The Phenomenon of Travelling Waves: A Review

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EARLY NEUROPHYSIOLOGICAL STUDIES

The travelling wave (TW) had its origins in some of the earliest of all neurophysiological investigations. For example, as early as 1934 Adrian and Matthews,[1] working on cats and rabbits, reported that neurons pulsate in small groups, and as they pulsate out of phase with each other, periodic waves of activity may spread over the whole cortex. After severe injury the action of convulsant drugs was to enhance the spread of these pulsations, often changing the direction of travel. The authors concluded that the cortex behaved as a freely conducting mass, with beats starting from one focus at one time and later from another area. The next year (1935) Adrian and Yamagiwa[2] reported out of phase alpha activity on the occipital regions of man and these phase differences later proved to be closely related to the TW phenomena.

In 1941 Libet and Gerard[3] reported that potential waves continued to travel after neuronal connections had been blocked or severed within the hemispheres of the isolated frog brain, dependent on the existence of intercellular currents. The TW induced by caffeine was simpler and of greater amplitude than most waves recorded from the surface, and these waves may travel from the olfactory bulb to the occipital pole with secondary and satellite waves firing back from the latter region. In 1950 Sloan and Jasper[4] noted that another neurophysiological phenomenon that travelled, viz., spreading depression, also could spread over a cortical incision. In 1944 Motokawa and Tsujiguchi[5] emphasized, as the basis of the TW, the phase differences in various regions, even to the extent of an actual phase reversal between occipital and frontal areas. Their theories to account for the TW included phenomena of (1) "physically-spreading," (2) "quasistanding wave" and (3) "physiological coordination." The latter was considered as the most suitable hypothesis with neurons viewed as tied with commissural fiber systems and their functional interrelationships determining the phase differences between various regions. In 1948 Cohn[6] confirmed the findings of Adrian and Yamagiwa that alpha rhythm could show transient phase shifts and developed a hypothetical model, based on the assumption of four functional oscillators in the upper and lower pericalcarine cortex of both hemispheres. In 1953 Mickle and Ades[7] showed that expanding patterns of positive potentials in the cortex of cats travelled for short distances at the rate of 1.5 m/sec. Thus, as a possible explanation for the TW many of these early investigations emphasized phase differences in the activity among different cortical regions and that waves seemed to travel from one place to another.

APPARATUS

The next important advancement was the development of apparatus to better view the TW. A two-dimensional array with 16 tuning units, called the "spectroheliograph," was used by Goldman et al[8,9] (1948, 1949) to study the phenomenon. The "toposcope" was next (Walter,[10] 1953), followed later by an improved "helical scan toposcope" (Shipton[11] 1957), photographing the input from 22 channel balanced amplifiers from electrodes covering the entire scalp. The "encephaloscope" of Livanov et al[12] (1956) was developed at that same time, using a matrix of 10 x 5 spots of light whose size was proportional to the potential at the corresponding electrode on the head. Also at this same time Petsche and Marko[13] (1955) continued their own development of toposcopic methods to investigate the TW. A few years later (1961) Rémond[14] had published his own method for constructing maps of potential distribution at different times, called chronotopographs. All of the latter work was done on man, but earlier in 1950

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Lilly[15] had described his "bavatron," a display of lights representing resting or evoked activity from many electrodes implanted into anesthetized animals. Topographic brain mapping devices are now available and likely are the most useful apparatus to investigate all aspects of the TW.

CONDITIONS FOR RECORDING THE TW

Abnormals

Even in abnormal conditions, like a midline brain tumor (Bechtereva,[16] 1960) or subacute sclerosing panencephalitis (Petsche et al,[17] 1961), the TW has been identified. In the former case, the travelling phenomenon was in the longitudinal direction and in the latter instance the velocity of the waves decreased with the progression of the disease.

Normals

REST

Goldman et al[9] (1949) were among the first to describe the TW at rest that could cross the entire skull, remain within a single lobe, or move either in a clockwise or counter-clockwise rotation. The frequency of rotation was about 9/sec, most pronounced with eyes closed in the waking state. The authors suggested that the alpha rhythm through the mechanism of the TW may represent a scanning process in the brain. In normal subjects, various authors have reported a change crucial or possibly required for the TW, viz., the difference in the phase of alpha rhythm throughout the head. During rest, Garoutte et al[18] (1959) found a time difference of 30-40 msec between the frontal and occipital alpha and Cooper[19] (1959) found similar delays. During hypnosis, Darrow et al[20] (1950) reported that there was an increased in-phase relationship between occipital and parietal and also frontal and parietal placements, suggesting that hypnosis may even decrease the possibility of recording the TW, assuming that phase changes enhance or may even be required for this phenomenon.

EMOTIONAL STIMULI

The importance of emotional stimuli in producing phase changes was emphasized by Darrow and Hicks[21] (1965) who reported that indifferent ideational verbal stimuli produced only a small increase in anterior leading of phase, but disturbing words produced an increase in "total diphasic reactions," suggestive of interaction between brain areas. A few years later Darrow[22] (1967) claimed that disturbed children with a behavior disorder showed a superabundance of these diphasic interareal phase reversals, confirmed by Martinius and Hoovey[23] (1971). Also, poorly cooperative aggressive individuals showed phase reversals with a prevalence of the anterior regions leading of alpha, in contrast to friendly, cooperative, or passive individuals who frequently showed occipital regions leading. Using emotionally-charged questions Berkhout et al[24] (1969) reported that phase lead and lag between frontal and occipital electrodes changed according to the semantic content of the questions used. Giannitrapani[25] (1970) found that verbal stimuli were associated with posterior leading of alpha on the occipital area, in contrast to noise or musical presentations, characterized by anterior leading, especially on the left side.

SENSORY STIMULI

Bechtereva and Zontov[26] (1962) studied the relationship between the phase of the EEG pattern and the timing of a stimulus, concluding that three time zones can be found within an alpha cycle for changing synchronization and, therefore, the phase relationships. Darrow[22] in 1967 found that a simple sensory stimulus elicited an increase in anterior leading of alpha as an example of the anterior-posterior phase changes. Shaw and McLachlan[27] (1968) presented visual, auditory and tactile stimuli and found anterior leading in most cases with the time-delay associated with the level of arousal. With a flicker visual stimulus (17/sec) Papakostopoulos et al[28] (1971) reported on a progressive phase change from the anterior to the posterior part of the head.

PHASE SHIFTS AND THEIR CHARACTERISTICS

Left vs Right

Lesèvre et al[29] (1967) found phase reversals only randomly distributed between the hemispheres, suggesting a basic synchrony of frequency and phase. Also, they reported a midline axis of symmetry at the points where there was the phase reversal of the alpha gradients. On the other hand, Liske et al[30] (1967) reported that normal subjects usually showed a phase lead on the right compared to the left, and the average shift was 0.83 msec to the right; the range was 4 msec to the left to 7 msec to the right. These findings suggested to the authors that the cerebral dominance for alpha more often resides in the right hemisphere since it more often exerted an average phase lead over alpha generated in the left hemisphere. Giannitrapani et al[31] (1966) found that the phase lead depended on handedness with the left leading in right-handers and right leading in left-handers. In 1970 the same author [25] further reported that the left lead from right-handers decreased with music or voice stimuli. Compared to normal controls, school children with behavior disorders showed the greatest spread of phase relationships between the two occipital areas

(Martinius and Hoovey,[23] 1971), suggesting that a TW would be more evident in the latter group.

CHARACTERISTICS OF THE TW

Animals

As early as 1950, Lilly[15] reported that auditory evoked potentials in cats spread in different ways away from the focus of activity initiated by afferent acoustical volleys, at times in determinable paths over time intervals as long as 1 sec. Barbiturate and sleep spindles also travelled and spread throughout various areas. Four and five years later Lilly and Cherry[32,33] (1954, 1955) added that more lively travelling occurred in wake than in deep anesthesia with velocities of 1 m/sec for the leading edge, but slowing to 0.1 m/sec for the trailing edge. The positive peaks were the most prominent, appearing as a "travelling mesa." Petsche and his colleagues have done considerable work on the TW in animals. In 1968, the latter author reported with Sterc[34] on seizure activity in rabbits and its spread at 0.1-0.5 m/sec, considering the spread to be purely a cortical event. Two years later Petsche and Rappelsberger[35] (1970) and also with Trappl[36] (1970) confirmed the primary role of the cortex in providing for the travelling phenomenon and also the intimate relationship between the TW and synchronization. The authors reported that at cytoarchitectural borderlines the field became distorted and may elicit other potential fields in these contiguous areas. Vertical incisions in cortex could prevent the fields from progressing across these boundaries. The polarity of the field that moved corresponded to the polarity of the more peaked or steeper phase of the grapho-elements, and usually the positive phases were the moving ones with a greater density or a steeper slope of equipotential lines, compared to the negative phase. In 1968, Bogdanovich and Knipst[37] confirmed in rabbits the presence of the TW phenomenon for 1-7/sec waves.

Man

One of the earliest studies on the TW in man was by Petsche and his colleagues[38] (1954), and this investigation dealt with the travelling of the spike and independently of the wave of the bilateral spike and wave complex. The travelling was parallel to the midline, slower over the frontal areas and more constant with regular than irregular patterns. Later in 1962 the same author[39] added that the TW was more constant for waves at the rates of 2-7 m/sec than for spikes at 4-15 m/sec. Earlier in 1955 Rémond[40] had claimed that the spikes were usually stationary and the waves were the portion that moved. In 1959 Foitl and Petsche[41] had described the TW from a dermoid cyst, noting a significant relationship between the velocity and frequency of the waves, more often (54%) travelling in the direction opposite to the amplitude gradient, compared to the same direction (24%). Petsche et al[42] (1972) summarized the TW as the cause, not the result, of the fact that EEG waves of uniform shape may be seen in large areas. To these authors the phenomenon likely deals with activity spreading along axons and dendrites plus several other complex processes involving synaptic delays.

Another early study on the TW and its characteristics was from Cooper and Mundy-Castle[43] (1960), utilizing the helical scan toposcope developed with Grey Walter at the Burden Neurological Institute. Velocities were often 2.4 m/sec for the alpha in the anterior-posterior (AP) direction, but ranged from 1-20 m/sec and had a mean of 5 m/sec. Occasionally in normals, but significantly more often in mentally disturbed patients, spread in the PA direction was seen. The higher frequency of alpha immediately after eye-closure, followed by a decreasing frequency (called the squeak phenomenon) appeared as the field then spread into the frontal areas. Taking a suggestion from Grey Walter[44] (1957), the authors speculated that individual alpha sources may vary in frequency independent of each other and that such variations can often be associated with increased mental activity. As a further explanation, the authors referred to the propensity of cortical cells to synchronize their oscillations dependent on the mutual induction or coupling between these cells. To them this synchronization may be influenced by a TW of activity, giving rise to progressive time differences in the peak amplitude of the waves recorded by channels arranged longitudinally.

Another investigator who has extensively studied the TW is Rémond. With his colleagues, Lesévre et al[29] (1967), Rémond found that chronotopographical maps of the alpha showed little evidence at that time for the TW. In the next year (1968) Rémond[45] claimed that moving fields actually exist and would be most evident from studying phase relationships directly on the brain surface, especially from a lissencephalic brain. He claimed that scalp recordings from the complex folded structure of the human cortex could only be suggestive of wave propagation. This author reported that the more peaked phase of the EEG wave was the one that seemed to travel, usually more often the positive phase, due to depolarization of the deepest layers. The alpha was usually maximal about 8 cm above the inion in the midline and the hill of that potential more often moved from anterior to posterior and from right to left. Often the potential reversed itself every 50 msec, making most of the head all negative or all positive at the same time.

With the complete cycle of negativity and positivity at 100 msec and therefore accounting for a 10/sec alpha rhythm, Rémond[45] finally concluded that the alpha was basically stationary and only certain kinds of pictures made it look like it was travelling. A few years later, this author joined his colleagues (Joseph et al,[46] 1972) in summarizing the behavior of alpha in 150 young adults and added data from mathematical simulations. From the human data, the authors reported that it was rare to see a fixed extremum of alpha on the midline and there was a great variety of alpha rhythms. Two different models were used to further investigate the travelling phenomenon: one with potentials out of phase between the hemispheres and the other with potential fields associated with a "wave of activity," spreading over the surface and causing a phase shift between the potentials. The phenomenon of travelling could therefore arise from (1) different frequencies; (2) phase shifts or (3) separation in space of two zones of maximal activity. The direction of the TW changed, according to whether the center region was of minimal or maximal potential, and the shorter wavelengths were associated with the greater phase shifts between regions. The authors speculated that transhemispheral TW were likely due to phase shifts in each hemisphere, not actual transhemispheral waves of activity. Furthermore, they concluded that waves of activity generally arose from anterior and lateral regions, gradually spreading through central and occipital regions, which were the areas of the maximal alpha. One of the final conclusions of these authors dealing with models was that one should discriminate in TW between (1) the phenomena that result from phase shifts between stationary potentials and (2) events that arise from the actual propagation of "waves of activity."

Another investigator making substantial contributions to this field was Lehmann[47] (1971) who described the maximal positivity of alpha usually on the precentral-central area and the maximal negativity on the occipital areas. However, after the maximum appears the next cycle of the alpha wave may show inverted polarities on those same regions. These maxima may "step clockwise or counterclockwise from area to area," referring to a phenomenon like the TW. Also, the smallest phase lag usually was seen between the two occipital areas. The de-emphasis of alpha solely on the occipital areas was also made by Sorel[48] (1971) who claimed that only 25% of cases show alpha rhythm confined to the posterior regions, since the majority showed the basal rhythm on the central and anterior regions. In the next year (1972), Lehmann[49] speculated that these data could be accounted for by three stationary generators oscillating at similar frequencies but with different phase angles. Comment was also made on sleep spindles with the maximal positive value migrating to the left at a speed of 1 m/sec. This speed of 1 m/sec was slower than the 8.5 m/sec for spike and wave complexes, which also moved at 2-3 m/sec. Lehmann concluded that the TW may be associated with stationarity of the maximal values of the field distribution, but with only minor changes in this distribution. Thus, according to the latter investigator, the travelling may not necessarily indicate an actual migration of the principal processes that produce the EEG waves.

Other contributions have come from Pozo-Olano[50] (1969) who described the "flow" of alpha mainly from anterior to posterior and from right to left. Peronnet et al[51] (1972) stated that the phase differences from 0°-180° could only be explained by propagation of activity from two independent generators at different depths of the same or similar frequency. Speeds were 0.5-8 cm/sec and this type of propagation corresponded to activity of synchronizing mechanisms rather than active propagation along dendrites (Gloor et al,[52] 1963). As a final comment on the review of relevant literature, Farley and Clark[53] (1961) used networks simulated by a digital computer in which each of the 1296 cells "had a probability of connection with their neighbor according to the distance from them." When groups of cells were stimulated, spreading waves were seen so that activity expanded to produce successive branches of activity proceeding clockwise around the edges of the nets. Thus, even with simulated computer networks, a type of TW could be seen.

SUMMARY

As early as 1934 evidence appeared in animals that waves of activity do not always remain stationary but can actually spread over the whole cortex. In the next year some of the earliest studies on the EEG of man showed phase changes of alpha activity that could account for the TW, which later was described when apparatus was built to better view it, especially in the 1950s. The TW has been described mainly as alpha activity that appears to travel both in abnormal and also normal conditions, including the resting state. The phenomenon seems to be enhanced with either external stimuli or endogenous emotional states, which increase phase changes on different brain areas. The travel has been described in all directions from the frontal to the occipital pole, and ear-

ly work suggests that the posterior-anterior direction may be more often found in abnormal mental states. The speed of travelling over the scalp has varied usually from 1-20 m/sec, but generally has been reported around 5 m/sec. Most investigators have reported that the positive phase is the one which most clearly travels. In exploring the phenomenon of the travelling wave, it is clear that maximal positivity and negativity of the alpha is not always on the occipital regions, as many clinical studies would imply; instead, the fronto-central areas in particular are often the focus of maximal alpha.

The neurophysiological basis for the TW likely includes the spreading of activity along axons and dendrites at rates consistent with the reported speeds of travelling for this phenomenon. Nunez[54] (1981) estimated, for the alpha rhythm, velocities in short and long neocortical interactions at 4-20 m/sec, matching propagation velocities in corticocortical fibers of 6-9 m/sec. Further explanations of the TW could be from the interactions of different frequencies or the same frequency, but with different phase relationships. New apparatus, like the Brain Mapper, will allow the formulation of pictures that in sequence will look like a wave that is actually travelling. One of the major interesting problems here is whether such a wave is actually or only apparently travelling. Another major question is whether such a travelling wave represents a scanning mechanism or a means of informational exchange between different brain areas. The present review indicates that further work is necessary to determine in a definitive way the answers to these latter questions.

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