of time. As a consequence, the intensity variation follows an exponential decrease. Indeed, according to Herbart, the quantity of inhibition must increase with time, in order to make the amount of time, be it greater or smaller, noticeable. The quantity of inhibition is the key factor in time perception. By reasoning on the exponential term, Herbart, in 1839, is able to give an estimate of the amount of time that is most conveniently perceived in consciousness: two seconds [1]. This order of magnitude corresponds in a very rough way to later estimates of the so-called 'specious present' especially dealt with by William James in his *Principles of Psychology* (1890). The kind of mathematical speculations developed by Herbart regarding the psychology of time is typical of his combination of mathematics, metaphysics, and common experience.

3. Time as a psychophysiological subject

In 1850, Hermann von Helmholtz measured the transmission velocity of the impulse in the nerve, a measurement that his master, the physiologist Johannes Müller, considered as impossible. As a consequence, all speculations regarding the simultaneous character of stimulation and conscious experience were discarded, and an entirely new field was opened for various kinds of experiments, some of which were conducted by Helmholtz himself. Relating the temporal aspects of conscious experience to the temporal properties of nervous impulses became a subject which was part of the new research program in psychophysics and psychophysiology carried out by many physicists, physicians and physiologists, such as Hermann Rudolf Lotze (*Medical Psychology or Physiology of the Soul, Medicinische Psychologie oder Physiologie der Seele*, 1852), Hermann von Helmholtz (*Handbook of Physiological Optics, Handbuch der physiologischen Optik*, 1856), Gustav Theodor Fechner (*Elements of Psychophysics, Elemente der Psychophysik*, 1860), Wilhelm Wundt (*Contributions to the Theory of Sense Perception, Beiträge zur Theorie der Sinneswahrnehmung*, 1862), Ernst Mach (*Lectures on Psychophysics*, *Vorträge über Psychophysik*, 1863), Hermann von Helmholtz (*The Sensations of Tone as Physiological Foundation for the Theory of Music*, *Die Tonempfindungen als physiologische Grundlage für die Theorie der Musik*, 1863), Adolf Höring (*Researches on the Sharpness of Hearing for the Quantities of Time*, *Versuche über das Unterscheidungsvermögen des Hörsinnes für die Zeitgrössen*, 1864), Ernst Mach (*Two Popular Lectures on Musical Acoustics*, *Zwei populäre Vorlesungen über musikalische Akustik*, 1865; *Introduction to Helmholtz's Theory of Music*, *Einleitung in die Helmholtz'sche Musiktheorie*, 1866), Wilhelm Camerer (*Researches on the Temporal Course of Voluntary Movement*, *Versuche über den zeitlichen Verlauf der Willensbewegung*, 1866), Karl Vierordt (*The Time-sense according to Research*, *Der Zeitsinn nach Versuchen*, 1868). To this impressive list, however, should be added the name of the first physiologist who spoke about time sense, Johann Czermak. Czermak, who held the chair of physiology at the University of Krakow, published in 1857 a paper in which he proposed the concept of this new sense, in addition to the sense of space already studied by Ernst Heinrich Weber. Czermak wanted to discover the physiological conditions of time perception. He planned to determine the smallest temporal interval that is perceived by the various senses (and may be different, depending on the particular sense), and also to study the perception of speed [2].

4. Fechner's psychophysics

The study of time and movement was dealt with in a small section of Gustav Theodor Fechner's *Elements of Psychophysics* in 1860 [3]. Fechner noticed that when two sensations follow each other too rapidly, they merge. He then asked the question of the length of the interval which is necessary for two sensations to be perceived separately. In order to understand the fusion phenomenon, he proposed that each sensation has a *Nachklang* or resonance. If the resonance of the first sensation is still strong enough when the second sensation arises, so that the differential threshold in intensity is not reached, both sensations merge. He then asks the question, whether this explanation is sufficient. In this discussion, he relies on a certain analogy with the sensation of space that was studied by Ernst Heinrich Weber in his pioneering experiments on the space sense of the skin, which is organised in circles of minimum diameter defining the spatial threshold and thus the subjective measurement of space. Fechner considers the possibility that the subjective measurement of time depends on internal 'psychophysical oscillations', in the same way as the subjective measurement of space depends on circles. The period of oscillation defines a threshold within which no time sensation occurs. Is it possible to find other arguments in favour of this hypothesis? Experiments on the intensity of visual sensations may give additional evidence. When white and black stimuli presented as sectors of a rotating disk follow each other more or less rapidly, this may create a uniform sensation if the differential threshold in intensity is not reached, or if the sensations of white and black follow each other rapidly. In connection with these phenomena, the question of the necessary time for a sensation to be perceived distinctly enough under different circumstances was asked. Experiments on the speed of reading texts printed in different sizes were performed. Experiments on the perception of the speed of astronomical movements (the speed of moving stars) were also performed. Indeed, since the work of Friedrich Wilhelm Bessel on personal equation in astronomical observations, astronomy was one of the main fields in which psychology and physiology (in this particular case the persistence of the visual sensation in the eye) could be relevant to physics. Generally speaking, the question of 'the time necessary for' a psychical experience to happen became a subject of many investigations.

5. Mach on time perception

From 1860 onwards, Ernst Mach tried to test the validity of the Weber–Fechner psychophysical law for time perception. In a paper on the time sense of the ear, in 1865, he was able to produce fundamental results [4]. He showed that time perception does not follow the psychophysical law and that the sense of hearing has the greatest temporal sharpness among all senses. The end of the paper is devoted to a far reaching philosophical discussion of the nature of time, which in Mach's view is nothing else than the 'presentability' (*Darstellbarkeit)* of all physical phenomena by each other. What Mach meant may be understood by considering the example of Foucault's pendulum: the rotation of its oscillation plane expresses the rotation of the earth, as mentioned later in Mach's *Mechanics*. In another paper on the space sense of the ear published in the same year 1865, Mach mentioned that the ear is capable of creating spatial representations. In 1875, he published a memoir on the sensations of movement, speed and acceleration (*Grundlinien der Lehre von den Bewegungsempfindungen*), in which he was able to prove the existence of a particular organ for equilibrium and movement in the inner ear, the semicircular organ. He showed also that the sensation of movement goes on when acceleration ceases, and that the sensation fades when acceleration keeps constant [5]. In about 15 years, Mach was able to carry out Czermak's research program. In the chapter on time sensations of his major work, *The Analysis of Sensations* (*Beiträge zur Analyse der Empfindungen*, 1886), Mach dealt with the theme of temporal errors, which had also been dealt with by other authors, including Wilhelm Wundt. Mach assumed that attention is unable to concentrate at the same time on two qualitatively different and simultaneous stimuli, with the consequence that one of them appears always later [6]. In 1872, Mach's collaborator V. Dvorak published the results of experiments in which two optical stimuli were delivered one after the other, to one eye and to the other one [7]. Under such circumstances, several kinds of spatial and temporal illusions could occur. A most remarkable result is the fact that successive stimuli may appear as simultaneous for a determined time interval of 1/8 to 1/6 s. The stimulus, which is attended to as the second one, appears thus as earlier. Mach himself did experiments on the time necessary for consciousness to go from one place to another. In *The Analysis of Sensation*, he mentions an experiment in which two red squares are successively attended to [8]. The second one, which is first seen in an indirect way, is seen as green, which means that it is seen by the attention as endowed with the complementary colour of the after-image, and thus, that the belated attentional process has already reached the stage of the positive after-image. To summarize, we have already dealt with several questions in Herbart's and Mach's works: the amount of time which is grasped by consciousness as a unity and as a convenient unit (the so-called 'specious present'), the differential temporal discrimination of the senses, the fact that the time sense does not obey the Weber–Fechner law, the perception of speed and acceleration, the role of the work of attention in temporal errors and the time of displacement of the attentional process.

6. Helmholtz and the psychophysiology of time

Hermann von Helmholtz's works on the velocity of the nervous impulse and on time perception are of a different branch, since they are of a more physiological character. His determination of the velocity of the nerve impulse in the frog had revolutionary consequences in physiology and psychology, since it implied that stimulation and perception were not simultaneous. In a lecture given in 1850 at the University of Königsberg, where he held a chair in physiology, Helmholtz made comments on the methods allowing one to make precise measurements of very small time intervals in order to study physiological phenomena, including sensations [9]. A major example of the kind of studies advocated by Helmholtz is given by the astronomer's personal equation, the variance in the judgement regarding simultaneity of different, auditory and visual stimuli, and its physiological basis. A simpler problem corresponds to successive stimuli of the same kind, impinging upon to the same nerve fibre. Below a certain time interval, two successive stimuli are judged as simultaneous. According to Helmholtz, about the same value of the threshold holds true for vision and audition: 1/10 s. In 1865, Mach will demonstrate the existence of different thresholds for these senses. Already in 1850, Helmholtz had perceived all experimental possibilities that were offered by his discovery of the conduction velocity in nerve fibres. Many of the major types of experiments and experimental paradigms that would be carried out later by him or by other experimentalists like Mach were described in this text, including the study of the time necessary for a conscious experience to develop. Thanks to an electromechanical device developed by Werner Siemens for artillery and telegraph, the measurement of very small time intervals of the order of several milliseconds could be performed. At that time, as shown by Frederick L. Holmes who studied Helmholtz's archives at the Berlin–Brandenburg Academy of Sciences, Helmholtz was also conceiving the project of studying the velocity of the nervous impulse on man, not only on frogs [10]. However, it was only in 1867 that he could start working on this subject, together with his Russian collaborator Nicolas Baxt. Two papers were published in 1867 and 1870, in which the results of measurements on man were given. The next obvious step was to establish the time necessary for a conscious experience to develop. An important paper on the time necessary for a visual impression to reach consciousness was published in 1871 by both authors [11]. The Helmholtz–Baxt experiments were based on the phenomenon of after-images, which allowed them to discuss the time-course of the conscious recognition of a stimulus after its cessation. They used rotating disks with open slots to create a visual stimulus of very short duration, followed by the appearance of an after-image on the retina. The after-image could be extinguished after a variable duration by a second, superimposed visual stimulus. The minimal value obtained by Helmholtz and Baxt for visual recognition to occur was 30 ms. Nicolas Baxt went on refining the same experimental procedure and published an additional paper on this subject, taking into account the time necessary for the extinction stimulus to reach consciousness. Baxt was able to demonstrate a relationship between the recognition time and the size and complexity of the stimulus (the number of recognizable objects it contains) [12]. Helmholtz used also the same experimental procedure to study attention. He was able to show that attention may be directed towards a point in visual space which is different from the fixation point of gaze.

7. Speculations regarding a possible frequency coding

This extraordinary burgeoning of experimental studies in physiology went with highly speculative and far-seeing developments. In his *Elements of Physiological Psychology* (*Grundzüge der physiologischen Psychologie*, 1880) Wilhelm Wundt held the view that perception is a discontinuous phenomenon, because of the fact that, when different stimuli are not simultaneously perceived, they tend to separate [13]. This same issue of discontinuity in perception arose more recently in the work of Ernst Pöppel. Much earlier than Wundt, Gustav Theodor Fechner [14a] and Hermann Rudolf

Lotze [14b] did not hesitate to formulate an important psychophysiological hypothesis on purely conceptual, philosophical and even metaphysical foundations. They shared the same kind of reasoning and held similar views on the nature of the transformation of a physical into a psychical process. According to the philosophical tradition, the soul is no extended being. Thus the only kind of magnitude that can be ascribed to it is an intensive one, which refers to the scholastic concept of the difference between extensive and intensive magnitudes, the former ones being additive, which is not the case for the latter. These metaphysical concepts were put in the context of physics and physiology in the eighteenth fifties and sixties, and used in the following way. The perceiving soul can only grasp the intensive aspects of the nervous, physical process that affects it. The nerve impulses may be considered to consist, by their succession, in an oscillatory process. One of the most striking features of this process is its frequency. Thus Fechner and Lotze agree on the fact that the soul perceives the frequency of the nerve impulses [14]. This metaphysical argument can be compared with the discovery by Edgar Douglas Adrian in 1926 of the fact that the varying intensity of a stimulus is transformed into a varying frequency of the nerve discharges [15]. To fully understand this latter point, we have to go from the German-speaking world to Great Britain. As a matter of fact, transfers of knowledge and expertise between the two scientific worlds did exist. For instance, Charles Sherrington visited Friedrich Leopold Goltz's laboratory in Strasbourg in 1884–1885 to study experimental neurology before going back to England.

8. James' correlation between neurosis and psychosis and the continuity of consciousness

The German-speaking and the English-speaking world had a common advocate, William James. In his *Principles of Psychology*, James raised some questions, which are still not answered in contemporary neuroscience, among which the question "to what cerebral process is the sense of time due?" is especially relevant to the present discussion. James fought against the view that consciousness is a discontinuous process, a view that was held by Wilhelm Wundt, who wrote in his *Grundzüge der physiologischen Psychologie* that "the psychological nature of our temporal intuition reveals itself as discrete" [16]. James derived his conclusion about the continuity of the stream of consciousness ("thought is sensibly continuous") from the oscillatory character of the nervous process that creates an overlap between neural oscillations and induces the summation of stimuli. "As the total neurosis changes, so does the total psychosis change. But as the changes of neurosis are never absolutely discontinuous, so must the successive psychoses shade gradually into each other" [17]. James tentatively explained both the continuity of consciousness and the duration of the 'specious present': "there is at every moment a cumulation of brain processes overlapping each other [...] The amount of the overlapping determines the feeling of the duration occupied." [18] James' speculations did enchant many readers, including the philosophers Henri Bergson and Edmund Husserl. The latter tried to devise a reflective method, the phenomenological method, which he applied to many kinds of problems, including the relationship between time and consciousness. He described the coexistence in consciousness of both dimensions, past and future, retention and protension. He was led to the conclusion that the temporal structure of consciousness is likely to be created by mechanisms that cannot be grasped by philosophical reflective consciousness and thus appear to it as passive mechanisms [19]. How the temporal framework of consciousness is created still remains to be explained. We have now to go back to nervous physiology as it developed in Great Britain and America in the early 20th century.

9. The all-or-none principle in nerve physiology and the frequency coding

In 1902, Francis Gotch, who studied nervous electrical responsiveness to single stimuli, stated the 'all-or-none' law that governs the transmission of the nerve impulses along the fibre [20]. In 1905, Keith Lucas showed that the same law applies to muscle fibres under an electrical stimulation. He worked in the laboratory of John Newport Langley, who succeeded Sir Michael Foster, the renovator of British physiology, in the chair of physiology at the University of Cambridge in 1903. Lucas' work on the excitable substances at the neuromuscular junction is a classical piece in the history of physiology. Regarding the 'all-or-none' principle, Lucas was able to work on isolated nerve fibres, to determine the number of muscle fibres innervated by a single nerve fibre and to study the behaviour of these 'motor units' [21]. In 1909, he showed that it has the same kind of scaled pattern that he had observed earlier on muscle fibres [22]. He thus extended the concept of an 'all-or-none' behaviour of the muscle fibre to the motor nerve fibre. Between 1912 and 1914, his student Edgar Douglas Adrian extended these observations to sensory nerve fibres and published a series of papers in which he showed that the amplitude of the impulse at a single point depends on the local state at this point, rather than on the intensity of the impulse [23]. In 1915, the Bostonian physiologist Alexander Forbes gave other arguments to give support to the 'all-or-none' law [24]. In 1922, he published a paper with Adrian on the all or nothing response of the sensory nerve fibre [25]. Both investigators were able to show that the response of a sensory nerve fibre to the excitation of the corresponding muscle is of the same kind that the response of a motor nerve once artificially stimulated. Forbes stretched the muscle with help of a spring or gave it an electrical shock to induce its contraction [26]. The same kind of technique was used by Adrian, who published in 1926 a series of three papers in which he showed that the frequency of the sensory response is proportional to the weight which stretches the muscle [27]. This fundamental discovery of the frequency coding of stimulus intensity had many theoretical consequences. Due to its quite general character, the frequency coding put an end to the old concept of a specific nerve energy which had been put forward by the German physiologist Johannes Müller in 1826 [28]. Generally speaking, the frequency coding received a strong functional significance. Much later, the German physiologist Ernst Pöppel stressed the discontinuous character of nerve action as the basic mechanism that creates the apparent continuity of consciousness.

10. Adrian on brain rhythms

In spite of his great achievements in physiology, Adrian missed for a while the discovery of the electroencephalogram by Hans Berger in 1929, which was done in a more clinical context. He apologized on several occasions for this lack of information. He explained that the electrophysiologists outside Germany were unaware of Berger's papers before 1933. Electrophysiologists were engaged in work on the peripheral nervous system and not on the central. Adrian mentioned that his own acquaintance with the electrophysiology of the central nervous system did not reach the level of the mammalian brain before 1933. But in 1931, while he was working with Frederik Buytendijk, he started to record electrical potentials in the isolated goldfish's brain, in which both researchers found some slow rhythmic potential changes in the brain stem. These slow rhythms could be "produced by the summation of brief potential changes (e.g., action currents in the nerve fibres) occurring repeatedly in different elements, the rise and fall of the curve being due to an increase and decrease in the number of elements which happen to be in the active state at any moment." [29] Another tentative explanation was that the slow waves "represent a slow change in the nerve cells or dendrites." Rapid waves were observed in the mid-brain. These rapid fluctuations could be ascribed to a "repeated synchronous activity in a group of neurones." Adrian then observed various rhythms, "synchronized reactions" in the water beetle's (*Dytiscus marginalis*) optic ganglion [30]. These results led him to the study of the rabbit's cerebral cortex in 1933. Working with Bryan Matthews, he studied the electrical activity produced in the rabbit's anaesthetized brain either spontaneously or by an injury (a cut of brain tissue or a puncture), or by a sensory stimulation, or by drugs [31]. Most of the paper is devoted to the discussion of the way the recorded (brief or slow) waves are produced by single neurones, acting in a synchronous or an asynchronous manner. Adrian and Matthews noticed that synchronized action could occur over large areas in the nervous system. When studying the existing literature on the subject, Adrian and Matthews found a reference to Hans Berger's work in a paper published in 1932 by Max Heinrich Fischer of the Kaiser-Wilhelm Brain Research Institute headed by Oskar Vogt in Berlin-Buch [32]. Fischer made records from the exposed brains of cats, rabbits, dogs and monkeys. He described spontaneous oscillations occurring at the cortical surface, other oscillations occurring under various sensory stimulations, and a characteristic response from the striate area to visual stimulations. At the Berlin-Buch Institute, other investigators, A.E. Kornmüller [33] and Jan Tönnies, did also work on the EEG in rabbits and monkeys. In America, brain potentials were recorded by S.H. Bartley and E.B. Newman as early as 1930. George Bishop worked with S.H. Bartley on evoked potentials in the visual cortex. They were able to record electrical phenomena in the visual cortex of the rabbit following electrical stimulation of the optic nerve. In a subsequent study, Bishop tried to investigate excitability changes in the optic pathway [34]. Indeed, the study of the electrical activity within the central nervous system received increased attention in the early nineteen thirties in several parts of the scientific world.

Going back to Great Britain, Adrian and Matthews recognized immediately the fundamental importance of Berger's discovery. They tried to verify it, and arranged a demonstration at a meeting of the Physiological Society in Cambridge on 12 May 1934. They started to use the terminology of Berger's alpha rhythm, and asked the question of how cortical neurons could produce such regular potential changes. Adrian met Berger in Paris in 1937. Meanwhile, the terminology of 'synchronized' vs. 'desynchronized' states became in use to describe the various patterns observed on the electroencephalogram. As stated by Giuseppe Moruzzi, "several lines of experimental evidence led to the conclusion that the slow potential oscillations found in the EEG and in the electrocorticogram were summation effects built from repeated brief unitary pulsations. These unitary beats, however, were much slower than the single action potentials obtained from motor or sensory fibres. Adrian's doctrine of the synchronization and the desynchronization of cortical neurones and the explanation of Berger's arrest reaction can now be found in every textbook and are regarded as the basic principles of electroencephalography." [35]

11. EEG, brain rhythms, and synchronization properties

The states of sleep and wakefulness became soon part of the new picture of brain potentials. One of the pioneers in the field, Alfred Loomis, wrote in 1937: "Largely by the development of a type of amplifier system specifically designed to faithfully record the unusual types of potential occurring during sleep, we have been able to establish very definite states of sleep which change suddenly from time to time, and to correlate these with movements, with dreams, and with external stimuli applied to the sleeping subject" [36]. The effect of external (auditory) stimuli on brain waves in sleep was described by Loomis in terms of synchronization, the brain waves behaving "as if the subject's cerebral processes had synchronized with the regularly repeated tone." Artificial synchronization of brain waves with the frequency of external stimuli may be found in other kinds of situations. In a paper on brain rhythms published in 1944, Adrian gave the results of some experiments on the collective working of brain cells: indeed, "regularity means that large numbers of brain cells must be working in unison at the same rate" [37]. This collective behaviour is beautifully shown in Berger's alpha rhythm, which appears when attention is displaced from one sense to another: for instance, the alpha rhythm appears in the visual area when the subject hears a sound. "The alpha rhythm is thus a rhythm of inattention, a positive activity which fills those parts of the cortex which are for the moment unemployed. It is not the basic rhythm of unstimulated nerve cells, and there must be some kind of competition between the message from the eyes and from the source of the alpha rhythm to decide which shall control the cortical areas" [38]. In order to study this competition between the alpha rhythm and the much more irregular sensory activity, Adrian created sensory messages endowed with a much more regular pattern: "This can be done, as far as vision is concerned, by making the field more or less uniform and lighting it with a flickering light. The nerve cells are then forced to work in unison at the frequency of the flicker." In order to produce a competition between the alpha rhythm and the flicker rhythm, Adrian devised an experiment in which the eyes were closed and the flickering light was delivered on the closed lids. In this kind of competition between rhythms, sometimes both rhythms could be seen to "co-operate if their frequencies allowed it." [39] "Such a combined rhythm usually took some time to build up as the two sets of waves had to be synchronized, but there was evidently an interaction between them and a tendency to remain synchronized as long as their frequencies were not too far apart." [40] This is a magnificent example of an artificial synchronization of brain rhythms.

In France, Alfred Fessard, who became a regular correspondent of Adrian, was perhaps the electrophysiologist who was most interested in the rhythmic properties of living matter, according to the title of the two volumes he published in 1936 [41]. In 1937, Fessard spent a semester at Cambridge, and worked there with Bryan Matthews on the so-called 'synaptic potentials', according to the terminology they proposed for these slow potentials that they were able to record on the sensory and motor roots of the spinal cord [42]. Fessard was also most interested in autorhythmic activities found in different structures such as nerve or muscle fibres, stretch receptors, ganglion cells etc., under certain experimental conditions. According to his pupils Pierre Buser and Robert Naquet, "his interest was to show that all such structures were able to develop autorhythmic states of activity when treated with different physical or chemical agents; autorhythmicity thus seemed to be a general property of isolated excitable preparations" [43]. Alfred Fessard devoted many studies with D. Auger and Angélique Arvanitaki to rhythmic activities in nerves, to the coupling or synchronization between neighbouring pulsating system and to the mechanisms of electric discharges in electric fishes [44].

12. Synchronized and desynchronized states, brain rhythms after the World War II

The vocabulary of synchronized versus desynchronized states was amply used in the fundamental studies of Moruzzi and Magoun (1949) to oppose slow-wave sleep to the waking state. They began their classical paper by the following sentence: "Transitions from sleep to wakefulness, or from the less extreme states of relaxation and drowsiness to alertness and attention, all are characterized by an apparent breaking up of the synchronization of discharge of elements of the cerebral cortex, an alteration marked in the EEG by the replacement of high-voltage slow waves with low-voltage fast activity" [45]. According to their own words, these authors "described the desynchronization of the EEG induced by brain stem stimulation and presented evidence that this alteration results from exciting a system of reticular relays ascending to the diencephalon" [46]. At the same time, Frédéric Bremer defended his view of sleep as deafferentation, based on his 'cerveau isolé' preparation. In his view, the fundamental property of synchronized self-rhythmicity in central neuronal aggregates revealed itself in the clearest way in this preparation [47]. After the discovery of REM sleep by Eugene Aserinsky and Nathaniel Kleitman in 1955, the synchronization vs desynchronization vocabulary was also applied to the different states of sleep, among other kinds of denominations like the ones in use for both sleep states: slow-wave sleep versus activated sleep or rapid sleep, rapid eye movement sleep versus non-rapid eye movement sleep. Michel Jouvet's terminology of paradoxical sleep [48] deserves particular attention, since it has the great advantage to escape the epistemological criticism of being caught in a purely dichotomic conceptual structure, which is the case of all other denominations. Regarding paradoxical sleep, Michel Jouvet discovered particular waves, endowed with an irregular pattern, in the brain stem. They were later shown in large cortical areas, mainly visual and auditory areas, and were consequently denominated as 'ponto-geniculo-occipital waves' by Marc Jeannerod.

In the late sixties and early seventies, Arlette Rougeul-Buser and Jean-Jacques Bouyer, among other researchers, discovered in the cat the equally unexpected phenomenon of synchronization episodes within states of wakefulness, which were currently described as consisting only in desynchronized activity. These rhythms of 'motionless wakefulness' appear on the somaesthetic cortex with a frequency of 12 to 18 Hz [49]. Other synchronization phenomena within wakefulness were described in the motor and parietal cortex of the cat or baboon when the animal was in a state of intense wakefulness, with a frequency of 35 to 45 Hz. They were discovered by Arlette Rougeul-Buser and Jean-Jacques Bouyer and were first denominated as 'rythmes d'hypervigilance' [50]. They were called later '40-Hz rhythms'. Other researchers (Wolf Singer, Rodolfo Llinas) took much interest in them and found them under other circumstances. Llinas, for instance, discovered them in paradoxical sleep [51]. Using magnetoencephalography, Llinas was able to observe a rostrocaudal phase shift of 40 Hz activity over the cortex during wakefulness and paradoxical sleep. The 40-Hz rhythms became the subject of many philosophical discussions about their meaning regarding the 'binding problem' of consciousness. Since the binding between various kinds of representations corresponding to various cortical areas is commonly viewed as a key for understanding consciousness mechanisms, and since synchronizations between rhythmic activities in different areas can tentatively be seen as a binding mechanism, the 40-Hz rhythm became a candidate for solving the enigma of consciousness. It was considered as providing a necessary temporal framework of consciousness. This idea was mainly substantiated in the works of Rodolfo Llinas and Wolf Singer. More recently, Mircea Steriade criticized these speculations. He observed the appearance of synchronized rapid rhythms within slow-wave sleep. This fact "was surprising to those who consider these oscillations as reflecting high cognitive processes and conscious events during waking and REM sleep. However, the fact that beta/gamma activity is voltage (depolarization) dependent explains the presence of fast activity during the depolarizing phase of the slow sleep oscillation." [52] Other kinds of rhythms, named 'very fast visual rhythms', occurring in the visual cortex during eye saccade and endowed with a range of frequencies varying between 50 and 132 Hz, were recently observed by Pierre Buser and Arlette Rougeul-Buser [53]. This discovery makes the picture of the electrophysiological correlates of attention more complex. The fascinating story of brain rhythms remains thus an open question that keeps its exceptional scientific and philosophical interest.

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