The visually evoked cortical potential and the cortical alpha rhythm: Their physiological basis and some behavioral considerations

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The Visually Evoked Cortical Potential and the Cortical Alpha Rhythm: Their Physiological Basis and Some Behavioral Considerations

In partial fulfillment of the requirements for the degree of: Doctor of Optometry

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Acknowledgements:

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Abstract:

Physiological models for the generation of the Visually Evoked Cortical Potential (VECP) and the Alpha Rhythm are discussed. Certain stimulus and response variables are considered with respect to their effects on the VECP and the Alpha Rhythm. Consideration is also given to the possible physiological significance of these gross surface cortical potentials relative to the scheme of information processing. A model for an internal attentional mechanism is developed.
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Introduction:

Hans Berger first described the human electroencephalogram in 1929. Since that time, much investigative work has been devoted toward developing a better understanding of the gross electrical potentials which are recorded from the surface of the scalp. In recent years, an analysis of these scalp potentials has become a rather widely accepted clinical tool for the evaluation of various central nervous system functions. It is the purpose of this paper to review the fundamental physiological principles which are the basis for two specific types of scalp potentials: the Alpha Rhythm, which is the principal component of the spontaneous electroencephalogram (EEG), and the Visually Evoked Cortical Potential (VECP). The latter is also frequently referred to as the Visually Evoked Response (VER). Some general considerations regarding the functional and behavioral significance of these cortical potentials will also be discussed.

General Considerations of Gross Surface Potentials:

When measuring gross surface potentials, it is necessary to use two electrodes since electrical potential (voltage) can only be described as a difference between two values of electrical charge. The recording electrode is positioned at some discreet location on the surface of the scalp and reflects the electrical charge at that point relative to the reference.
electrode. The reference electrode is usually placed on an ear lobe or a mastoid process since these regions are generally considered to be electrically inactive with respect to the signal of interest; i.e., they behave as a "ground". A typical scheme for the recording of VECPs and the Alpha Rhythm is illustrated in Figure #1.

The difference in electrical potential which exists between the recording and reference electrodes represents the signal which is fed into the amplifier. The amplified signal, however, is a composite of all the electrical field changes which are "seen" by the recording electrode. This raw signal will contain much electrical activity which is of no interest to the investigator (i.e. muscle potentials). The undesired activity will frequently mask or conceal that component of the raw signal which is of interest and makes it necessary to remove this "noise" from the raw signal with the techniques of time-averaging or frequency filtering. Time-averaging a raw signal has the effect of "amplifying" only those components of the signal which are temporally locked to the stimulus in a consistent manner. Frequency filtering means that only those components of the signal whose frequencies lie within a specified range of values will be amplified.

It must be remembered that the recording electrode reflects the summed electrical field changes at a particular point on the surface of the scalp. In fact, electrical activity (displacement of charge) in any part of the body will manifest itself as a minute potential field shift at the recording electrode. This occurs as the result of electrotonic transmission through
Typical Scheme for the recording of VECPs and the Cortical Alpha Rhythm:

"A" is the standard location for placement of the recording electrode approximately 1 cm antero-superior to the inion. "B" and "C" indicate other possible recording electrode locations. The reference electrode is shown on the ear lobe at "I". "F", "P", "T", and "O" indicate frontal, parietal, temporal, and occipital lobes of the cortex. "Fz", "Pz", and "Oz" refer to standardized reference locations for placement of electrodes in EEG recording. The electrode at "A" is optimally situated for recording VECPs generated in immediately underlying occipital cortex. Figure taken from Sokol (44)
the electrolytes of the tissue spaces which lie between the site of electrical activity and the site of the recording electrode. As the site of electrical activity becomes further and further removed from the recording electrode, however, the magnitude of the recorded potential shift will become less and less as a result of the tissue impedence. By the same token, the nearer to the recording site the electrical activity occurs, the larger will be the measured potential change at the recording electrode. Of course, the amount of potential attenuation which results from transmission through the tissue spaces will depend to a large extent on the nature of the tissue which must be traversed; different tissue types having different values of impedence to current flow.

Electrotonic spread of current, as described above, must be differentiated from the other principal means by which electrical activity in one part of the body can manifest itself at distant locations: axonal transmission within the nervous system. A prominent difference between these two methods of electrical transmission is their respective propagation velocities. Electrotonic transmission occurs almost instantaneously, while axonal transmission has a velocity of approximately 3 to 100 meters per second (depending on the type of fiber).

The Visually Evoked Cortical Potential (VECP or VER):

When a visual stimulus is presented to the eye, the retinal image is encoded as a series of electrochemical impulses and transmitted along the axonal processes of the retinal ganglion cells. These axons proceed without interruption as the optic
nerve to the chiasm and, thereafter, as the optic tract until they reach the lateral geniculate nuclei (LGN) where they make synaptic contact with neurons of these nuclei. See Figure #2 for a description of the visual pathways.

The LGN is located in the thalamus and is classified as a "specific" sensory relay nucleus. The specific thalamic sensory relay nuclei have cortical projections which terminate in discreet areas of primary sensory cortex. These specific nuclei are differentiated from thalamic nuclei whose axons are diffusely projected to widespread areas of the cortex (non-specific) and thalamic nuclei which do not project to cortex but communicate with lower brainstem nuclei, the basal ganglia, and other thalamic nuclei. (4,5)

The activity which reaches the LGN from the optic tract is integrated and projected to primary visual cortex (Brodman's area 17) along the optic radiations (geniculo-calcarine pathway). The fibers of the optic radiations terminate in layer #4 of striate cortex and make synaptic connections with granular cells and the large apical dendrites of deeper pyramidal cells. See Figure #3 for a highly abbreviated description of striate cortex cytoarchitecture.

Arrival of impulses in the pre-synaptic terminals of the optic radiation fibers will cause changes in the polarization of the post-synaptic membranes. The polarity changes of these post-synaptic membranes is due to the movement of ions across the membrane and represents a net displacement of charge. It is this shift of charge across the post-synaptic membrane which is the most likely source for the potential changes which are
Illustration of the Visual Pathways From the Retina to Visual Cortex:

The lateral geniculate nuclei (bodies) lie at the lateral border of the Thalamus and are the only thalamic nuclei shown in this diagram. Illustration taken from Newell and Ernest (43).
Cytoarchitecture of Visual Cortex:

Specific geniculo-cortical afferent (S) is seen terminating on granular cell (G) and large pyramidal cell (LP) in layer #IV. Non-specific thalamo-cortical afferent (NS) makes synaptic contact with the large apical dendrite of the large cortical pyramidal neuron (LP). Intracortical fiber (I) is seen making synapses with superficial apical dendritic processes of large pyramidal cell (LP). A small pyramidal neuron is also shown (SP). Not all of the different types of cortical elements are shown in this figure.
recorded on the surface of the scalp. Simultaneous polarity changes in the dendrites and cell bodies of a large number of neurons would represent a relatively large net displacement of charge.

A highly coordinated afferent volley of impulses from the optic radiations would presumably cause simultaneous polarity changes in large groups of cortical neurons and would be reflected as a potential shift at the surface of the scalp. Following the initial volley of impulses to layer #4 of cortex, the activity would be relayed to groups of neurons in deeper and more superficial layers of the cortex and would result in polarity changes in these neuronal groups. These later synchronized polarity changes would also be reflected as potential shifts at the surface of the scalp. It may be assumed that these stages of activity include activity at synapses which result in either depolarization (excitatory) or hyperpolarization (inhibitory) of the post-synaptic membrane. The direction (polarity) of the scalp potential shifts will be dependent upon the depth and spatial orientation of the active neuronal populations and also upon the relative contributions of synaptic activity which causes depolarization of the post-synaptic membrane and synaptic activity resulting in hyperpolarization of the post-synaptic membrane.

As mentioned earlier, the potentials which result from these synchronized patterns of depolarization and hyperpolarization would be electrotonically conducted through the tissue spaces which are interposed between the site of neuronal activity and
the recording electrode. These tissues would include the overlying cortex, the meninges, cerebrospinal fluid, skull, and the scalp. Although the impedance of these tissues attenuates and "smears" the cortical potentials, a comparison of the evoked-response waveforms recorded directly from the surface of the cortex has shown that there is very little difference in the character of the response recorded from the surface of cortex and the response which is recorded from the surface of the scalp.

A. Transient VECPs:

Transient evoked potentials are also referred to as "single flash evoked potentials" since, in this method, the stimulus is presented for only a brief period of time. This allows an analysis of the cortical response to a single afferent volley. When multiple responses must be analyzed, as in signal averaging, the stimuli are spaced far enough apart (usually 1-2 sec.) so that the cortical response to a stimulus will be completed before delivery of the next stimulus.

The evoked cortical response to a temporally discreet visual stimulus has a characteristic pattern which may vary from one subject to the next, but is fairly consistent for any given subject. Figure #4 is representative of a typical time-averaged transient VECP to a flashed checkerboard pattern. The figure represents the change in surface potential as a function of time. It must be remembered that the electrode reflects the algebraic sum of all the potential changes which manifest themselves at that particular scalp location.
The Transient VECP:

A typical transient VECP in response to a "flashed" check pattern is illustrated here. The stimulus is presented at zero time. Latencies (implicit times) may be determined as the peaks of positivity and negativity. Many other systems of nomenclature have been used to designate the various components of the transient VECP. This system was used for the purpose of simplicity. See text for a detailed description of the transient VECP.
and at that particular point in time. The trace represents the summed changes in electrical potential (both positive and negative) as a function of time and reflects the sum of all neural activity (both hyperpolarizations and depolarizations) in the underlying cortex. As mentioned earlier, the polarity of the response is dependent upon the nature of the postsynaptic activity (hyperpolarization or depolarization) and also upon the depth and spatial orientation of the synchronously active neuronal populations. The amplitude of the response will depend on two basic factors: the temporally additive nature of the positive and negative components, and the total number of neurons participating in synchronous activity. In summary, the surface-recorded potential changes reflect the temporal and spatial summation of all the electrical activity in underlying cortex.

Synchronized activity within a neuronal population will occur in a particular temporal relationship to the delivery of the stimulus. This time period which separates the stimulus from the observed cortical response is called the response "latency". The latency depends primarily upon the speed of axonal conduction along the visual pathways and also upon the number neurons which must be sequentially activated in order to activate the particular neuronal group. It should be remembered, however, that the initial afferent volley to layer #4 of cortex will be highly synchronized and it is only following this initial synchronous volley of impulses that activity is communicated to the various neuronal subsets which
participate in generation of the later surface potential changes.

B. Physiological Correlates of the Transient VECP:

At the present time, there is little understanding of the precise neural events which give rise to the characteristic components of the transient VECP. This is largely the result of difficulties in defining the patterns of cortical activity which result from an afferent volley and also the problem of relating these spatio-temporal patterns of activity to the potential field changes recorded from a surface electrode. There is, however, a general agreement among investigators that the principal mechanism for generation of the surface potential changes is the patterns of graded post-synaptic dendritic potentials and that action potentials make only a small or insignificant contribution.

Attempts to determine the relationships between surface potentials and the activity of individual neurons have compared the records of potentials recorded from the surface of cortex or scalp with simultaneously recorded intracellular potential shifts. Creutzfeldt has proposed that the surface recorded potentials result from the vertical spread of activity along the large apical dendrites of cortical pyramidal neurons. These dendritic potentials occur as the result of synaptic activity involving axonal-dendritic and axonal-somatic terminations from several sources including: (i) specific and non-specific thalamo-cortical afferents, (ii) intracortical fibers, and (iii)
recurrent collaterals from neighboring cortical neurons. These relationships are illustrated in figure #3.

According to the Creutzfeldt model, the original surface positivity (component P1) results from a highly synchronized afferent volley to the deeper parts of the pyramidal neurons. This afferent volley consists of impulses arriving along the specific sensory thalamo-cortical projections and making excitatory synapses resulting in depolarization of the pyramidal membrane. The following surface negativity (component N1) is the result of a combination of (i) impulses arriving along non-specific thalamo-cortical afferents making excitatory depolarizing synapses with more superficial pyramidal dendritic processes and (ii) recurrent collaterals from neighboring cortical neurons which make inhibitory hyperpolarizing synapses with the soma of the pyramidal neurons. The second surface positivity (component P2) is correlated with the spread of hyperpolarization from recurrent inhibitory collaterals to the more superficial cortical areas along the pyramidal apical dendrites. This second surface positivity is interrupted by a second negative-going component (component N2) which results from secondary activity of the non-specific afferents and intracortical fibers which make depolarizing excitatory synapses on the more superficial pyramidal apical dendritic processes.

Creutzfeldt's model suggests that the synchronous activity of deeper depolarizing (excitatory) synapses will be "seen" at the surface of cortex or scalp as a fast transient positivity and that this positivity will gradually change to a

13.
surface negativity as the deeper depolarization is electrotonically conducted to more superficial areas of the cortex along the apical dendrites of the pyramidal neurons. The model also suggests that synchronized activity of hyperpolarizing (inhibitory) synapses will be seen as a fast transient surface negativity followed by a gradual reversal of polarity as the potential spreads vertically along the apical dendrites to more superficial cortex. The reverse of these relationships would be expected for depolarizing or hyperpolarizing synaptic activity which occurred at pyramidal apical dendritic processes in superficial cortex followed by the spread of this potential along the apical dendrites to deeper cortical areas.

Creutzfeldt's model assumes that the observed surface potential changes are due exclusively (or at least primarily) to the electrical activity of pyramidal neurons. The fact that these neurons are all regularly arranged with long apical dendrites which are perpendicularly orientated to the cortical surface would suggest that they may be optimally suited for generation of the electrical field effects seen at the surface of cortex or scalp. Using the effects of topically applied strychnine and bicucilline, however, Towe has demonstrated that deeper cortical neurons make only a small or insignificant contribution to the surface potential and that it is primarily the more superficial cortical neurons lying in layers #2 and #3 which determine the characteristic surface potentials of the sensory-evoked cortical response. (8,21,22)
It must be pointed out that both Towe's and Creutzfeldt's models are based upon data obtained from investigations which used sensorimotor cortex of cat and that application of these models to the human VECP involves assumptions which may have varying degrees of validity. There seems to be a general agreement among most investigators, however, that the processes which reflect information processing in primary sensory cortex of cat can be assumed to similar to the processes which reflect the same levels of information processing in the human primary sensory cortex.

C. Significance of the Transient VECP:

Many attempts have been made in an effort to correlate individual components of the transient VECP with various levels of sensory information processing and, although certain components of the transient response do appear to be correlated with different physical characteristics of the stimulus, the relationships between observed cortical behavior and the subjective experience of perception remain unknown. It seems reasonable to refer to these two general classes of variables as stimulus (external) variables and response (internal) variables.

As discussed in section B, the earlier (short latency) components of the transient VECP reflect earlier stages of cortical sensory information processing and the later (long latency) components of the transient response reflect later stages of cortical processing. It could be assumed that the later components reflected "higher" levels of information processing and it has, in fact, been suggested that the later components
of the transient VECP are most closely related to psychological variables while the earlier components are most closely related to stimulus variables. The correlations which have been found to exist between the various components of the transient VECP and the different stimulus and psychological variables provide the basis for the use of the VECP in measuring certain aspects of human perceptual behavior.

Among the stimulus variables which have been demonstrated to show a correlation with the transient VECP are stimulus intensity, the spatial structure (pattern) of the stimulus, and the color of the stimulus. In order to avoid a consideration of refractive error, accommodation, pupillary diameter, and ocular fixation variables, the stimulus will be defined as the stimulus which is delivered to the retina.

It is generally accepted that as the intensity of the stimulus is increased, the amplitude of the VECP will also increase until a "saturation" level of intensity is reached. At the saturation level of intensity, the amplitude of the VECP will then level off and may even decrease as the intensity of the stimulus is increased further. It has also been demonstrated that an increase in stimulus intensity is accompanied by a decrease in the latency of all components of the transient VECP.

The character of the transient VECP in response to a spatially structured stimulus field is distinctly different from the transient response to a blank (homogeneous) stimulus field. These differences are reflected primarily in polarity reversals of some components and the presence or
absence of other components in the response. There is also
evidence that the character of the transient VECP to a spat-
ially structured field is dependent upon the orientation of
the pattern within the stimulus field and also upon the detail
(size (acuity size) of the spatial pattern. These
last two effects can be assumed to be the result of orientation
and contrast sensitive mechanisms within the visual system.
Differences in the transient VECPs to different colored stim-
uli have been reported although it is not clear whether these
differences reflect a true "color" response or a response to
differences in stimulus luminance which result from differences
in spectral sensitivity to the different stimulus wavelengths.
(2pg90-109)

Psychological (internal) variables have been extensively
studied in order to determine their relationship to the VECP.
Among the many which have been investigated are the variables
of stimulus "meaning", the intelligence of the subject, and
the attentional status of the subject. It has been suggested
that the amplitude of the later components of the transient
VECP may reflect the level of meaning which the stimulus has
for the subject under the experimental conditions employed
(2pg146-148,3pg40+305) to elicit the response. Stimulus meaning,
however, must be operationally defined within the context of
the experimental conditions and is, therefore, difficult to
control. The difficulty in controlling for stimulus meaning
suggests that these observations are, at best, questionable.

Various investigators have shown that measures of VECP
latency, variability, and waveform asymmetry are correlated with conventional measures of the subject's intelligence. (2pg132, 3pg305,40)

This correlation does not necessarily imply a functional relationship between intelligence and the character of the VECP although it has been proposed that these measures may reflect some aspect of the subject's "neural efficiency". The amplitude of the components of the transient VECP have also been shown to be positively correlated with the subject's level of attention to the stimulus. These attentional effects seem to be more pronounced in the later (longer latency) components of the response. Attentional effects on the transient VECP are discussed in greater detail later in this paper.

It can be assumed that the transient VECP contains much information with respect to the functional processing of visual information. The manner in which the known stimulus and psychological variables might contribute to the character of the VECP remains poorly understood and one might suppose that there are many more variables which have not yet been identified. The development of an understanding of these relationships, however, will establish the VECP as a valuable instrument for the clinical and non-clinical evaluation of human visual behavior.

D. The Steady-State VECP:

As the interval between two successive stimuli in a repetitive series becomes shorter than the duration of the transient response, the earlier components of the cortical response to an individual stimulus will interact with the later components
of the cortical response to the immediately preceding stimulus. With sufficiently high stimulus frequencies, the cortical responses to the stimuli will overlap and the response pattern assumes a 'periodic' character having the same frequency as the stimulus. Thus, the most distinguishing feature of the steady-state VECP is the fact that the individual components seen in the transient VECP can no longer be differentiated.

The fact that the individual response components of the transient VECP can no longer be distinguished in the steady-state VECP may be the result of (i) the linear superimposition of the individual transient response components in time, or (ii) cessation of cortical processing mechanisms which generate some of the individual response components due to an inability to operate at these higher frequencies, or (iii) a fundamental change in the operation of the cortical processing mechanisms.

Following the first few cycles of cortical activity, the response pattern becomes stabilized as a "dynamic steady-state" in which no particular response cycle can be associated with any individual stimulus cycle. In spite of this fact, it is possible to measure response latency with the steady-state VECP although the latency determination is not as straightforward as latency determinations from the transient VECP. Once the response has assumed a steady-state character, the sinusoidal response pattern will maintain a constant phase (time) relationship to the repetitive stimulus. See Figure #5 for an illustration of a steady-state VECP and its relationship to the stimulus.
Steady-State VECP in Response to a Sinusoidally Modulated Stimulus:

Upper trace represents the response to a sinusoidally modulated visual stimulus (lower trace). The steady-state VECP has the same frequency as the stimulus modulation frequency and will maintain a constant phase shift (\( \phi \)) with respect to the stimulus. The latency of response may be determined as an integral (N) multiple of stimulus cycles (360 degrees) plus the phase shift.
The Alpha Rhythm:

The alpha rhythm was first described by Berger in 1929. It is the principal component of the spontaneous electroencephalogram and has been officially defined by the International Federation for Electroencephalography and Clinical Neurophysiology as follows: "......rhythm at 8-13 Hz occurring during wakefulness over the posterior regions of the head, generally with higher voltage over the occipital areas. Amplitude is variable but mostly below 50 microvolts in the adult. Best seen with eyes closed or under conditions of physical relaxation and relative mental inactivity. Blocked or attenuated by attention, especially visual, and mental effort." This definition is entirely empirical and does not rely on an understanding of the physiological events which are responsible for the generation of the alpha rhythm. Although the spontaneous EEG has received widespread clinical application for many years, its physiological basis is still only partly understood and much controversy exists with regard to the generation and functional significance of the alpha rhythm.

A. Site of the Physiological Generator of Rhythmic Activity:

There is an almost universal agreement among investigators that the rhythmic genesis of the cortical alpha rhythm occurs in the thalamus. As mentioned earlier, the thalamic nuclei may be differentiated into two general classes on the basis of their communications with other CNS locations. The specific thalamic nuclei have cortical projections which terminate in discrete cortical areas. Examples of specific thalamic...
nuclei would include the sensory nuclei: lateral geniculate (vision) which projects to calcarine cortex, medial geniculate (hearing) which projects to superior temporal cortex, and ventralis posterior (general body sensations and taste) with its projections to post-central gyrus. Electrical stimulation of the specific projection nuclei results in activation of only that region of primary sensory cortex which receives afferent projections from that nucleus.

The other general class of thalamic nuclei would consist of those thalamic nuclei which do not project to discrete regions of cerebral cortex and would include nuclei which communicate with other thalamic and sub-thalamic centers, basal ganglia, hypothalamus, other sub-cortical centers, and also nuclei which project diffusely to widespread areas of cortex (the non-specific or diffuse thalamic nuclei). It is with regard to the projections of the non-specific nuclei that the greatest disagreement among investigators exists. This non-specific thalamo-cortical projection system was originally believed to be composed of projections from the midline and intralaminar thalamic nuclei and it was assumed that these nuclei had projections to large areas of the cortex. (1pg13, 12,13,14)

This model was based primarily on the demonstration that large areas of cortex could be activated by stimulation of the midline and intralaminar nuclear groups.

Current evidence, however, suggests that the widespread cortical activation which results from stimulation of the midline and intralaminar nuclei probably is the result of...
intrathalamic connections between the midline-intralaminar group and the specific (sensory) thalamic nuclei. The question of whether or not the midline-intralaminar nuclei have direct projections to widespread cortical areas remains largely unresolved at this time. It has also been suggested that the reticular nucleus (thalamus) might be the final neuronal element in the non-specific cortical projection system although Golgi-impregnation studies have shown that cortical projections from reticular nucleus are unlikely.

Rhythmic cortical activity characteristic of cortical alpha spindles may be elicited by electrical stimulation of many thalamic nuclei. Normal patterns of cortical spindles may be elicited following destructive lesions of the midline and intralaminar nuclei provided that the specific projection nuclei are left intact. This suggests that many thalamic nuclei may participate in the initiation and generation of spindle activity and also suggests that rhythmic activity which develops in one nucleus will most likely spread to other thalamic nuclei by virtue of an extensive network of intrathalamic connections. The relay of this rhythmic activity to cortex, however, seems to be dependent upon the specific thalamic projection nuclei.

B. Physiological Basis of the Rhythmic Activity:

Spindle activity within a thalamic nucleus is characterized by rhythmic synchronized activity in a large number of neurons. A typical thalamic spindle is shown in Figure #6 and represents
Simultaneously Recorded Spindle Activity in Thalamus and Cortex:

Both sets of recordings represent extracellular activity which was simultaneously recorded from a medial thalamic nucleus (Th. Med.), a laterally located thalamic nucleus (Th. Lat.), and the postcruciate cortex of cat. Note the perfect synchrony of the top three spindles and the bottom thalamic spindles. The lower cortical spindle is poorly synchronized with the two thalamic spindles. It can be seen that the spindles are all composed of rhythmic activity on the order of 10 Hz. See text for a more complete description. Figure taken from Andersen & Andersson (1)
the extracellular potential changes for a population of neurons in a thalamic nucleus. Several features of the spindle are immediately obvious. The amplitude of the rhythmic activity gradually builds to some maximum value and then gradually decreases. The periodic nature of the activity within the spindle is also seen to be approximately 10 Hz. At the beginning of the spindle, only a few neurons are synchronously active. As more neurons are recruited into the spindle activity, the amplitude of the thalamic spindle will increase to a maximum value and then decrease as the activity within the neuronal group becomes desynchronized. The following model has been suggested as the most likely mechanism for the generation of thalamic spindle activity.

Afferent excitatory input to a thalamic nucleus will cause an initial discharge of action potentials along the axons of those neurons whose membranes received a threshold level of depolarization. These neurons have axon collaterals which make excitatory synapses with interneurons lying within the same thalamic nucleus. The interneurons, in turn, make inhibitory synapses on a large number of neurons, all within the same nucleus. As a result of this network of axon collaterals and inhibitory interneurons, threshold depolarization of even a single thalamic neuron by an excitatory afferent input will result in the synchronized hyperpolarization (inhibition) of a large number of neurons within the nucleus. This inhibitory hyperpolarization is very intense and lasts for roughly 100 milliseconds. Following this 100 msec period of hyperpolarization,
the previously inhibited group of neurons will synchronously fire (generate action potentials) due to post-inhibitory facilitation. Axon collaterals from these excited neurons will activate a large number of inhibitory interneurons and the cycle will repeat itself as larger and larger numbers of neurons are recruited into the rhythmic activity. See Figure #7 for a highly schematic representation of this model.

As increasing numbers of neurons become rhythmically active, the maintenance of synchrony within the larger neuronal network becomes more unlikely and the number of neurons participating in the synchronized activity will gradually decrease. It is this pattern of gradually increasing synchrony of neural activity which builds to a maximum and then decreases (becomes desynchronized) which is responsible for the typical extracellularly recorded thalamic spindle. Although the model assumed that initiation of spindle activity resulted from excitatory input to a thalamic nucleus, it seems reasonable to assume that the same pattern of rhythmic activity could result from the spontaneous activity of a thalamic neuron.

The rhythmic activity of a particular thalamic nucleus is diffused throughout the thalamus due to the variety of intrathalamic connections which exist between nuclei. Thus, the rhythmic activity which begins in any of the thalamic nuclei will most likely result in synchronized activity of neuronal populations in other thalamic areas. The synchronous activity is relayed to cerebral cortex along the axons of the specific projection nuclei and causes rhythmic volleys of post-synaptic...
**Figure #7**

Thalamic Neuronal Group #1  Thalamic neuronal Group #2

*Sequence of Spindle Development:*

Legend:
- resting projection cell
- discharging projection cell
- inhibited projection cell
- resting inhibitory interneurons
- discharging inhibitory interneurons
- excitatory synapse
- inhibitory synapse

Model for the Development of Thalamic Spindle Activity:

Top figure shows relationships within a single population of neurons and between two populations. Bottom figure illustrates sequence of development of the rhythmic thalamic spindle activity. Both figures taken from Andersen & Andersson (1). See text for a description of the model.
potentials in the cortical neurons with which they make synaptic contact. The surface-recorded alpha rhythm represents this pattern of synchronized post-synaptic potentials in the underlying cortex.

The fact that widespread regions of cortex are usually involved in alpha spindle activity at the same time was originally thought to be the result of thalamic nuclei which projected to large areas of the cortex (a non-specific projection system). It seems more likely, however, that this widespread cortical alpha behavior is the result of intra-thalamic spread of spindle activity which is then relayed to specific regions of cortex along the specific projection fibers. Further support for a purely specific thalamo-cortical relay of thalamic spindle activity to cortex is the fact that cortical alpha spindles of different frequencies may be recorded from different cortical areas. This would presumably reflect the different frequencies of rhythmic activity which develops in the specific thalamic nuclei which project to these cortical areas.

C. Possible Significance of the Alpha Rhythm:

Although a good deal of speculative material may be found in the literature, the functional significance of the alpha rhythm remains unknown. It has been pointed out that the thalamus is capable of receiving a brief afferent volley from lower levels of the CNS and transforming this brief signal into a rhythmic volley of impulses (to cortex) which lasts for hundreds of milliseconds and having a characteristic
frequency of approximately 10 Hz. It has also been demonstrated that a stimulus (at cortex) whose frequency is 10-20/sec, and whose duration is greater than 100 msec, is most effective in physiological activation of cortex. This observation has led some investigators to propose that the thalamic rhythmic mechanism may operate for the purpose of converting afferent information from peripheral receptors into trains of impulses which are optimal for cortical processing.

Within this context, the alpha rhythm which is observed during periods of low levels of sensory input to thalamus would simply represent the spontaneous generation of rhythmic thalamic activity through the mechanism of recurrent inhibitory circuits described earlier. This does not imply that the rhythmic activity serves any particular "function" but suggests, rather, that it represents a state of thalamic "rest". In other words, when there is no active processing of sensory information, the thalamic nuclei are free-running, and this spontaneous pattern of activity is manifest as alpha spindles in cortex. It has also been proposed that the alpha rhythm may reflect the activity of a central "scanning" mechanism which would operate as a method for the focus (or gating) of attention to a particular sensory modality. Although it is not clear how this gating operation might be performed, there is a strong correlation between the level of attention to a stimulus and the level of alpha activity being produced. Therefore, it is likely that the alpha mechanisms are physio-
logically related to central attentional mechanisms, although they may not be functionally related.

It seems reasonable to assume that there may be some advantage in maintaining a highly organized pattern of activity among the neurons of the primary cortical sensory areas. One could speculate (and I emphasize the term, speculate) that cortical neurons which are maintained in a pattern of rhythmic depolarization are optimally "tuned" for the reception and integration of an afferent volley. Future investigations will be required in order to determine whether the alpha rhythm has some functional significance or whether it is, indeed, simply a physiological artifact of spontaneous thalamic activity.

A Physiological Model for Attentional Effects on the Alpha Rhythm and the VECP:

The preceding discussion has dealt primarily with evidence in support of theories which attempt to define the physiological basis of the alpha rhythm and the VECP. Using this information as a theoretical precedent, a mechanism for the operation of attentional variables within the scheme of sensory information processing will now be considered.

Attention is a psychological variable and is assumed to be internally generated. As with other psychological variables, there exists the obvious problem of developing a precise and consistent definition; although each of us may relate to our own subjective states of "attention" and "inattention". The 19th century psychologist, William James, defined attention

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as follows: "Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration of consciousness are its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which is a real opposite to the confused, dazed, scatterbrained state which in French is called "distraction"."

A further problem in dealing with psychological variables in scientific investigation is that these variables must be measured with indirect means. For this reason, attention is usually operationally defined within the context of the experimental procedure or else it is assumed to be reflected in some other variable which can be quantitatively determined. An example of an operational determination of attentional state would be those investigations which attempt to control attention by providing the subject with different instructional "sets". These procedures demand that the subject make some specific response which is based upon an accurate description of the stimulus. It is assumed that this discrimination-response demand will maintain attention to the visual stimulus at some higher level than if the subject were merely instructed to "watch the screen". It is further assumed that the accuracy of the subject's responses will reflect the level of attention to the stimulus discrimination task. An example of an indirect measure of attention would be the use of the alpha rhythm, since it is an almost universally accepted
observation that the amplitude of the cortical alpha activity is inversely correlated to the level of attention.

A. Attentional Effects on the VECP:

Numerous investigators have suggested that the amplitude of the VECP (and also the amplitude of other modalities of sensory-evoked cortical potentials) is positively correlated with the level of attention to the stimulus used to evoke the cortical response. (2,3,23,24,25,26,27,28,31) In other words, the amplitude of the VECP would be expected to be greater with greater attention to the stimulus and smaller with lower levels of attention to the stimulus. Implicit in this suggestion is the possibility that these different levels of cortical response reflect the operation of some internal mechanism which is functionally related to the subject's attentional status.

This attentional mechanism would provide a means for the selective facilitation of sensory signals which are of "interest" to the subject, while at the same time exerting an inhibitory or blocking effect upon sensory signals which are not of interest. The facilitated sensory input would result in the activation of cortical processes responsible for the conscious perception of the stimulus. Inattention to afferent sensory input, however, would presumably result in an inhibition or blocking of this input at some lower level of the CNS and would prevent the level of cortical processing which is necessary for a conscious perception of that stimulus to be formed. It, therefore, seems reasonable to assume that the observed attentional effects on the character of the VECP might
reflect the different levels of processing which the sensory signals attain.

B. Attentional Effects on the Alpha Rhythm:

As mentioned earlier in this paper, it is an almost universally accepted observation that the amplitude of the cortical alpha rhythm is inversely related to the subject's level of attention. This means that one would expect to find a high level of attention associated with a low level of cortical alpha activity and a low level of attention associated with a higher level of cortical alpha activity. Within this context, attention may be directed either to an externally applied stimulus or to some internal cognitive task. It might also be assumed that this attentional effect on the level of cortical alpha activity is representative of the same general internal attentional mechanism which is responsible for the observed attentional effects on the VECP.

C. Physiological Model for an Internal Attentional Mechanism:

The thalamus, with its association to the reticular activating system, has long been implicated as a functional region for the regulation of cortical activation or arousal. Almost every afferent signal terminates in the thalamus before being projected to cortex. In light of this fact, the thalamus is ideally situated for the operation of a generalized mechanism which could selectively facilitate the processing of those sensory signals which are of interest and inhibit or block the processing of those sensory signals which
are not of interest. A thalamic "gating" or attentional mechanism could presumably operate on the sensory signals either at the level of the thalamic sensory nuclei or at the level of sensory cortex. This cortical level of influence would most likely depend upon the activity of the non-specific thalamo-cortical projection system which is independent of, and parallel to, the specific sensory thalamo-cortical projections. Both of these thalamic projection systems have been described earlier in the paper.

An attentional mechanism which operates by attenuating sensory transmission of unattended afferent signals through the specific thalamic nuclei would be expected to result in a decreased amplitude of all early (and probably also the later) components of the VECP which was evoked by the unattended stimulus. Attentional effects which result from inhibition or attenuation of cortical processing of the unattended sensory input from specific sensory thalamic nuclei would be expected to show an attenuation (reduced amplitude) of those components of the VECP which reflect the level of cortical processing which is being operated upon (inhibited) by the attentional mechanism. As mentioned earlier, this cortical attentional effect would probably be dependent upon activity in the non-specific thalamo-cortical projections.

The available data suggest that inhibition (blocking) of the unattended stimulus probably occurs both at the level of the thalamus and at the level of sensory cortex; and that the inhibition of the specific sensory thalamic nuclei, as well as
the inhibition at the level of sensory cortex, are the result of inhibitory connections of the non-specific thalamic nuclei.

If it is assumed that the operation of the attentional mechanism is directed by some cortical process, then one is confronted with the problem of determining how this cortical direction is effected at the level of the thalamus. It seems likely that this occurs as a result of inhibitory inputs to the non-specific thalamic nuclei from orbital cortex.

Orbital cortex is located on the inferior aspect of the frontal lobes and is functionally located within the limbic system. This is particularly interesting since it is known that the limbic system is intimately involved in emotional and other complex psychological behaviors.

The input to the non-specific thalamic nuclei from orbital cortex arrives via the descending medial forebrain bundle and enters the thalamus at the inferior thalamic peduncle. Interruption of this pathway by means of destructive lesion or reversible cryogenic blockade results in two distinct effects: (i) an increase in amplitude of all components of the transient VECP and (ii) a reduction of spontaneous cortical spindle activity. It should also be pointed out that the non-specific thalamic nuclei have projections to orbital cortex and that this implies the existence of a functional "loop" between these two areas.

It was suggested earlier that the attentional mechanism operates by means of a tonic level of inhibitory activity
which is imposed upon the specific sensory thalamic nuclei and sensory cortex by the non-specific thalamic nuclei. Those sensory signals which are of interest (i.e. those sensory signals which are attended) will be transmitted through the specific sensory thalamic nuclei and processed in sensory cortex due to a decrease in the inhibitory effect upon that particular sensory "channel". The decrease in inhibition of that sensory channel is, in turn, the result of inhibitory input to the non-specific thalamic nuclei from orbital cortex. In other words, activity in orbital cortex produces an inhibition of non-specific thalamic nuclei; and this results in decreased inhibition (facilitation) of the specific sensory nuclei and sensory cortical areas which are involved in processing the signal of interest. Figure #8 illustrates the functional relationships involved in this theoretical model of an attentional mechanism.

In this manner, the attentional mechanism can select which sensory signals will be "processed" by cortex and which sensory signals will not be processed. When one considers the large numbers of sensory signals which are constantly being delivered to thalamus from the peripheral receptors, and the relative inability of the cortex to deal effectively with this entire barrage of information, then the value of such a selective mechanism is obvious.
Functional Connections Among the Components of a Model for a Theoretical Attentional Mechanism:

Excitatory (+) and inhibitory (-) connections are shown. Only those pathways which are relevant to the model are illustrated. See text for a description.
Conclusion:

This paper has proposed a physiological model for the generation of two types of surface-recorded cortical potentials and has suggested their possible significance with respect to several variables of human behavior. These models, however, are far from complete. In spite of this, it can be assumed that a more complete model is impending and that a better understanding of the physiological basis for these cortical potentials will ultimately lead to a more comprehensive understanding of the "nature of perception".
References:


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