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THE CORTEX AS INTERFEROMETER: THE TRANSMISSION OF AMPLITUDE, FREQUENCY AND PHASE IN CORTICAL STRUCTURES*

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Abstract—Concerning the perceptual phenomenon of object constancy: an object may be represented exhaustively in all its transformations only by introducing *phase* operators (as well as amplitude). The transmission of phase and a metric capable of handling phase in the central nervous system is thus requisite. Interferometry meets these requirements. The occurrence of interferometry in the cortex is shown to be feasible.

The cortex, it is suggested, codes frequency spatially and in the time domain. This permits phase, also, to be represented by latency changes in the time of arrival of patterning upon the cortex. Latency changes are effected by delay methods and may be considered as a kind of *temporal* modulation of frequencies.

For interferometry to work a carrier and a metric must be provided by the brain. The temporal carrier for cortical information can be constituted of indigenous cortical rhythms synchronized by a thalamic trigger. Great flexibility of measuring power is needed in order to account for the generation of information by the brain. The dipole can be shown to provide the metric capable of just such power.

INTRODUCTION

ONE OF the central issues in the study of visual perception is how "object constancy" is achieved. In order to have object constancy certain requisites have to be met in the transmissive aspects of the system considered. The view will be detailed here that it is requisite that the degree of freedom of the encoded "description" of the perceptual object remain constant in the face of changes in other aspects of the code.

The relation between constancy of the degrees of freedom of the encoded "description" of the perceptual object and "object constancy" will not be discussed here as the problem is covered adequately elsewhere in the psychology literature [1-3]. What will be discussed, however, is the problem of how the degrees of freedom may remain invariant in the face of encoding in the central nervous system. Neural transmission is affected by electrical coding. For the degrees of freedom of encoded electrical information to remain invariant, transformations on both the amplitude and phase of the electrical information must be transmitted. It is for this reason that the question of the encoding of phase in the brain is addressed.

It is common to view the cerebral cortex in electrical terms. But the descriptive mathematics and physics of electromagnetic theory find applications not only in the electrical but also in the optical field [4] where phase relations are taken account of regularly. Since cerebral cortex has both an input and output it may be described in terms of a transfer

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function between the two. This is also the case with a lens, the functioning of which can be described in electromagnetic terms. It is therefore cogent to use to advantage in an attempt to understand cortex, the quantitative descriptions which apply to optical information processing when they are applicable.

Electrical input can be described exhaustively in terms of amplitude, frequency and phase. It has been shown [5] that in an optical system information modulation can be described exclusively in terms of operations of *amplitude contrast* and *phase contrast*. It is well known that changes in the intensity of the external stimulus produce correlated changes in amplitude of responses in the cortex [6-7]. However, the phase of the light waves reflected from the external object appears undetected by the eye. Yet, phase can be generated in the central nervous system. For example, after a Fourier transformation of the pattern of intensities upon the eye "pseudofrequencies" and "phase" would be available. Unfortunately the transmission of phase has not up to now been studied directly in the brain. Yet GABOR [8](p. 384) has shown that it is not possible to find a matrix representation of sound such that arbitrary phase shifts applied to it could never be detected.

In this paper the suggestion is made that modulation of transmitted information in the cortex is carried out by the relative delay in conduction of parts of the encoded signal. This implies that frequency in the central nervous system is coded in the time domain and must be represented by the patterns of arrival of thalamo-cortical impulses.

The nature of the frequency code in the visual system raises a problem, however. In the auditory system signal frequency is readily detectable and so a clearly stipulated bit of information can be defined objectively [9, 10]. In the visual system, on the other hand, wavelength in white light is undetected as the carrier of information about edges. Thus, the absolute unit can only be defined physiologically i.e. background activity of a certain sort (e.g. positive d.c. activity) is needed against which the input is "contrasted" for registration to take place. The "minimum ray characteristic" [11] in Herzian wave theory indicates that the absolute unit of information measurement can, in certain circumstances, be undefinable. In this case what is necessary instead is an electrical contrast background. The work of BISHOP [12] and of BARTLEY [7] will be reviewed to show that, in fact, only during positive d.c. activity in the cortex is an input to the visual cortex registered.

Using macroelectrodes TUNTURI [13] in the dog and HIND [14] in the cat demonstrated spatial representation of frequencies in the auditory mode. Experimenters using microelectrodes [15] have cast doubt on tonotopic organization at this level.

If frequencies are coded spatially in the central nervous system, then phase must be represented temporally, i.e. by the time of arrival of electrical patterning upon the cortex. This method of coding will be called coding by "arrival patterns". A start was made on the study of electrical patterning in the cortex [16] but no recent work has been done.

As a rule, information is always relative to a carrier. Yet the carrier of cortical information has never been defined. This carrier need not be considered a frequency carrier. GABOR [9](p.431) noted that the Fourier integral method considers phenomena in an infinite interval, *sub specie aeternitas*. Thus Fourier's theorem makes of description in time and of the spectrum two mutually exclusive methods. GABOR's important and neglected analysis shows the strict interdependency of frequency and time—a relationship of vital concern to communication theory. The carrier could thus be a periodic structure, and subject to the physics of such structures [17]. As I have postulated that cortical structures represent frequency in time domain terms, it would seem reasonable to suppose that the carrier is

The fact that modification of information in the cortex takes place spatially as well as temporally implies the existence of *interferometry* in the cortex. Interferometry entails analog measurements of added and subtracted components—not a digital metric. LASULEY [18] and PRIBRAM [19] have already seriously suggested that the cortex processes information in a way reminiscent of wave front reconstruction. The specific proposal has been made that recognition may be based on instantaneous cross correlations among arrival patterns constituted of the spatial configurations of postsynaptic potentials which are generated. Thus, cortical function has been viewed as an example of holography [20]. The present writer has taken this approach still further by drawing the connection to visual illusions [21]. Here, it will be shown that functionally, the interferometric operations in cortex proceed by delay methods, i.e. they provide a temporal example of holography. Holographic models of temporal recall [22–24] have been presented, but fall short of adequately explaining storage in the central nervous system: the notion of a signal, interacting with a delayed part of itself and stored, may explain associative recall, but it does not explain the recognition of the signal itself.

To provide the necessary medium for interferometry between the carrier's periodicity and sensory input, the cerebral cortex must thus be constituted of a complex of analog and digital elements that is isotropic when activated by the thalamic trigger mechanisms alone, and anisotropic when affected by other input. Mechanisms to produce delay sufficient to pattern gross potentials are indeed available. These mechanisms make it likely that frequency is coded spatially into time domain (cf. Fig. 1) and that phase exists as a measure on the time of arrival of two disparate inputs.

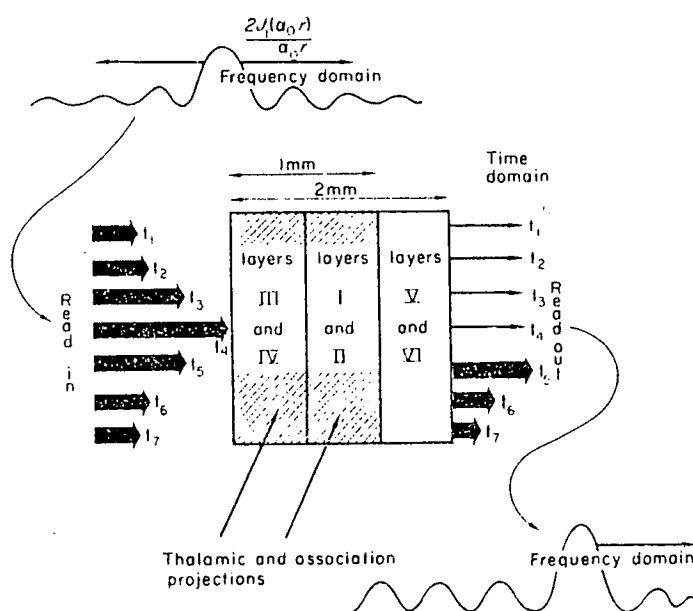


FIG. 1. Translation of frequency domain into time domain in the cortex. Arrow thickness indicates magnitude of potential. Cross-hatching indicates interferometry.

FUNCTIONAL STRUCTURE OF THE CEREBRAL CORTEX

Some of the structural details of the cortex remain the same in all mammals [25]. The arrangement of the synaptic articulations through which nerve impulses are transmitted, i.e. the plexuses of dendritic and axonal branches, remain constant. Indeed, axodendritic synapses would appear to exist in immature cortex [26]. Cell number, cell size and form vary, however, and in the lower mammals there no longer appear certain types of cells found in monkey and ape. Yet all mammals share approximately the same kind of cortical engineering. According to LORENTE DE NÓ "the reduction of the number of cells with short axons, without essential modification of the long links in the chains of cortical neurons, makes the cortex of the mouse the "skeleton" for the human cortex" [25]. Diagrams of the cortex of the mouse are used by LORENTE DE NÓ as a "first approximation for interpretation of experimental results obtained in the higher mammals" [25](p. 309).

LORENTE DE NÓ [25] classifies cortical cells into four types:

1. Cells with descending axons often reaching the white substance to be continued by a fiber of projection or of association.
2. Cells with short axons ramified in the proximity of the cell body, often within a homogeneous zone of the dendritic plexus.
3. Cells with ascending axons ramified in one or several cortical layers.
4. Cells with horizontal axons.

CLARE & BISHOP [27] presented evidence of four groups of fibers activating cortical neurons:

1. Conducting at 50 m/sec;
2. Conducting at 25 m/sec; stimulation of both these fiber groups results in responses initiated by spikes although they are superposed on a surface positive wave and followed by a negative phase. BISHOP & CLARE [28] showed that these slow phases are of dendritic origin.
3. Conducting at 8-10 m/sec.
4. Conducting at 1 m/sec.

Thus the input itself, relayed from inferior structures could be subjected to delay of certain aspects of its arrival patterning.

CLARE and BISHOP [29] inferred the following sequence of cortical firing: afferent radiation fibers immediately activate the short-axon cells of the fourth layer of the cortex, which in turn activate a first group of pyramidal cells lying at about the same level. These pyramidal cells fire their axons which leave the cortex by way of the subcortical white matter. Recurrent branches of these main axons ramifying within the cortex activate a second group of pyramidal cells. This alternate firing continues until a segment has run its course. The synaptic times between each pair of successive responses are less than 1 msec, which indicates that transmission is from axon to cell body.

According to O'LEARY [30] the essential anatomical characters of the cortex from the point of view of interpreting electrical potentials are:

1. The vertically oriented elements each consisting of a pyramidal cell body, an ascending dendritic shaft, and a descending axon.
2. The chief intracortical connections are established through the collateral arborizations of the axons of pyramidal cells and the variety of short axon arborizations which occur at different levels of the cortex.
3. In the sensory cortical areas the cortex is primarily activated through entering afferents which arborize at a level of the cortex corresponding to the granule layer (iv); in the precentral cortex the apparently but not necessarily equivalent afferent plexus arborizes at a more superficial level, probably articulating directly with superficial pyramids of medium size.
4. The activation of the whole cortex would appear to proceed through intracortical circuits arising from cells situated within the confines of the plexus of arborizing afferents. The arrangement of all contained elements is such that adequate records of cortical activity can only be expected from an intact cortex containing all of the various vertically disposed elements.

It may therefore be seen that a columnar arrangement provides a functional unit of cortex. This paper will thus underline this vertical aspect of functioning.

THE SPATIAL AND TEMPORAL DISPERSION OF INFORMATION IN THE CORTEX

According to the view presented here, the potential changes necessary to provide interferometry are not generated transcortically but by "arrival patterns" upon the cortex from inferior structures. Thus any study which afflicts the cortex with knife cuts, wires or any other interruption of horizontal conduction [31] and produces no behavioral deficit, does not rule out the possibility of cortical arrival patterns constituted vertically. The case for electrotonic spread in the cortex is very tenuous [32]. However, just as in the case of a rope held in the hand and flicked at the wrist, wave formations of electrical activity viewed at the surface of the brain may be considered as a spatial dispersion of information *without dispersion of travel of the constituent elements*. Such a phenomenon is common in geophysics [33] and oceanography [34] and lends itself to time series analysis description [35]. The vertical columnar activity of cortical units constitutes a horizontal pattern of differences in activity over time. This notion thus leads to an up-to-date *law of mass action* [36] in that there is a horizontal spread of *information* but no horizontal mechanical spread of *energy*.

If frequencies are thus represented spatially, then a dispersion of information occurs through the medium to a large degree. Also with the spatial representation of frequencies, phase becomes represented in the time domain. In the following reviewed studies, it will be shown that the patterning of electrical activity upon the surface of the cortex is the outcome of modulated activity within the columnar units of the cortex effected by delay. The relation of within-cortex delay modulations to surface-cortex phase representation over time will be indicated.

The relation between EEG phenomena and surface dendritic activity finds some advocates; others see the relation between cellular discharge and the EEG. CREUTZFELDT *et al.* [37] relate the origin of potential changes in different neuronal parts and the spread of potentials along the somadendritic membrane to the EEG. They state that at the end of a high frequency stimulation series in the specific thalamic nuclei, the EEG record may show a large positive swing which returns slowly within 300-500 msec. to the baseline. This positive swing is accompanied by a slow hyperpolarization of cellular membrane potentials which decreases with a similar time course.

A surface electrode located above the apical dendrites will "see" a potential which is the result of several mechanisms: a quick depolarization of the soma or near soma membrane (fast EPSP after VL stimulation), will first be "seen" as a surface positive potential and then change into a negative one, whereas a fast polarization (beginning of large synchronized IPSPs or repolarization after spike potentials) will be first "seen" as a surface negative potential before the polarization changes the rest of the membrane.

The data of SUZUKI and OCHS [38] support the author's supposition. Weak surface stimulation produced a purely negative surface potential restricted to the superficial layers. Stimulation below 0.5 mm, however, produced a biphasic positive-negative response. This means, in the author's analysis, activation of apical dendrites in the former case, and of deep structures close to the soma in the latter case.

The primary surface negativity after VL stimulation is considered to be due mainly to the synchronous afferent volley; the primary EPSP which appears on the crest of the primary positivity may add to the surface positivity if it is assumed that the specific afferents terminate mainly deep on the soma-dendritic membrane. The corticofugal spike discharge adds to the surface positivity. The primary negativity may be partly due to the electrotonic depolarization of the dendrites and is enhanced by the secondary slow EPSPs, which might even be due to the excitation of ascending recurrent collaterals.

The authors suggest that the beginning of the IPSP (fast transient localized on or near the soma) plays an important role in shaping the primary surface negativity during single stimuli. The primary surface negativity may be considered a mixture of transients from depolarization to polarization at or near the soma. The frequently observed late negative wave especially during slow stimulation at 3-4/sec can be explained by the slow tertiary IPSP. In some cases the decay of the IPSP leading to relative negativity of the soma-dendritic membrane may lead to a surface negativity. The suggestion is that ADRIAN's [39] "superficial" response, (the first negative potential), is correlated with excitatory responses either in the dendrites or soma-axon. The "deep" response, (the ensuing positivity), corresponds to the IPSP.

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It matters little to the present argument whether the interaction processes within the cortex are dependent upon the potential changes occurring at a synapse or an ephapse—the output will still be electrical. The conception of cortical “arrival patterns” depicting phase in temporal terms draws attention to the spatial interactions of cortical activity without, however, postulating *transcortical* conduction of such activity.

The transmission of phase within the medium provided by the cortex is documented obliquely in many studies. One can note that both amplitude and frequency changes in auditory stimulation find correlated changes in the cortex [40]. NEFF *et al.* [41] and NEFF and DIAMOND [42] showed that bilateral, though not unilateral, ablations of AI, AII and EP in the cat leads to a severe deficit in the ability to localize sounds in space. The ability to spatially localize in the auditory system, therefore, must be dependent upon the *transmission of phase relations between the stimulation at the two ears*. To suppose an anatomical correlate of right and left in one hemisphere is unrealistic.

It is impossible to distinguish between left and right spatial locations for sounds by intensity differences alone for the following reason: suppose at the cortical level *all* cells fire to either *R* or *L* stimulation. Suppose a sound loses 1/2 its effect by traveling around the head. If there are two inputs *a* from *R* and *b* from *L*, a cell may have to distinguish between ($a/1/2b$) and ($1/2b/a$), i.e. between a *R* or *L* sound in space. If the cell “knows” *a* is right and *b* is left it will be able to do this. However, the cell fires to both inputs and therefore it cannot have this “knowledge”. Suppose *all* cells fire only to a *R* stimulus or to a *L* stimulus. In this case the comparison occurs elsewhere than at the cellular level. Suppose *some* cells fire by both *R* and *L* stimulation. By virtue of *R* and *L* specific cells *a* is registered as *R* and $1/2a$ as $1/2R$; *b* is registered as *L* and $1/2b$ as $1/2L$. The firing of the binaurally activated units (which require *both* inputs) indicates only *one* sound in space. However, the comparison ($R > 1/2L$) or ($1/2R < L$) by the specific cells still has to take place. As these monaurally activated units could be interconnected this could be achieved. But this comparison of the two inputs (as frequency is spatially located) would be spatial and the registration would be in terms of phase.

In the auditory system there is an immediate conversion from frequency to spatial location at the sensory level. In the visual system there is no such sensory conversion because frequency is undetected. However, the treatment of spatially located areas of excitability as if they were spatially located “pseudofrequencies” means that for purposes of information transmission both auditory and visual systems may be treated alike. As already noted, from the fact that a spatial dispersion of frequencies occurs, it follows that phase exists in the time domain.

A CARRIER FOR INFORMATION IN THE BRAIN

Except where there exists a “preformism” between stimulus and reception in the case of primitive structures, there must be a “carrier” or coherent “predictable” source on which modulations may effect a noticeable change. The difference between the temporally unmodulated coherent source and its modulation would constitute a source of information. Reference has already been made to regular cortical activity which is triggered by thalamic input. This is a coherent source. The possibility for cortical interferometry can be seen by considering the differences and similarities of augmenting and recruiting responses.

MORISON and DEMPSEY [43–46] showed that both recruiting and augmenting waves increase the amplitude of cortical response to repetitive (5–10/sec) shocks to the thalamus. JASPER and HANBERY [47–49] have shown that the pathways for recruiting and augmenting waves represent different processes.

Recruiting waves are surface negative with long latency (ca. 15–30 msec) and with a smaller surface positive phase occasionally preceding and often following. Complex polyphasic forms are common. Recruiting waves are most easily elicited by stimulation of the medial one-third of the thalamus and occupy the upper dendritic layers of the cortex. They are maximally recorded in cortical regions other than the primary sensory projection areas with a distribution and morphology similar to that of spontaneous slow wave “recruiting spindles” seen in barbiturate narcosis and sleep.

Augmenting waves have a latency of approximately 10–20 msec, and follow repetitively elicited primary sensory responses to stimulation of thalamic radiations at the same optimum frequency for recruiting responses. An augmenting wave is an increasingly large negative wave with a peak 5–15 msec, later than the peak of the specific response negative wave.

JASPER [50] found that auditory, visual and somato-sensory responses evoked peripherally and in the relay nuclei were unaffected by reticular or medial thalamic stimulation, although the delayed waves after the primary response were usually suppressed. JASPER and AJMONE-MARSON [51] showed facilitation of the surface-negative phase of the primary response to optic nerve or lateral geniculate stimulation by a simultaneous negative wave from the medial thalamus. The negative phase of the sensory response might be depressed by an "intralaminar response" and the latter might be depressed following the optic stimulus.

BISHOP [12] found in some cases with rabbit as subject, that even where the spontaneous rhythm of the cortex is low, weak shocks to the optic nerve are effective only when they fall in certain phase relationships with an inherent cortical rhythm which is not accompanied by a potential fluctuation in the record. An interval of about 0.2 sec or multiples of this can be found at which successive shocks will be equally effective. A slight change of *phase* relationships at the same frequency, will alter the amplitude of the whole series of responses. A slight change of *frequency* will cause an alternating slow increase and decrease of successive responses in a manner strictly corresponding to beat frequency phenomena.

A single volley from the optic nerve synchronizes corticothalamic circuits even if they are asynchronous and their summated responses then follow periodically as part of the cortical response to stimulation. BISHOP remarks that the series of spikes which appear on the main cortical discharge may represent the repetitive discharges of cortical *visual* elements; when not appearing as separate spikes, temporal dispersion may fuse them to a smooth elevation. BISHOP states (p. 313): "The evidence points, then, to a peculiar circumstance of cortical stimulation. The afferent impulse alone is in general unable to traverse the higher neurones of the visual pathway, but it is able to activate the parallel coordinating pathways which in turn facilitate the visual pathway to passage by afferent impulses. The significance of such a mechanism for vision is not apparent."

However effective the first maximal shock to the optic nerve, the response to the second is maximal only after a 0.2 sec interval, being absent during an interval of 80–100 msec, after the first. The cortex is thus accessible to a second stimulus only after the first stimulus has completed the circuit through the successive elements of the cortex. Even with maximal stimuli, facilitation by corticofugal pathways is essential for passage of the critical synapses.

Thus two coincidental impulses are required to fire a synapse. One from the periphery and one from the cortex is necessary for input from the visual pathway to cause a response in the cortex. The frequency of the necessary cortical discharge is 5 per sec and would appear to be triggered from the thalamus. This could serve as a coherent "carrier" to optic nerve discharges of higher frequency—not a "carrier" that is frequency modulated, however; there is, rather, a *temporal modulation of frequency*. Its action, (as it is suggested that positive d.c. activity is required for registration of input), is that of a band pass filter in the time domain.

As early as 1830 Cauchy obtained the result that for waves with wave lengths large compared with the distance between point masses in a one-dimensional lattice, velocity is independent of wavelength.

Let d = distance between regularities: 5 per sec (in our example)

a = reciprocal wavelength

V = phase velocity

ν = frequency

then v is a periodic function of a with period $1/d$ and $V=v/a$. It can be shown, therefore, [17](p. 7) that all ambiguity in wavelength and direction of motion is removed if a is restricted to the interval:

$$-\frac{1}{2d} \leq a \leq \frac{1}{2d}$$

except in the two special cases where

$$a = \pm \frac{1}{2d}$$

Unambiguous frequency modulation can only occur if the carrier frequency (v_c) is twice the modulating frequency (v_m) or more:

$$v_c \geq 2v_m$$

GABOR [9] and STEWART [52] have shown the reciprocal relationship of frequency and time (t) in information transmission:

$$\Delta f \cdot \Delta t \approx 1$$

this implies therefore:

$$t_c \leq \frac{t_m}{2}$$

We shall return to the meaning of t_c later. In the sense that a cortical rhythm of 5 per sec provides maybe 5×100 msec, "windows" per sec (of positive d.c. activity), t_c could be considered 100 msec.

There are two interesting but probably coincidental outcomes to this line of reasoning: if one considers the 5 per sec frequency as a temporal occurrence, then from

$$t_c = \frac{t_m}{2},$$

t_m is 10 per sec; 10 c/s is also the so-called alpha rhythm. Perhaps the slowest "temporal-frequency" able to modify the inherent cortical rhythm is the alpha rhythm; GABOR [9] (pp. 452-453) conducted preliminary experiments with a "frequency converter" in the auditory mode. He estimated the best "window length" for the unambiguous transmission of information would be 100 msec. This was our supposed estimate for t_c . A smaller interval (i.e. a higher frequency) results in informational loss. These two observations could be circumstantial; may be they are not.

BISHOP *et al.* [53] recorded between a surface electrode on the lateral gyrus and one in the subcortical white matter in the visual cortex of cat. The investigators consider the augmenting phenomenon to be correlated with stimulation of slowly conducting corticopetal fibers passing near to the lateral geniculate nucleus and mingling with radiation fibers to the cortex. When augmenting and recruiting waves were recorded from the same locus, augmenting waves could be occluded by preceding recruiting responses (possibly with some facilitation of the primary response) and vice versa. Both recruiting and augmenting waves occupy the same (0.4-1.0 mm) upper region of the cortex.

LANDAU *et al.* [54] investigated the interactions of several varieties of evoked responses in the visual and association cortex of cat. It was found that the optic response was practically always greatly facilitated during high frequency (80-200/sec) intralaminar stimulation. Surface positive current depressed the positive and exaggerated the negative phase of the specific response, surface negative current doing the reverse. Tetanic stimulation of the medial thalamus induced large well-synchronized waves in the cortex but whose frequency bore no relation to the stimulus frequency. Post-tetanic potentiation of the callosal response was accompanied by depression of the optic radiation or no change in it. The response in the lateral gyrus, however, was sometimes partially occluded by a tetanus (100-200/sec) to the optic radiation. Callosal, recruiting and direct cortical responses all involve local graded activity in dendritic tissue as only occlusive interactions were seen when any of these sites were stimulated.

The authors state that two general types of mechanism appear to be involved, which can affect different regions of the same neuron. One is the specific sensory response, which is transmitted at and above the IV cortical layer to the lower poles of pyramidal cells. The second type of activity is generated via axons impinging directly on apical dendrites of pyramidal cells.

Their experiments suggest that the superficial layer of the cortex is a collecting net for various impulses from many loci. Any type of response activating apical dendritic terminals may show interactions with any other activity occupying the same dendrites, and all such activities should be capable of affecting the excitability of the axon spike generator.

If radiation afferents are stimulated and the cortex is directly stimulated [51] in appropriate time relations, the negative phase of the diphasic wave following stimulation of the specific thalamic radiation interferes with the simple negative wave response to antidromic synaptic activation of dendrites, and vice versa.

CLARE and BISHOP [27] conclude that the essential features of central nervous system rhythmicity are predominantly functions of the excitability cycle of dendritic synapses, such as may be exhibited in relative isolation in the recruiting responses of apical dendrites of cortex.

THE VALUE OF A DIPOLE IN PROVIDING A METRIC

It has already been stated that phase modulations could take place by delayed conduction. If these methods of delay were carried out digitally, then the cortical engineering involved would be unwieldy. Analog processes which provide delay are far more plausible. The interactions of disparate inputs are presumed, therefore, to take place by analog summations and subtractions. A dipole fulfills this requirement and will be addressed in this section. First, studies will be reviewed showing that analog interactions can take place within the cortex modifying the activity of the cortical rhythm, then the dipole itself will be considered.

TRAUBKA and ROETLING [55] have shown how objects of known shape may be detected in a slowly varying background by thresholding the cross correlation of the object seen with an aperture mask consisting of two narrow bands, one of positive transmittance and the other of negative transmittance, close to and on opposite sides of the object outline.

In the sensori-motor cortex in the *cerveau isolé* or barbiturate anaesthetized cat, spindle waves recorded from the surface are composed of alternating excitatory and inhibitory post-synaptic potentials [56]. The investigators postulate that these potentials are generated by the radially oriented pyramidal neurons and location of the synaptic activity to be along the extent of the apical dendritic shafts of these neurons, probably including the soma membrane and basal dendrites as judged by large amplitude of PSPs recorded with intracellular microelectrodes. Referring to other studies with microelectrodes [57, 58], the authors consider spindle waves to exert a modulating or "gating" action upon the excitability of cortical neurons. In this study, too, a dissociation was found between surface dendritic and soma membrane potentials. Increased firing of pyramidal tract neurones with slow positive shifts in potential occurred with spindle waves of surface negative sign. Spontaneous slow waves of 300 msec, duration were noted at a frequency of 3 per sec. Slow surface waves were inhibitory and intracellular oscillations are composed of excitatory (depolarizing) and inhibitory (polarizing) components of 5-17 mV amplitude. STEFANIS and JASPER [59] stimulated axons in the pes pedunculi and recorded the antidromic responses in cortical pyramidal tract neurons with intracellular microelectrodes. The antidromic IPSPs were found to originate mainly from synaptic sites of the soma membrane close to the spike trigger zone. Both EPSPs and IPSPs could be recorded from the same neurons, indicating, perhaps, that collateral connections can be modified with respect to their excitatory or inhibitory effects.

CLARE and BISHOP [60] consider apical dendrites to affect the cell body electrotonically and the conduction downward to be decremental, local and not all-or-none. The conduction velocity in dendrites is slow: CHANG [61] reports 2m/sec along the surface of the motor area. In previous attempts to account for such slow wave phenomena, it was noted that following a striate cortex response, the 5 per sec after discharge often broke up into bursts of shorter waves, the briefest of which, approximately 15 msec, in duration, corresponded to the duration of the primary specific response.

For our purposes the interesting observation was made that since apical dendrites exhibit no absolutely refractory period, a second response initiated during the first sums with it. By repetitive stimulation a continuous negativity can be maintained. Thus modulation of stimulation afferent to dendrites alone could induce potential wave forms of any duration.

CLARE and BISHOP [29] showed that in the upper 0.3 mm of the cortex, when there are few cell bodies and a high concentration of dendrites, single electric shocks applied to the cortical surface give rise to surface negative waves of 15 msec, duration. Below the cortical surface, the electrode elicits a surface

positive wave succeeded by a surface negative wave. When cell bodies are reached, spikes are superposed on the surface positively. At the base of the cortex, the record is the same as that of the cortical response to optic nerve stimulation.

The propagation of the dendritic impulse upward in the cortex is so slow that with a conduction distance of less than 2mm, the surface of the cortex may remain positive for 5-10 msec, before the dendritic impulse arrives to reverse the potential.

In present day computers with analog to digital conversion input-output devices, there is an absolute zero level given for the digital measurement which should be aligned with the absolute zero of analog measurement. It is questionable, however, whether an analog measuring device is truly analog with an absolute zero. A dipole, however, would appear to dispense with an absolute zero and is a true analog measuring device with great flexibility due to its equilibrium properties.

BISHOP and CLARE [28] investigated the response of the cortex to direct cortical stimuli applied at different depths. Agreeing with ADRIAN's [39] early work, the negatively responding elements acting at the surface were inferred to be either apical dendrites or horizontally oriented short axon cells of the first layer. The positive component was assigned to the activity of elements deep in the cortex and the negative to elements near the cortical surface. This relation indicated propagation of activity upward from below in the normally activated response thus suggesting the feeding to a dipole.

Two negative components were recorded in the response to stimulation. The earlier is weak but greatly accentuated by strychnine; when strychninized cortex is activated via the radiation, the usual positive wave precedes the exaggerated negative; when strychnine spikes occur spontaneously, the surface negative spike may or may not be preceded by a positive corresponding to that of the specific response.

In the normal discharge to afferent stimulation, the earlier negative wave represents antidromic conduction along apical dendrites; this response is not usually maximal and strychnine accentuates it. The later negative wave of the specific response arises from below in the IV layer of the cortex and may represent the response of the fusiform cells of layer VI.

When the suprasylvian cortex was stimulated on the surface, the upper third of the cortex showed a surface-negative reaction. It was shown that there is a failure of conduction of dendrites from below; the speculation is that decremental conduction must take place along apical dendrites from below, as practically all pyramidal cells have apical dendrites and many dendrites from lower layers reach the surface.

Direct activation of the optic area gave the same results as obtained from the suprasylvian gyrus, eliciting a surface negative wave of 10 msec, duration. Stimulated below 0.5 mm, recording between surface and deep electrodes, there occurred an initial positive spike superposed upon the surface positive phase of the diphasic response. With the stimulating electrode at greater depth, a second spike followed the first, followed by a third. The authors consider that the negative response to optic nerve stimulation is assignable to conduction in apical dendrites. The surface positive phase is considered the activity of basal dendrites of pyramidal cells and is non-conductive.

Following surface stimulation, the shallower of 2 recording electrodes becomes negative close to the surface, but the deeper lead fails to show any activity. Apical dendrites are capable of downward conduction under some conditions. When strychnine is applied to the optic cortex, its effect is to cause increased dendritic response to optic nerve stimulation, and also sets of spontaneous waves (strychnine "spikes") assignable to the activity of dendrites.

A sequence of at least three prominent spikes indicated that three groups of cell bodies discharged successively. Recording at different depths within the cortex revealed that the cells involved are the pyramidal cells, and that the later groups to fire in the sequence are those which on the average lie shallow in the cortex.

ADRIAN's [39] initial investigation of the direct cortical response described two kinds: a "superficial response" surface negative and lasting from 10 to 20 msec, and a "deep response" surface positive of the same duration or longer. The superficial response was thought to spread along either dendrites or Cajal cell fibers in the molecular layer. The deep response was thought to spread synaptically over neurones deeper in the cortex. The "dendritic response" spreads decrementally to a distance of 1 cm, which is a greater distance than the lateral maximum spread of dendrites—4 mm.

OCHS [62] considers the direct cortical response to be due to directly activated cortico-cortical fibers terminating on pyramidal cells in the responding area in two groups: an upper group on dendrites causing a surface negativity and a lower one on somas giving a surface positivity. The potentials are considered post-synaptic of the pyramidal cell. Again this suggests the occurrence of a dipole.

OCHS and SUZUKI [63] showed that the negative wave of the direct cortical response is transmitted by neuronal elements present in the molecular layers. This was shown by a molecular layer preparation where the cortical layers below the uppermost layer and, in addition, the cortico-cortical fiber path below the cortex were cut. Such cuts did not block transmission of the negative wave. Another type of transmission

link was shown after making cuts through the whole of the cortex. The responses transmitted were positive-negative DCRs with a longer latency and preceded by a small fast spike wave.

LANDAU *et al.* [64] analyzed evoked cortical potentials under the influence of polarizing currents. Although the major surface positive wave is diminished by surface positive polarization and increased by surface negative polarization, the initial radiation spike is affected in the opposite way.

Using the isolated frog brain, GERARD and LIBET [65-67] blocked synaptic conduction with nicotine but found electrical waves of regular shape still present in the cortex. Large caffeine waves, which travel at about 6 cm per second were not abolished by nicotine and often not even by a complete transection of the entire cerebrum. They proposed that the cortical sheet behaves as does a polarized layer.

MORRELL [68] showed that an auditory stimulus, which by itself evoked no response in rabbit cortex, produced a 0.5-1 mV SP shift if the auditory stimulus was followed by electrical stimulation of the center median nucleus.

RUSINOV [69] reported the appearance of slow potential changes in the visual area when a light stimulus came to evoke a defense reflex. ROWLAND and GOLDSTONE [70] demonstrated SP shifts of 100-200 mV to a 2/sec click or flash stimulation if the latter were reinforced by offering the animal food 2 sec after the sensory stimulus.

BURES [71] showed that the development of conditioned responses can be blocked by KCl induced spreading depression in the cortex of the rat. Spreading depression was identified by the negative slow potential change which is believed to reflect massive neuronal depolarization.

The data of MORRELL, RUSINOV, BURES and ROWLAND and GOLDSTONE indicate not only that changes in learning are reflected in changes in the steady potential, but also that learning is blocked when the steady potential is negative (BURES).

The data from strychnine studies should be viewed in the light that strychnine solution ($10^{-2} - 10^{-3}$) causes the cortex to become 200-300 mV, negative to the ventricle or sub-cortical white matter. Negative aftermaths also follow spikes induced by surface application of curare.

O'LEARY and GOLDRING [30] believe that all electrical phenomena can be gathered under the workings of the pyramidal cell which presents a resting potential gradient along the length between its subsurface dendritic plexus and its soma.

I have thus marshalled the evidence to show that a "metrical system" exists in the brain. The ability to measure means that one source of input may modulate the effects of another but without the use of occlusive devices such as all-or-none inhibition or excitation. Effects can be additive and subtractive. Conceptions of digital neural nets have long been in vogue that seem to the present writer to have badly misled students of brain functioning. Digital elements are required merely to transport earlier happenings of an analog nature. The neural-net notions of digital firing have been concerned with *information transmission*, which would appear to be a less important problem than that of *information engenderment*, which can be handled by the concepts proposed here.

CONCLUSION

Concerning the perceptual phenomenon of object constancy: an object may be represented exhaustively in all its transformations only by introducing *phase* operators (as well as amplitude). The transmission of phase and a metric capable of handling phase in the central nervous system is thus requisite. Interferometry meets these requirements. The occurrence of interferometry in the cortex is shown to be feasible.

The cortex, it is suggested, codes frequency spatially and in the time domain. This permits phase, also, to be represented by latency changes in the time of arrival of patterning upon the cortex. Latency changes are affected by delay methods and may be considered as a kind of *temporal* modulation of frequencies.

For interferometry to work a carrier and a metric must be provided by the brain. The temporal carrier for cortical information can be constituted of indigenous cortical

rhythms synchronized by a thalamic trigger. Great flexibility of measuring power is needed in order to account for the generation of information by the brain. The dipole can be shown to provide the metric capable of just such power.

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Résumé—A propos du phénomène de la constance des objets, on admet qu'un objet ne peut être représenté de façon exhaustive selon toutes ses transformations que par l'introduction des opérateurs de phase (aussi bien que d'amplitude). La transmission de la phase et un système capable de la mesurer au niveau cérébral sont ainsi réclamés. L'interférométrie permet de satisfaire ces conditions. On montre la possibilité de l'interférométrie au niveau du cortex.

On suggère que le cortex code la fréquence spatialement et temporellement. Ceci permet aussi que la phase soit représentée par les modifications de latence dans le temps d'arrivée du "patterning" sur le cortex. Les modifications de latence sont effectuées par des méthodes de retard et peuvent être considérées comme une espèce de modulation temporelle des fréquences.

Pour qu'il puisse y avoir interférométrie, un système de transport et de mesure doit être fourni au cerveau. L'effecteur temporel de l'information corticale peut être constituée par des rythmes d'origine corticale synchronisés par un déclencheur thalamique. Une grande flexibilité du pouvoir de mesure est réclamé pour rendre compte de la génération de l'information par le cerveau. On peut montrer que le dipôle procure le système de mesure capable d'un tel pouvoir.

Zusammenfassung—Zum Wahrnehmungsphänomen der Konstanterhaltung des Objekts ist zu sagen: Ein Objekt kann in all seinen Umgestaltungen allein durch Strukturen, die auf die Phase ebenso wie auf die Amplitude der Schwingungen einwirken, erschöpfend dargestellt werden. Die Übertragung von Phasen und ein Meßelement im Zentralnervensystem, das auf Phasenverschiebungen anspricht, sind daher notwendig. Die Interferometrie erfüllt diese Bedingungen. Es wurde gezeigt, daß Interferometrie im Cortex möglich ist. Man muß annehmen, daß die Hirnrinde durch räumliche und zeitliche Verschiebungen der Frequenz eine Chiffrierung bewirkt. Dies erlaubt der Phase auch, durch Latenzwechsel bei der Ankunft der mustererzeugenden elektrophysiologischen Vorgänge auf den Cortex repräsentiert zu werden. Latenzwechsel werden durch Verzögerungsmethoden hervorgerufen und können als eine Art zeitlicher Modulierung der Frequenzen betrachtet werden.

Um Interferometrie wirksam werden zu lassen, müssen ein Träger- und ein messendes System von Gehirn vorgesehen sein. Das zeitliche Trägersystem für corticale Information kann aus den eigenständigen corticalen Rhythmen, die durch thalamische Strukturen synchronisiert werden, gebildet werden. Es wird eine große Flexibilität der messenden Kräfte benötigt, um die Erzeugung von Informationen durch das Gehirn zu ermöglichen. Es kann gezeigt werden, daß der Dipol ein für eine derartige Kraft empfindliches Meßelement darstellt.