Neural Coherence and the Content of Consciousness

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INTRODUCTION

On the one hand Dr. John's paper is a reintegration of previous animal work originally published during the period 1959 to 1977, and on the other hand, it is a refocusing on a subset of this work translated to human subjects.

The subissue in Dr. John's paper is the content of consciousness and not, specifically, the operation of consciousness. Previously, Dr. John helped to show why it is anatomically and functionally helpful to distinguish between the operation of consciousness and the content of consciousness (Thatcher and John, 1977). To briefly review, the "general operation of consciousness" (GOC) is characterized by longer time intervals and relatively time invariant processes such as sleep, wakefulness, arousal, and coma. The GOC is a relatively tonic state, with slow adjustments of the levels of arousal (i.e., on the order of minutes and hours), such as occur during changes in levels of awareness and/or drowsiness and mediated by reticular-limbic and thalamic excitatory control systems. In contrast, the "content of consciousness" (COQ is defined as the momentary collection of sensations and thoughts that we would call the "present moment," which is temporally and hierarchically nested within the GOC and is mediated by the coherent activation of large ensembles of neurons. William James referred to the content of consciousness as the "specious present," which he defined as that "interval of time (about 1 to 7 seconds) when an event that belonged to the present is distinctly perceived as the past" (James, 1890). A finer temporal grain of the content of consciousness is provided by the psychophysical experiments of Efron (1967, 1970a,b) and others (Fraisse, 1963; Shallice, 1964) that demonstrated an approximately 20- to 200-ms "perceptual frame" in which nearly simultaneous events were integrated into a perceptual whole. Subsequent EP studies have indicated that the duration of the frame increases as a function of the complexity of the integration, especially as shown in P400 studies (Thatcher, 1976, 1977a). As Dr. John pointed out in 1977, the running average summation of the content of each of the approximately 20- to 200-ms perceptual frames may represent a temporal limit of the momentary content of consciousness (Thatcher and John, 1977). Experimentally, the duration of the integrative perceptual frame varies de

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pending on the salience and sensory modality of the stimulus (Efron, 1970a, 1970b). However, explicit to the concept of a perceptual frame is a temporal limiting process which itself could be defined as a general operation of consciousness; i.e., when temporal boundaries are invoked then a defined general operation is necessary to govern the onset and offset of the integration process. This emphasizes further that a general operation and the content of the operation are temporally nested.

Dr. John's paper is a revisitation and reintegration of these views, with experimental emphasis on the COC involving coherent neural activity. Dr. John presented many similar findings as early as *1975* (Thatcher and John, 1975). In the 1975 paper Dr. John used temporal principal component analyses with Varimax rotation (TPCVA) of evoked potentials in a delayed matching paradigm using noncontingent probes that preceded and followed the delivery of information. Dr. John found a similar interstimulus interval response in 1975 that he reports in his present paper (i.e., a P1 vs. P2 effect). During the period from 1974 to 1980 a series of delayed matching from sample experiments were conducted in the Brain Research laboratories which supported Dr. John's findings (Thatcher, 1976, 1977a,b, 1978, 1980; Thatcher and Maisel, 1979). This work was reviewed and summarized in a publication entitled "Functional Landscapes of the Brain: An Electrotopographic Perspective," in which the results of both SPCA and TPCVA analyses were presented in a series of DMS experiments (Thatcher and Maisel, 1979). It is interesting to note that not only was a similar P1 vs P2 effect observed but that the strength and persistence of the effect increased as a function of task demand (Thatcher and Maisel, 1979; Thatcher, 1980).

THE ISSUE OF ZERO PHASE LOCKING

Zero phase locking of coherent neural activity during perception and memory is a topic that Dr. John has also significantly contributed to (John and Killam, 1959; John, 1961, 1967, 1972; John and Morgades, 1969a,b; Ramos et al. 1976a,b,c). His work in this area predates the currently popular experimental rediscovery of "zero phase lag coherent neural activation" in animals (Singer, 1994; Gray et al. 1989; Eckhorn et al. 1988; Murthy and Fetz; 1992). For example, experiments by John and Morgades (1969a,b) and Ramos et al. (1976a,b,c) showed that clusters of coherent multiunit activity can be elicited from widespread brain regions of the cat during stimulus generalization. Most importantly, the pattern of coherent multiunit activation often reflected the temporal characteristics of a remembered stimulus (see reviews of this work by John, 1967, and Thatcher and John, 1977).

As for Dr. John's present paper, what is especially unique and important is the finding of five spatial principal components (SPCs) capable of accounting for 90% of the variance of scalp voltage patterns which appear to reflect coherent activation of large ensembles of neurons. The finding that the loadings of these SPCs were similar during different cognitive tasks and in different subjects suggests fundamental subsets of organized neural resources that are common to all people performing these tasks. The interesting presence of a P1 vs. P2 difference landscape suggests further that these SPCs reflect a binding process that brings together spatially distributed fragments of the past to evaluate the immediate present.

A MODEL OF EEG COHERENCE AND NEAR ZERO PHASE

Dr. John's DMS findings inspired me to revisit some old thoughts about the role of near zero phase lag. For example, let us consider that in Dr. John's study that a "General Operation" is the process of "binding" through near zero phase lag (NZL) and that this stable state enables coherent neural activity to produce the "content of consciousness."

In this light, two critical and still unanswered questions remain: (1) what are the mechanisms by which distributed neural ensembles become coherently active at zero phase lag? and (2) what are the mechanisms by which neural resource is allocated through zero phase lag coherent activity? The answer to the first question appears closer to an explanation than the second. For example, mathematical and simulation studies by Grossberg and Somers (1991) demonstrate that zero phase locking between connected networks occurs whenever two conditions are met: (a) there is strong coupling and (b) there is some form of delay (or inhibition) involved in the coupling between networks. Other workers have postulated a specific role of feedback and feedforward inhibition in the creation of synchronized zero phase locked neural activity (Lytton et al., 1992; Traub et al., 1996). Thus, strong coupling and delays appear to be necessary and essential elements in the establishment of zero phase lag coherent neural activity. However, precisely which brain regions (e.g., thalamus, reticular formation, limbic cortex, etc) control the spatial and temporal distribution of inhibitory and excitatory drives at a given moment of time is very complicated and, likely, task specific. Dr. John's present paper suggests the presence of a finite set of spatial constraints that operate on ensembles of cells, thus producing the five basis functions of the SPC. Although the relative activation or loading for any given set of spatial constraints varies from task to task and subject to subject, nonetheless, it is suggested that the combination of a limited set of constraints is sufficient to explain the allocation of neural resource. This is an interesting idea, one that deserves further experimentation.

The second question is more fundamental than the first question and, also, more difficult. Recently, I had the pleasure of working on the problem of neuronal resource allocation while at the National Institutes of Health. The experiments involved the neuronal mechanisms .by which human voluntary movements occur using multimodal registration of EEG, MRI, and PET (Thatcher et al., 1993a,b, 1994). EEG coherence and phase measures were obtained before and after finger movements and specific patterns of neuronal activation were observed to correlate with the allocation of resources that underlay the finger movements. A neural network switching model was developed in which loops of cells behaved similar to spinning tops or gyroscopes. The justification for this view was the computation of strong second derivatives involved in the dynamics of neuronal switching could not be explained by standard neural network models that involve nearly instantaneous switching dynamics.

One hypothesis is that phase locking serves to link associated features in different neural systems to form a coherency of spatially organized phase and frequency relationships within and between neural networks (Grossberg, 1976; Grossberg and Somers, 1991; von der Malsburg and Schneider, 1986; Baldi and Meir, 1990). According

to this hypothesis, phase shifts represent neural network "punctuation marks" or "delimiters."

In the motor movement studies by Thatcher et al. *(1994),* a phase shift at the beginning of a movement reflects a spatial expansion process whereby the neural networks that may potentially mediate the motor response are first identified and labeled as members of a functional set whereby the members of the functional set are phase locked into a shared or coherent network of resource readiness during which different combinations of neural networks are decoupled and recoupled for the mediation of different aspects of movement. A phase shift at the end of a movement represents the release of neural networks and coupled resources from their phase locked state so that neural elements are free to form new configurations or to become part of future motor movements and future phase locked configurations (Thatcher et al., *1994;* Thatcher, *1995).*

In order to link Dr. John's EEG coherence observations, previous studies of human scalp EEG coherence have shown that short (e.g., 1 mm to 1 cm) and long (e.g., 1 to 30 cm) distance connections exhibit different spatial gradients of coherence (Thatcher et al., *1986;* Pascual-Marqui et al., *1988).* For example, short distance connections exhibit a "diffusion" gradient of change with distance characterized by a negative exponential, while long distance connections exhibit a cyclical spatial gradient, depending upon the location of cortico-cortical fasciculi (Thatcher et al., *1986).* If we assume that the number and strength of synaptic inputs are constant and invariant, then the mean value of coherence at different interelectrode distances is primarily a function of the number of short and long distance connections. The empirically derived equation to describe human EEG coherence based upon short versus long distance connections can be modified so that the strength of synaptic coupling is a function of the number of short and long connections:

$$C_{ij} = A_{ij}e^{-kd} + B_{ij}e^{kd}\sin kd \qquad\qquad \textbf{Eq.}(1)$$

where C_{ij} is the magnitude of coupling as measured by coherence between systems *i* and *j* based upon the interelectrode distances between *i* and *j,* A_{ij} and B_{ij} are coefficients for the short and long distance systems, respectively, *k* is a constant, and *d is* scalp interelectrode distance in centimeters. This equation has successfully accounted for over *90%* of the variance of scalp derived human EEG coherence (Thatcher et al., *1986;* Pascual-Marqui et al., *1988).*

Although the action of the short and long distance connections are somewhat independent and even competitive, for the purposes of the present study by Dr. John, let us assume that the number of short and long distance connections is constant and that changes in EEG coherence are due solely to changes in the strength of the synaptic inputs impinging on *i* or *j* through the short and long distance connection systems. Accordingly, changes in EEG coherence over time are

represented by the first derivative of strength of synaptic drives $\dfrac{dC_{ij}}{dt} = S_{ij}$ \qquad Eq.(2)

A parsimonious aspect of the above description of scalp recorded EEG coherence is that a common mathematical model can be used to describe both the single unit findings of John and Morgades (1969b), Gray et al. (1989), and Eckhorn et al. (1988), the EEG coherence findings of Thatcher et al. (1994) and the present John study. For example, the classical method of modeling coupled oscillators is based on the observation that at its limit cycle, a oscillator can be described by a single parameter, its phase 0_{ij} The dynamics of a population of N interaction oscillators can then be approximated by the system

$$\frac{dq_i}{dt} = w_i(t) + f(q_i \cdots q_n)$$ Eq. (3)

where the variables w;(t) are the uncoupled internal frequencies within neural loops and $f(q, \dots q_n)$ is the function that describes the coupling among the oscillators. The behavior of Eq. (3) is very simple, for example, if the frequency of two oscillators w, and w_2 are sufficiently close, then the system "phase locks", i.e., it has a stable periodic solution which is independent of time. For $|W_1 - W_2|$ sufficiently large then the system drifts with the faster oscillator attracting the slower one (Ermentrout and Kopell, 1990). Assuming a constant coupling strength then Eq. (3) becomes

$$\frac{dq_i}{dt} = w_i(t) + K\sin(q_i - q_j)$$ Eq. (4)

This is the most common method of modeling multiunit neural network oscillators (Cohen et al., 1982; Baldi and Meir, 1990; Kopell and Ermentrout, 1986). A further refinement of this model was used by Baldi and Meir (1990) to account for both short and long distance coupling of shared stimulus features. According to their model, the phase of a neuron or a group of coherently oscillating neurons within a cortical column was represented by

$$\frac{dq_i}{dt} = w_i(t) + n_i(t) + K_{ij}\sin(q_i - q_j)$$ Eq. (5)

where $n_i(t)$ is Gaussian noise with a fixed variance. The frequency w is 0 except in the regions activated by the stimulus. For example, in an excited region the frequency w is set to a constant value which is maximal for neurons tuned to the optimal stimulus orientation and near 0 for oscillators associated with the orthogonal orientation. This aspect of their model was described by an amplitude-dependent coupling function K_{ij} :

$$K_{ij}(t) = A_i(t)A_j(t)K(d(i,j))$$ Eq. 6

where $K_{ij}(t)$ is a function of coupling strengths which are dependent on the distance between i and j and also the amplitude of the activity at those sites. A;(t) and $A; (t)$ are the amplitudes, defined by the number of action potentials per unit time, which are 0 everywhere except in the excited regions and $K(d(i,, j))$ assumes that the short and long distance connections are isotropic.

Since we know that short and long distance connections are not isotropic, we pro-

pose to modify Baldi and Meir's (1990) model by adding pathway and amplitude threshold parameters which provide boundaries that define the amplitudes and preferred pathways necessary for phase locking to occur. For example,

$$K_{ij}(t) = A_i(t)A_j(t)K(d(i,j))F(A_j - T_k) \qquad \text{Eq. (7)}$$

where T_k is some threshold value of average depolarization in a population of neurons, A_i is the average of the neural activity in a neighborhood of i, Aj is the average of the neural activity in a neighborhood of *j*, $K[d(i, j)]$ is defined by Eq. (1), and the function $F(x) = 1$ if $x \geq 0$ and 0 if $x < 0$.

We define preferred pathways as those pathways with properties such as: (1) the highest density of connections, and/or (2) the pathways with the greatest synaptic strengths, and/or (3) synapses in nearest proximity to the axon hillock. Formally, we represent the distance function *d(i, j)* as

d(i,j) = | 1 for an i and j preferred pathway
           |
           | 0 for an i and j non-preferred pathway

Likewise, we define the amplitudes of activity $A_i(t)$ and $A_j(t)$ as

$A_i(t)$ and $A_j(t)$ = | 1 for an i and j from excited regions i and j
                         |
                         | 0 for an i and j from non-excited regions i and j

According to this model, phase locking occurs between excited populations of neurons whose frequency of oscillations w has increased to some critical value and which are coupled as part of a preferred pathway. In the Thatcher et al. (1994) hand movement experiment, the preferred pathways would involve the connection systems of the hand region of the motor cortex and the prefrontal, thalamic, and other regions involved in the mediation of hand and finger movements. The phase locking would represent a "labeling" process whereby the neural resource most likely to mediate the motor response would be identified and linked.

Similarly, according to this model EEG coherence changes in Dr. John's DMS study reflect the action of coupled oscillators in which resource allocation occurs through the rapid spatiotemporal self-organization of neurons involved in the comparison of the present to the past. The five spatial SPC patterns of coherent activity observed by Dr. John may represent the strongest five of the stable oscillatory modes of neural self-organization based on short and long distance connection systems (Eqs. 5 and 7). A careful computer simulation of this model, however, is necessary before its value to the important issue of the "content of the present" can be assessed.

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