

Thoughts on the Meaning of Brain Electrical Activity

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Recordings of electrical brain activity have provided a rich field of data. These data are harvested at at least two scales of inquiry: scalp recordings from humans have accessed cognitive aspects of the mind/brain relationship, and microelectrode recordings in animals have delineated circuits involved in sensory and motor processes. As yet, there are few studies that have attempted to reconcile the findings obtained at these different scales. It is such reconciliation that we are attempting in experiments performed in our Center for Brain Research and Informational Sciences. A progress report follows.

L'enregistrement de l'activité du cerveau a fourni des données très riches qui ont alimenté au moins deux niveaux de recherche. Les enregistrements de surface chez l'humain ont permis d'étudier les aspects cognitifs de la relation esprit/cerveau tandis que les enregistrements par microélectrodes chez les animaux ont délimité les circuits sous-jacents aux processus sensoriels et moteurs. Jusqu'à maintenant, il y a eu peu d'études qui tenté de réconcilier les données obtenues à ces deux niveaux. C'est objectif que visent nos expériences au Center for Brain Research and Informational Sciences. Cet article présente un rapport d'étape.

THE ELECTROENCEPHALOGRAPH

We recently completed an experiment which showed that electrical activity recorded from the scalp of humans changes its configuration on average 100 times per second. We initially recorded and displayed, on a videotape, the squared amplitude of the brain electrical activity and noted that the encoded colour representation changed much more rapidly than we expected from the years of watching the running EEG on paper or on an oscilloscope screen. (The video was shown at the conference.) In order to quantify our observation we developed a scalar representation based on drawing a line that connected the location of maximum squared amplitude during a 5msec period with the location of the maximum squared amplitude recorded during the follow-

ing 5msec period. We surveyed 19 locations (in the standard 10-20 electrocap configuration) over a 30sec epoch. As the maximum amplitude moved repeatedly between the same two locations, the line between those locations became thicker. The stability of the patterns of scalars over different epochs is shown in Fig. 1.

Note that the rate of change of the electrical brain activity varies from approximately 68 to 168 per second but that the scalar patterns are practically identical whether the recording epoch is 5.5 or 20sec. The patterns do change, however, when the person engages in a mental task, as can be seen in Fig. 2. These observations suggest an answer to a persisting problem in relating brain function to psychological processes, a problem enunciated clearly by Karl Lashley (1942, p. 306):

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My thanks go to Basil Hiley and Kunio Yasue as well as to Ilya Prigogine for help in interpreting the mathematics presented here. Any remaining errors are not their responsibility—they are due to my remaining stuck in a highly dense spectral domain.

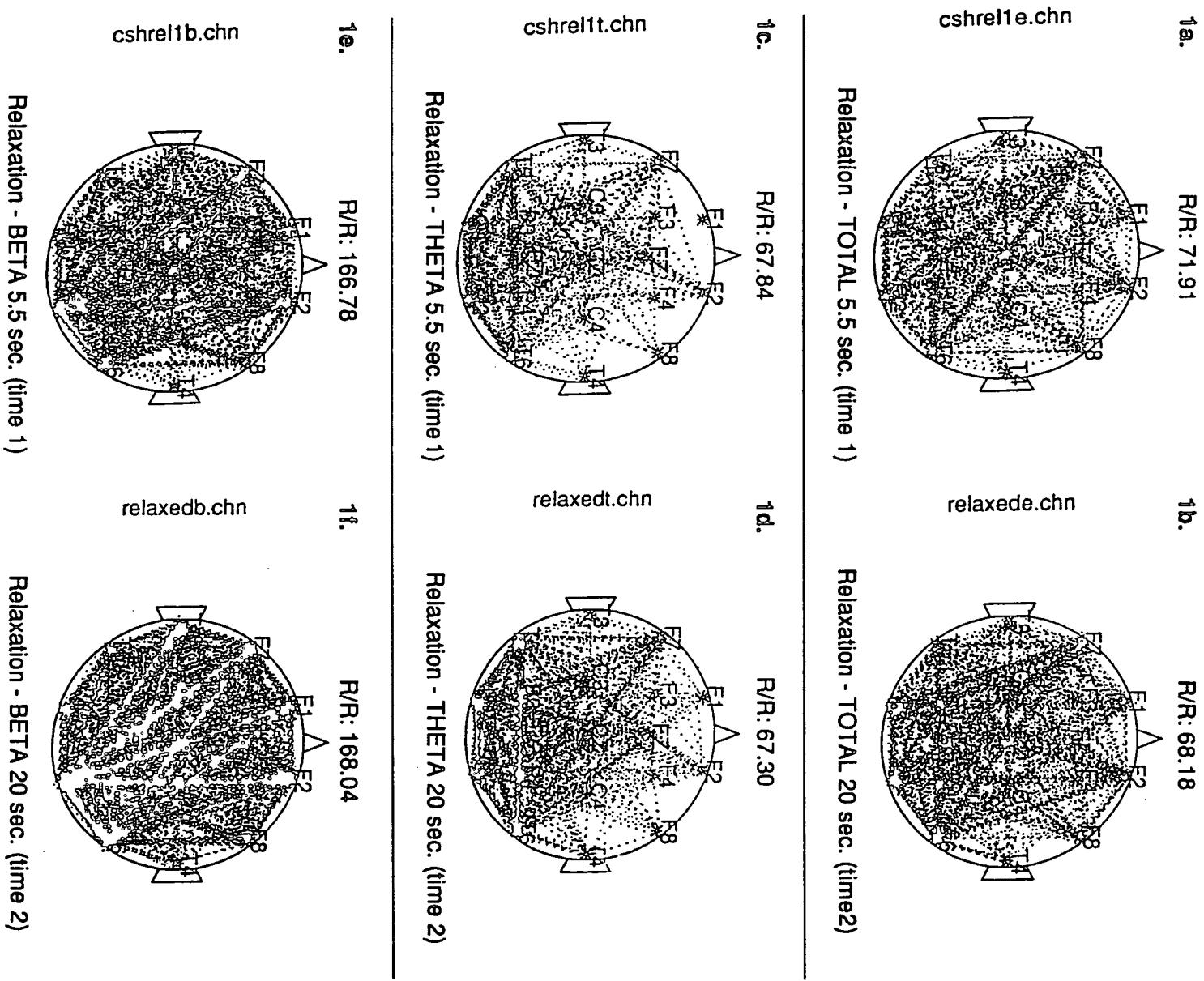


FIG. 1. Scalar representation of two different portions (early and late) and two data set lengths (5.5 and 10.0sec) of the baseline condition: Fig. 1a and 1b, total; 1c and 1d, theta; and 1e and 1f, beta.

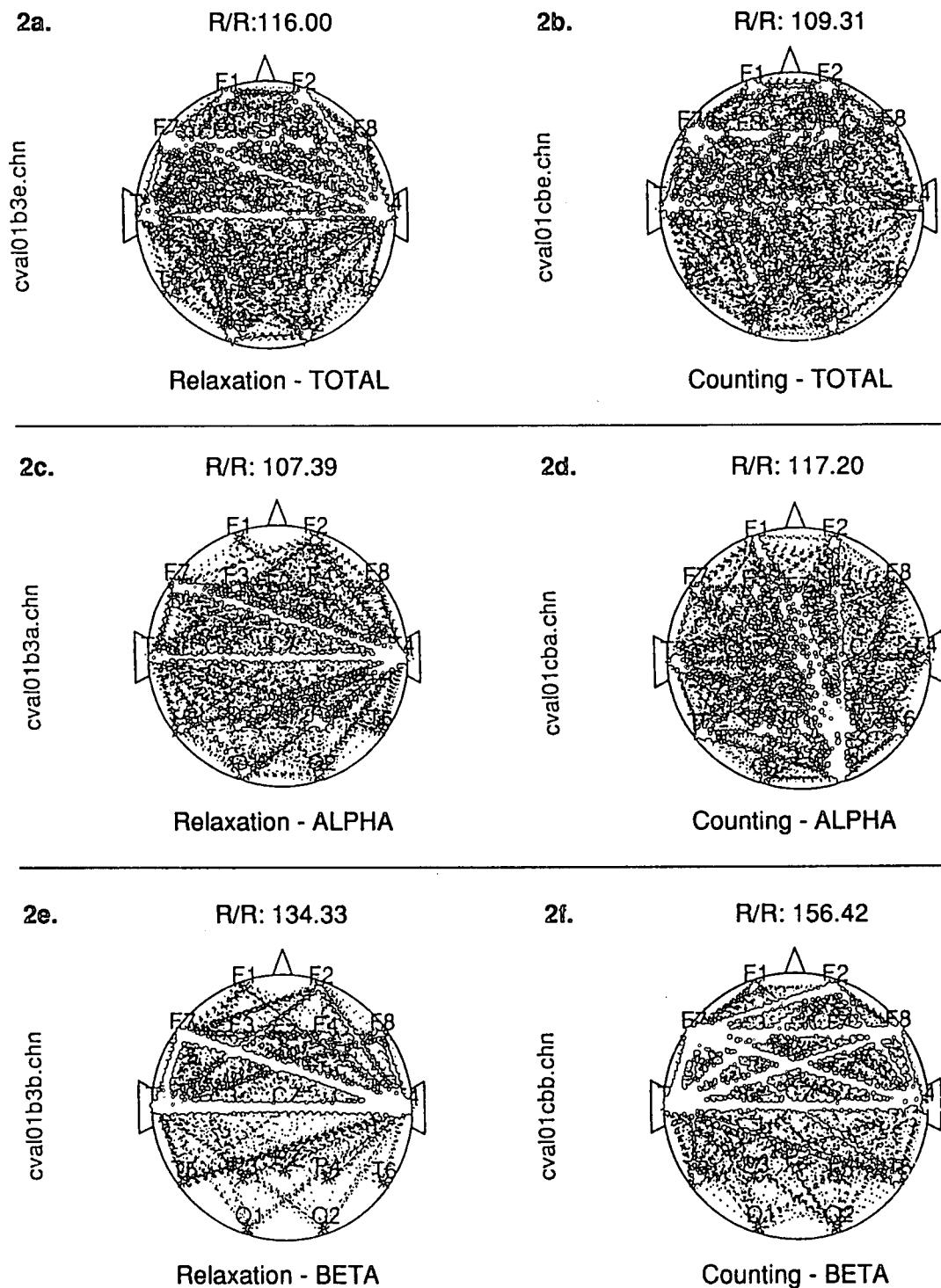


FIG. 2(a-f). Scalar representations of recrudescence in total, alpha, and beta EEG during resting and counting backwards.

Here is the dilemma. Nerve impulses are transmitted over definite, restricted paths in the sensory and motor nerves and in the central nervous system from cell to cell through definite intercellular connections. Yet all behavior seems to be determined by masses of excitation, by the form or relations or proportions of excitation within general fields of activity, without regard to particular nerve cells. It is the pattern and not the element that counts. What sort of nervous organization might be capable of responding to a pattern of excitation without limited specialized paths of conduction? The problem is almost universal in the activities of the nervous system and some hypothesis is needed to direct further research.

For almost half a century we have known that the EEG recorded from the scalp does not so much reflect an accumulation of nerve impulses as it reflects the graded polarizations (hyper- and depolarizations) of synapses and the fine-fibred axonic and dendritic cortical connection web (e.g. Adey, 1967; Creutzfeld, 1961; Green, Maxwell, & Petsche, 1961; Green & Petsche, 1961; Li, Cullen, & Jasper, 1956; Verzeano & Laufer, 1970; Verzeano & Negishi, 1960)¹. It is in these graded polarizations that patterns of excitations (and inhibition) need to be sought.

GRADED POLARIZATIONS IN THE BRAIN'S CONNECTION WEB

However, it is nerve impulses that we can readily record with microelectrodes, nerve impulses that are generated in order to inform one part of the nervous system what is going on in another part. This has given rise to viewing the functions of the brain and especially those of the cerebral cortex in terms of its circuitry. Though circuitry is certainly an important aspect of brain function, by themselves circuits cannot account for the psychological processes emphasized by Lashley in the earlier quotation.

As a metaphor, the old vacuum tube serves admirably. The tube's circuitry has interposed within it a plate. Minute changes in the charge of the plate provide patterns in an otherwise stable transmission of energy. These patterns, these

designs, constitute the information processing capabilities of early computers.

George Bishop (1956), in a definitive essay that discussed "the natural history of the nerve impulse", reviewed the evidence for attending another aspect of neural activity, an aspect analogous to that served by the plate in the vacuum tube. Bishop indicated that graded slow potentials, hyper- and depolarizations, are more general as well as more primitive than the impulses that probably developed when the early metazoans became too large. He cites the evidence that the cerebral cortex still operates largely by means of connections characteristic of primitive neuropil, the most appropriate mechanism for the production of a state, as contrasted to the transmission about such states. On the basis of such evidence, I suggested (Pribram, 1971, p. 105) that:

Nerve impulses and graded potentials are two kinds of processes that can function reciprocally. A simple hypothesis would state that the less efficient the processing of synaptic arrival patterns into axonic departure patterns, the longer the duration of the designs of the graded dendritic microprocess.—In short, nerve impulses arriving at synapses generate a graded potential dendritic microprocess. The design of this microprocess interacts with that already present by virtue of the spontaneous activity of the nervous system and its previous 'experience.' The interaction is modulated by inhibitory process and the whole procedure produces effects akin to the interference patterns resulting from the interaction of simultaneously occurring wave fronts. The graded potential processes thus act as cross correlation devices to produce new figures from which the patterns of departure of nerve impulses are initiated. The rapidly paced changes in awareness could well reflect the duration of the correlation process.

One way of portraying the two different modes of operation of the brain cortex is to record, from the same microelectrode, with low and with high pass amplification. We find (Fig. 3) that the slow graded activity recorded with low pass filtering precedes the high pass filtered spiking recorded from the same electrode 75% of the time during sensory stimulation (in 2369 recordings). This indicates that, just as for intracellular recordings from axons, that depolarizations and hyperpolarizations precede the generation of action potentials (spikes). Thus, as in the case of the vacuum tube plate, the graded activity "programmes" the

¹ The situation is much the same as it is with the electroretinogram, where the alpha and beta waves reflect retinal activity that is entirely devoid of nerve impulses.

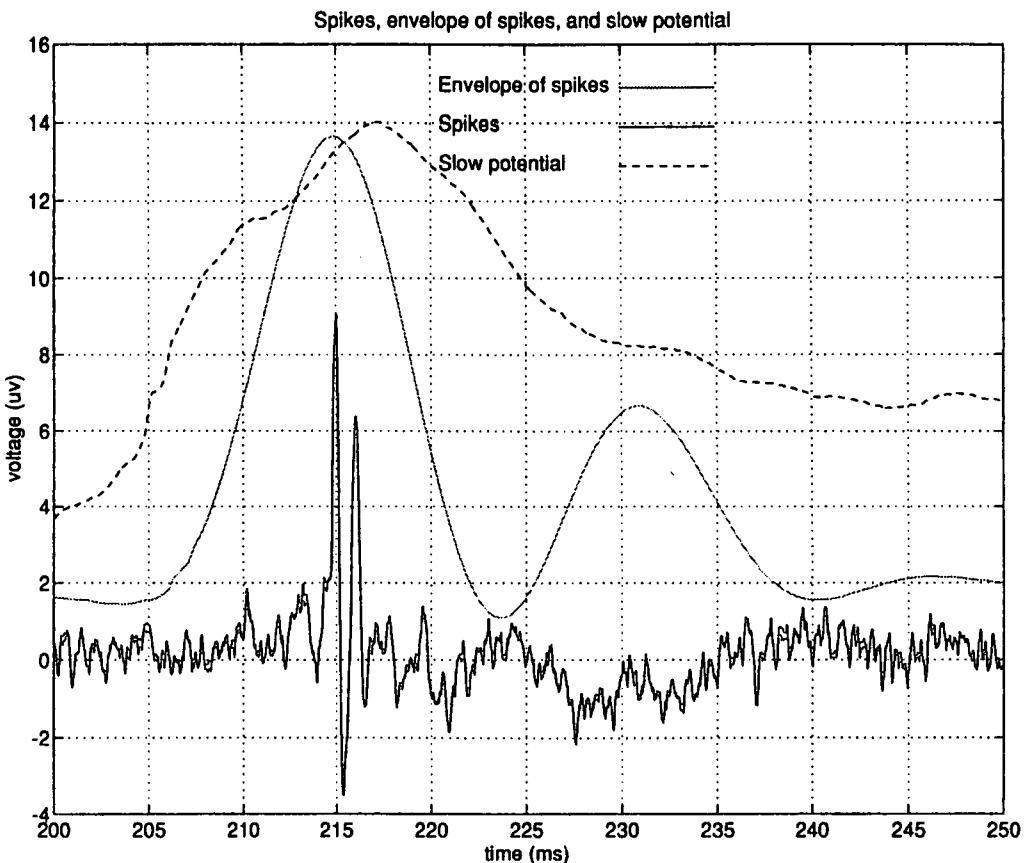


FIG. 3. An example of the relationship between spikes and multi-unit bursts to coincident local field potentials. Note that the ascending slope of the field potentials precedes that of the spikes and bursts. If the field potentials were a consequence of the burst, the peak should coincide with or come later than the maximum number of bursts.

output of the axon from which recordings are made. The graded activity intervenes between the input and the output relation of the neuron.

The evidence available at that time, albeit indirect, was reviewed to support the hypothesis that the graded processes recorded with low pass filtering, presumably occurring in dendrites, are coordinated with awareness. This evidence did not, however, include the displays of designs of dendritic processes that are the critical underpinnings of the hypothesis.

THE CONFIGURATION OF DENDRITIC FIELDS: A SPECTRAL DOMAIN

Such displays are readily provided, thanks to Kuffler (1953), who devised a technique that maps the configuration of dendritic activity from microelectrode recordings of nerve impulses from the axons connected to those dendrites. Kuffler applied to microelectrode recordings from the optic nerve the clinical technique of mapping

the visual field of a subject. Instead of obtaining a verbal or instrumental response from the subject, Kuffler obtained the response from a single axon: A dramatic increase (or decrease) from baseline spontaneous activity in the number of nerve impulses. The visual field of that axon is described by the area in the visual environment over which a stimulus is registered by the response of the axon. David Hubel, in a lecture at Stanford University, pointed out that such a visual "receptive" field actually represents the functional dendritic field of that axon under the conditions of visual stimulation.

During the 1960s and 1970s many laboratories, including mine, mapped these functional dendritic fields in the visual system. Their shapes change from concentric (bull's eye) to elongated as one proceeds from optic nerve to cortex. Mathematical descriptions and computer simulations can be fitted to these shapes (for review see, for instance Pribram, 1991, Lectures 1, 2, 4, 5). Here I present similar shapes obtained from recordings made from axons in the somatosensory cortex of rats

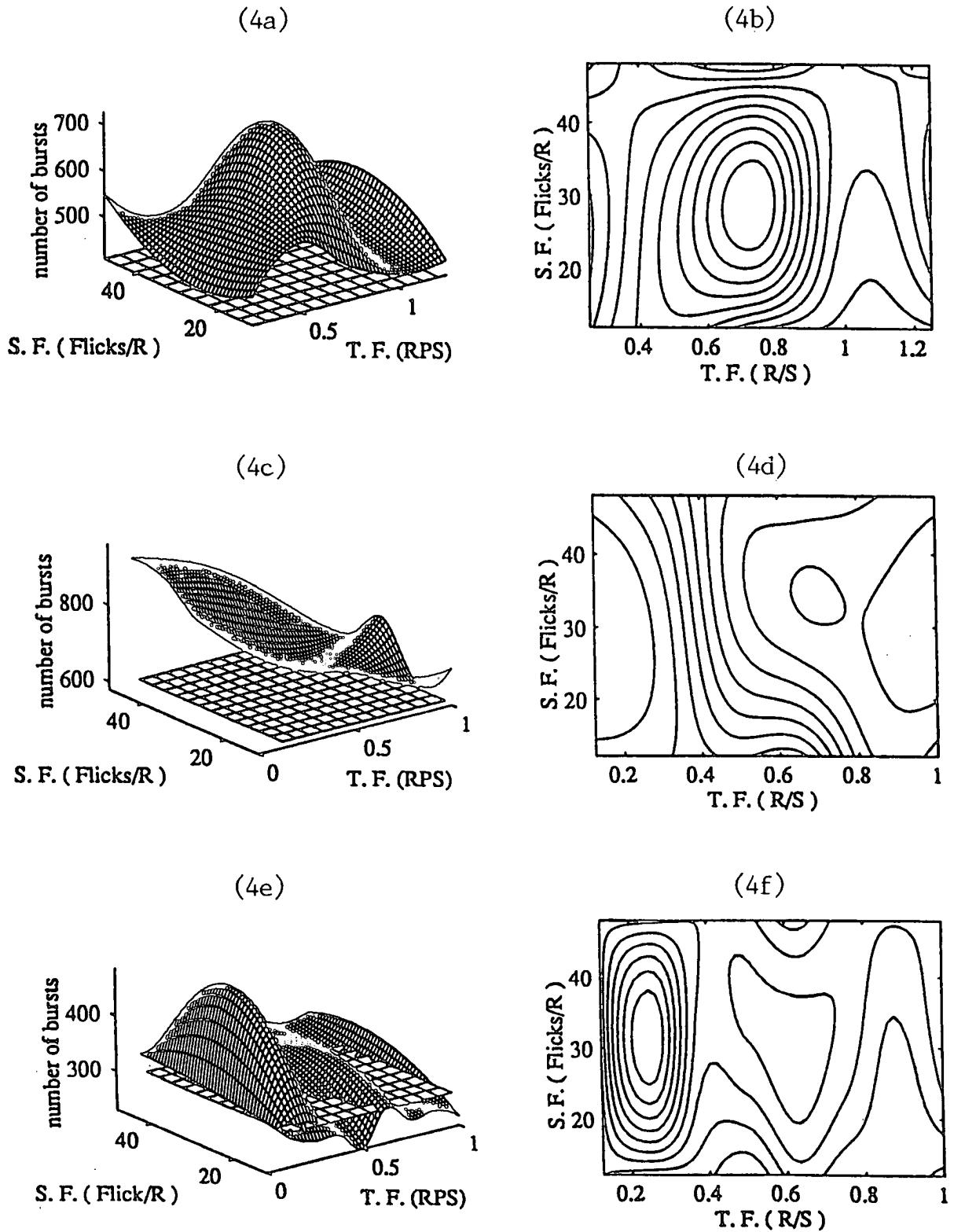


FIG. 4(a-f). Examples of receptive filled manifolds and their associated contour maps derived by an interpolation (spline) procedure from recorded whisker stimulation. The contour map was abstracted from the manifold by plotting contours in terms of equal numbers of bursts per recording interval (100sec). Each figure shows baseline activity (no whisker stimulation) at a given electrode location as a gr-plane located in terms of number of bursts per 100sec.

(see Fig. 4). There are several characteristics of the shape of these maps that are important to the hypothesis under consideration. First, these maps represent whisker stimulation in the spectral ("pure" frequency) domain, since variations of the stimulus are made by changing the spatial frequency (spacings of grooves) of cylindrical gratings and the temporal frequency (speed of rotation) with which the whiskers are engaged. The spectral representation emerges as a "density" of whisker stimulation, which enfolds both the spatial and the temporal aspects of the stimulation. As a corollary, in such a representation "information" about space and time becomes distributed over the reach of the mapping.

Second, the functional dendritic field can thus be mapped as a surface distribution. One way to look at surface distributions is to consider them to be produced by nodes of interference among wave forms with different origins. The dendritic connection web receives inputs from arbours originating in a variety of axons. As suggested by Eccles (1958), these inputs can be conceived as forming wavefronts. But this conception is not critical. When we additionally mapped the orientation of the spatial frequency grating (the orientation of the grooves), we were able to plot neuronal population vectors based on regression to a sinusoid. However, these vectors capture only the most obvious aspects of the surface distributions; all of its subtleties are ignored.

THE TEMPORAL HOLD

What does this concern with surface distributions that map a spectral domain gain us? Llinas, at this conference, and several other laboratories (e.g. Singer, 1993) have tackled the so-called binding problem by indicating coherence among neural oscillators (oscillation indicated by raster plots, see Fig. 5). Periodicity in the density distribution of nerve impulses (recorded from single axons) can be shown to be produced either by sensory input, or in Llinas' hands by input from the intralaminar nuclei of the dorsal thalamus. These investigators have emphasized the temporal dimension of their findings, but, as came out in the discussion of Llinas' results at this conference, it is the temporal binding of separate spatial locations that is at stake.

Elsewhere (Pribram, 1966, p. 179), I suggested that such a "temporal hold" is necessary to:

. . . the flexible rearrangement of memory processes. This temporal hold is assumed to be accomplished through an operation similar to that which gives rise to a temporary dominant focus in the experiments of Zal'manson working with Ukhtomski (1927). (In these experiments they applied a pattey of filter paper soaked in strichnine to an appropriate location on the motor cortex which resulted in a shift of a conditional reflex from one leg to another.) Without regulation by such a hold mechanism, the organism fluctuates inordinately among temporal signals and thus produces only a jumble of arrival patterns.

The Contingent Negative Variation (CNV), the expectancy wave of the EEG, was suggested to represent such a temporal hold. Initially this negative variation was recorded deep to the frontal lobe of the brain, which suggested a basal ganglion or limbic origin. Of interest in the light of Llinas' results obtained from stimulation of the intralaminar group of nuclei is that, with the collaboration of a medical student (McKegney, 1958), I had traced, by way of the retrograde degeneration technique, connections from the intralaminar complex to the perirhinal cortex (as well as to the basal ganglia), an area currently held responsible for many of the devastating effects on memory resulting from resections of the medial portion of the temporal lobe².

Binding by way of a temporal hold that produces coherence can readily be calculated in the space-time domain provided there are only a few oscillators involved. When coherence must be calculated over many locations as is done in computerized tomography (CAT and PET scans and fMRI) and in the presentation at this conference

² The intralaminar complex becomes more prominent as one proceeds from rat to cat to monkey to man. Also, this complex divides the thalamus into two divisions: One projects to the convexal cortex to include the posterior part of the frontal cortex and the parietal, occipital, and temporal regions. This division maintains an anterior-posterior axis, which reflects the anterior-posterior axis of the cortex. By contrast, the other, more medial division, which projects to the far frontal (prefrontal) and cingulate cortex, loses this anterior-posterior topological correspondence. This difference in thalamocortical organization is one reason for classifying the far frontal cortex with the limbic formation. (The other is that resections of the far frontal and limbic cortices produce deficits in delayed alternation behaviour in monkeys whereas resections of the convexal cortical regions do not; the reverse is true for simple sensory discriminations.) For review see Pribram (1954, 1958).

jun19, Stimulation Rate= 4 Hz, Groove Width= 0.8mm

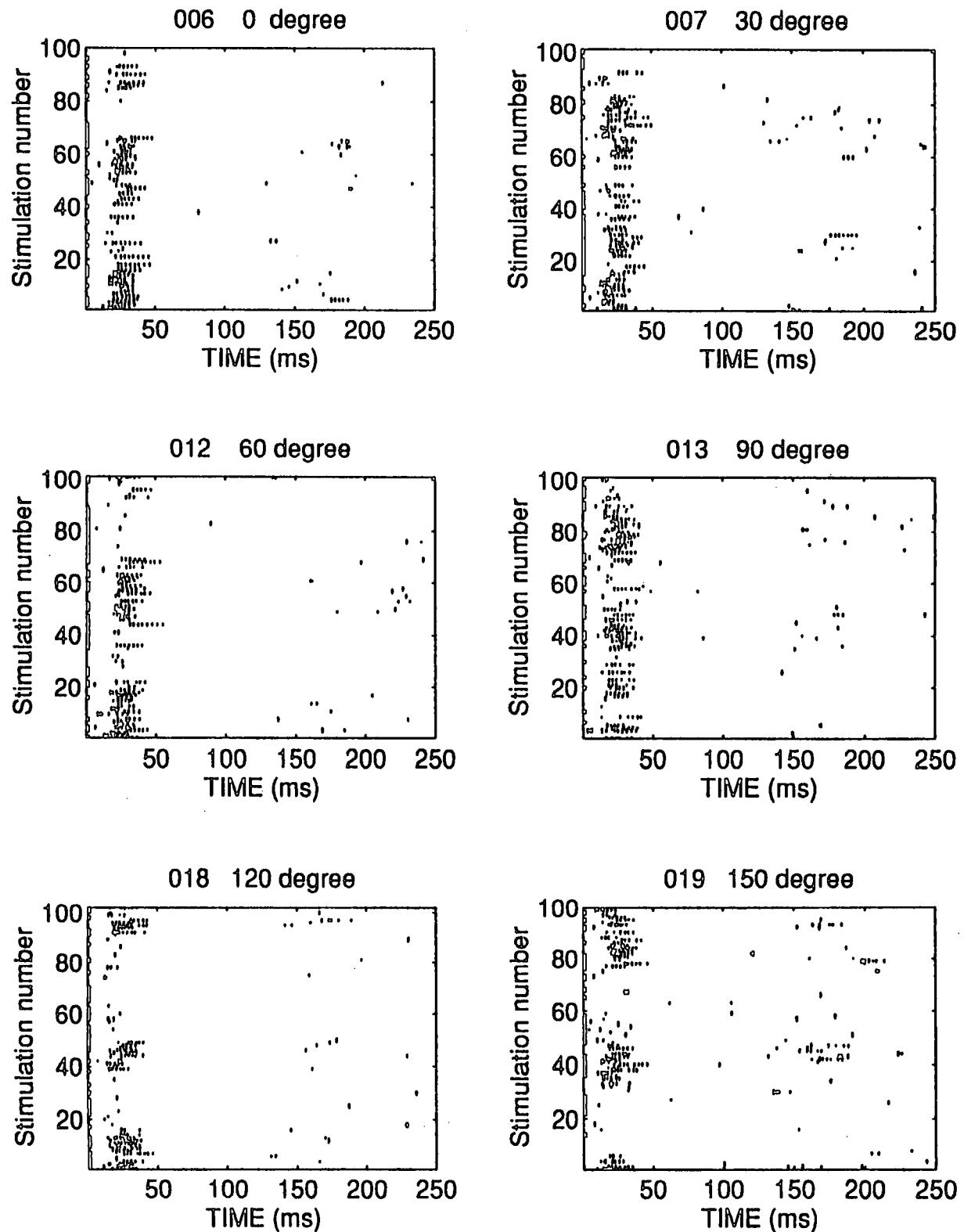


FIG. 5. Raster plots showing periodicity of single-neuron firing as a function of a sweep of a rat's whiskers across an 8mm grating. The sweep was initiated by electrical stimulation (stimulation number) of the 5th cranial nerve at the rate of 4Hz. Although this is not readily seen in this figure, the neural periodicity is *not* identical with the sweep rate, especially when rates of 8 or 12Hz were used. Note that the periodic burst occurs only within the first 50msec of each sweep.

by Petsche for determining different patterns of the EEG that characterize listening to different musical compositions, the computations are facilitated considerably when they are carried out in the spectral domain (by using an FFT or similar algorithm). My suggestion, in keeping with my hypothesis, is that if it is easier for the computer to perform the algorithm in this domain, it is likely that it is easier for the brain to do it that way.

SCAN-PATHS

The analogy with tomography raises an issue that needs to be addressed: We do not perceive in the spectral domain. How is the inverse transform implemented, so that processing can shift back from the spectral to the space-time domain? The spectral domain is time symmetric. What is needed is a mechanism that breaks time symmetry. Prigogine (e.g. 1994) has noted that under certain conditions, the time symmetry inherent in the spectral domain can be broken. He has suggested that under these conditions scattering (dissipation of energy) is persistent rather than transitory; that is, the system is an open, not a closed one. Open systems provide opportunities for a range of possibilities for different futures³. Whether Prigogine's formulation is the correct one or not, the important point of his programme is that open systems are open to possibilities. When a path is taken, a choice is made among possibilities (e.g. by the formation of an attractor) such that the path not taken is forever lost, and time symmetry is broken.

This emphasis on paths brings Prigogine's formulation regarding the breaking of time sym-

metry into register with the issue addressed here regarding the mechanism whereby an inverse transform accomplishes a return from the spectral to the space-time domain. Effron (1989) has shown the importance of scan-paths to visual and other sensory processing. Bolster and I (Bolster & Pribram, 1993) have shown, by recordings of the electrical activity of the parietal, temporal, and far frontal intrinsic "association" cortices of monkeys while they were choosing among single or conjoined features, that these brain systems are involved in the construction of scan-paths. Other evidence (reviewed by Pribram, 1960, 1974, 1991) indicates that these parts of the cortex operate back onto the primary sensory pathways to help organize the sensory input.

Individual scan-paths, when externalized as eye movements (which they need not be), do not look directed any more than do the individual "paths" taken by the maximum squared amplitude recordings shown in Fig. 1. But when scans are tracked over time, patterns tend to centre on the more "informative" parts of a figure (Bagshaw, Mackworth, & Pribram, 1970). Thus, on the basis of the evidence that is demonstrated in Fig. 1, the temporal hold (as demonstrated in Llinas' experiments) can result in brief "moments" iterated until a pattern of scan-paths accomplishes a percept. On the basis of our experiments and those of Petche's presented at this conference, the duration of such a neural moment to approximate 100th of a second on average (in the range from 5 to 20 msec) and that of the temporal hold would be coordinate with the span of attention.

A MODEL

The following example shows how a system operating in the spectral domain can be constructed from scan-paths; specifically, how hippocampal (limbic) function can interact with operations in the cortical convexity to facilitate learning.

The example takes into consideration Jeffrey Gray's and J.N.P. Rawlins' (1975) proposal that the hippocampal formation acts as a comparator; D.S. Olton's (1983) and my own (Pribram, 1971) emphasis on its function as a memory buffer; Abraham Amsel's (in press) experiments regarding the effects of hippocampal manipulations on vicarious trial (and error) performances; and E. Roy John's (1967) demonstration that electrical responses are evoked in limbic structures during and only during early phases of learning.

³ Mathematically, Prigogine's discussion concerns certain generalized quantum and/or classical systems driven by (non-self-adjoined) Hamiltonian operators (for quantum systems) and/or Liouville operators (for classical systems) which are "chosen" so that their time developments are kept contractive (i.e. lose information) and dissipative (i.e. lose energy). My interpretation (Pribram, 1994) of his equations is that damping terms eliminate the imaginary component of non-square integrable Eigen functions due to their evolution operator (e.g. a Hamiltonian). Thus, undertaking a "path", choosing, making implicit or explicit directed movement—whether as attention to input, as intending an action or as thought (i.e. rummaging through memory)—breaks time symmetry. The path taken "loses information" or better stated, loses uncertainty in Shannon's formulation, and, in the terminology of nonlinear dynamics, forms an attractor in a dissipative process.

Specifically, the example attempts to resolve some apparently discrepant findings regarding the results of microelectrode recordings of the activity of single neurons or small groups of such neurons during performances of rats in mazes. The discrepancy is that under some conditions, a path in space is outlined by the recordings; under other conditions, spatial cues appear to be represented in a distributed fashion.

The current formulation was instigated by another presented by J. McClelland and Bruce McNaughton (McClelland, 1996). The McClelland-McNaughton model takes into account only the latter's finding of a representation in hippocampal neurons of a path in space. Thus their model directly matches hippocampal activity with the activity of the cortical convexity (as would be expected of a comparator). On the input side such a model is plausible. However, their model also demands such a comparative process on the output side. This is implausible in view of results obtained by Paul MacLean and myself (Pribram & MacLean, 1953) when mapping cortical connectivity by strychnine neuronography. Although we were readily able to show multiple inputs to the hippocampal formation, we were totally unable to activate *any* isocortical region by stimulating the hippocampal cortex. The finding was so striking that MacLean (1990) developed the theme of a schizophysiology of cortical function.

On the other hand, such outputs are plentiful to the amygdala, to the n. accumbens septi, and to other subcortical structures via the fornix. Confirmation of the difference between input (encoding) and output (decoding) operations involving the hippocampal formation has recently come from studies in humans using fMRI (Gabrieli, Brewer, Desmond, & Glover, 1997). Encoding into memory was found to activate the parahippocampal cortex, which includes the entorhinal cortex (which receives input from the remainder of the isocortex), whereas decoding (retrieval) was found to activate the subiculum which (Gabrieli, et al., 1997, p. 265) "provides the major *subcortical* output of the hippocampal region via the fornix".

The subcortical nuclei do not have the laminar structure of cortex and so are poor candidates for the point-to-point match a computer would ordinarily be conceived to implement. On the other hand, a match could readily be achieved if the comparison would involve a stage during which processing involved a distributed stage, much as when a holographic memory is used to store and

retrieve information (for instance with holofishes). It is the evidence that such a distributed store is, in fact, built up in the hippocampal formation during learning that makes such a model plausible.

Landfield (1976) and O'Keefe (1986) have developed such a model. O'Keefe (1986, pp. 82-84) reviews the evidence and describes the model as follows:

Attempts to gain an idea of the way in which an environment is represented in the hippocampus strongly suggest the absence of any topographic isomorphism between the map and the environment. Furthermore, it appears that a small cluster of neighboring pyramidal cells would map, albeit crudely, the entire environment. This observation, taken together with the ease that many experimenters have had in finding place cells with arbitrarily located electrodes in the hippocampus, suggests that each environment is represented many times over in the hippocampus, in a manner similar to a holographic plate. In both representation systems the effect of increasing the area of the storage which is activated is to increase the definition of the representation.

A second major similarity between the way in which information can be stored on a holographic plate and the way environments can be represented in the hippocampus is that the same hippocampal cells can participate in the representation of several environments (O'Keefe & Conway, 1978; Kubie & Ranck, 1983). In the Kubie and Ranck study the same place cell was recorded from the hippocampus of female rats in three different environments: All of the 28 non-theta cells had a place field in at least one of the environments, and 12 had a field in all three environments. There was no systematic relationship amongst the fields of the same neurone in the different environments. One can conclude that each hippocampal place cell can enter into the representation of a large number of environments, and conversely, that the representation of any given environment is dependent on the activity of a reasonably large group of place neurones.

The third major similarity between the holographic recording technique and the construction of environmental maps in the hippocampus is the use of interference patterns between sinusoidal waves to determine the pattern of activity in the recording substrate (see Landfield, 1976). In optical holography this is done by splitting a beam of monochromatic light into two, reflecting one beam off the scene to be encoded and then interacting the two beams at the plane of the substrate. In the hippocampus something similar might be happening. . . . The beams are formed

by the activity in the fibers projecting to the hippocampus from the medial septal nucleus (MS) and the nucleus of the diagonal band of Broca (DBB).

Pioneering work by Petsche, Stumpf and their colleagues (Stumpf, 1965) showed that the function of the MS and DBB nuclei was to translate the amount of activity ascending from various brainstem nuclei into a frequency modulated code. Neurons in the MS/DBB complex fire in bursts, with a burst frequency which varies from 4–12Hz. Increases in the strength of brainstem stimulation produce increases in the frequency of the bursts but not necessarily in the number of spikes within each burst (Petsche, Gogolak and van Zweiten, 1965). It is now widely accepted that this bursting activity in the MS/DBB is responsible for the synchronization of the hippocampal theta rhythm.

The November 1995 issue of *Scientific American* shows how such a holographic matching process could work. Of course, in this quotation (Psaltis & Mok, 1995, p. 76), the matching process works by way of illuminating crystals, and the neural substitutes for this would be surface distributions of dendritic polarizations in somatosensory cortex, as shown in Fig. 4:

Given a hologram, either one of the two beams that interfered to create it can be used to reconstruct the other. What this means, in a holographic memory, is that it is possible not only to orient a reference beam into the crystal at a certain angle to select an individual holographic page but also to accomplish the reverse, illuminating a crystal with one of the stored images gives rise to an approximation of the associated reference beam, reproduced as a plane wave emanating from the crystal at the appropriate angle.

A lens can focus this wave to a small spot whose lateral position is determined by the angle and therefore reveals the identity of the input image. If the crystal is illuminated with a hologram that is not among the stored patterns, multiple reference beams—and therefore multiple focused spots, are the result. The brightness of each spot is proportional to the degree of similarity between the input image and each of the stored patterns. In other words, the array of spots [weights in a layer of a PDP network] is an encoding of the input image, in terms of its similarity with the stored database of images.

Putting this together with the McClelland-McNaughton model, which is based on data

that do show a representation of the *path* taken by an animal down an alley maze, encoding in the hippocampus may be both holographic-like and patterned in space and time. The hypothesis is that as multiple paths become represented in the hippocampal formation, a transformation into holographic-like surface distribution in the spectral domain is effected. When a particular path is subsequently sought, the buffer operates much as does the holographic memory described earlier. Actual paths construct the holographic memory and scan-paths activate the comparator to retrieve a particularly appropriate actual path. Essentially, the process implements a shift in coordinates from space-time (configurational) to spectral and back to configurational.

The shift of coordinates is suggested to take place by way of scanning, that is, constructing a particular path. Computational models such as those proposed by Harth, Unnikrishnan, and Pandya (1987) and by Yasue, Jibu, and Pribram (Pribram, 1991) have been developed for vision to account for the shift in coordinates as a result of such a choice. In the Yasue et al. proposal, Euler-Lagrange equations correspond to *paths* taken in configuration space (space-time coordinates). The shift from spectral to the configuration coordinates has been demonstrated in the visual system both at the thalamic and cortical level. Electrical stimulation of temporal or frontal lobe cortex enhances or diminishes the extent of the inhibitory surrounds and flanks of dendritic receptive fields in thalamus and cortex so that the sensory channels can either become multiplexed or fused. As the dendritic fields can be described in terms of a space-time constraint on a sinusoid such as the Gabor elementary function, the constraint is embodied in the inhibitory surround of the field. Enhancing the surround enhances processing in configuration coordinates; diminishing the surround enhances the sinusoidal (spectral domain) aspects of processing. Thus, the development of scan-paths operates on the inhibitory process that characterize the fluctuations of the polarizations of the dendritic connection web.

END-THOUGHTS

In a way, it is a miracle that we can garner meaning from the recording of brain electrical activity. Imagine what you might learn from placing electrodes on top of a computer to determine which program is in operation (or even whether the program is in hexadecimal, ASCII, or C++). Or,

take a single wire and stick it into the guts of the computer (and hope you won't short anything out) to find out in machine language what is going on. Despite such odds, by hard work and, what is essential, by synthesizing the results with those obtained with other techniques, meaning has been harvested from recordings of brain electrical activity. Have we got it totally right as yet? Probably not. But when I think back to what we knew half a century ago about how the brain operates to organize our perceptions and our memory and our behaviour, I can only be optimistic: 24,000 neuroscientists are in the trenches ready to seize the next vantage.

REFERENCES

- Adey, W.R. (1967). Intrinsic organization of cerebral tissue in alerting, orienting, and discriminative responses. In G.C. Quarton, T. Melnechuk, & F.O. Schmitt (Eds.), *The neurosciences* (pp. 615-633). New York: The Rockefeller Press.
- Amsel, A. (in press). On cognitive maps, vicarious trial-and-error, and impulsivity. In K.H. Pribram (Ed.), *Brain and values*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Bagshaw, M.H., Macworth, N.H., & Pribram, K.H. (1970). The effect of inferotemporal cortex ablations on eye movements of monkeys during discrimination training. *International Journal of Neuroscience*, 1, 153-158.
- Bishop, G. (1956). Natural history of the nerve impulse. *Physiological Review*, 36, 376-399.
- Bolster, B., & Pribram, K.H. (1993). Cortical involvement in visual scan in the monkey. *Perception and Psychophysics*, 53(5), 505-518. Austin, TX: The Psychonomic Society.
- Creutzfeld, O.D. (1961). General physiology of cortical neurons and neuronal information in the visual system. In M.A.B. Brazier (Ed.), *Brain and behavior* (pp. 299-358). Washington, DC: American Institute of Biological Sciences.
- Eccles, J.C. (1958). The physiology of imagination. *Scientific American*, 199, 135-146.
- Effron, R. (1989). *The decline and fall of hemispheric specialization*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Gabrieli, J.D.E., Brewer, J.B., Desmond, J.E., & Glover, G.H. (1997). Separate neural bases of two fundamental memory processes in the human medial temporal lobe. *Science*, 276, 264-266.
- Gray, J., & Rawlins, J.N.P. (1975). Comparator and buffer memory: An attempt to integrate two models of hippocampal function. In R.L. Isaacson & K.H. Pribram (Eds.), *The hippocampus, Vol. I and II* (pp. 159-196). New York: Plenum.
- Green, J.D., Maxwell, D.S., & Petsche, H. (1961). Hippocampal electrical activity III. Unitary events and genesis of slow waves. *EEG Clinical Neurophysiology*, 13, 854-867.
- Green, J.D., & Petsche, H. (1961). Hippocampal electrical activity II. Virtual generators. *EEG Clinical Neurophysiology*, 13, 847-853.
- Harth, E., Unnikrishnan, P., & Pandya, A.S. (1987). The inversion of sensory processing by feedback pathways: Model of visual cognitive functions. *Science*, 237, 184-187.
- John, E.R. (1967). *Mechanisms of memory*. New York: Academic Press.
- Kubie, J.L., & Ranck, J.B. (1983). Sensory-behavioural correlates in individual hippocampus neurones in three situations: Space and context. In W. Seifert (Ed.), *Neurobiology of the hippocampus* (pp. 433-447). London: Academic Press.
- Kuffler, S.W. (1953). Discharge patterns and functional organization of mammalian retina. *Journal of Neurophysiology*, 16, 37-69.
- Landfield, P.W. (1976). Synchronous EEG rhythms: Their nature and their possible functions in memory, information transmission and behaviour. In E.H. Gispen (Ed.), *Molecular and functional neurobiology*. Amsterdam: Elsevier.
- Lashley, K.S. (1942). The problem of cerebral organization in vision. In *Biological symposia, Vol. VII, Visual mechanisms* (pp. 301-322). Lancaster, UK: Jacques Cattell Press.
- Li, C.L., Cullen, C., & Jasper, H.H. (1956). Laminar microelectrode analysis of cortical unspecific recruiting responses and spontaneous rhythms. *Journal of Neurophysiology*, 19, 131-143.
- MacLean, P. (1990). *The Triune brain in evolution: Role in paleocerebral functions*. New York: Plenum Press.
- McClelland, J. (1996). Role of the hippocampus in learning and memory: A computational analysis. In T. Ono, B.L. McNaughton, S. Molotchnikoff, E.T. Rolls, & H. Nichijo (Eds.), *Perception, memory and emotion: Frontier in neuroscience* (pp. 601-613). Oxford: Elsevier Science.
- McKegney, F.P. (1958). Telencephalic projections of the midline and intralaminar nuclei in the cat. *Yale Journal of Biological Medicine*, 30, 415-428.
- O'Keefe, J. (1986). Is consciousness the gateway to the hippocampal cognitive map? A speculative essay on the neural basis of mind. *Brain and Mind*, 59-98.
- O'Keefe, J., & Conway, D.H. (1978). Hippocampal place units in the freely moving rat: Why they fire where they fire. *Experimental Brain Research*, 31, 573-590.
- Olton, D.S. (1983). Memory functions and the hippocampus. In W. Seifert (Ed.), *Neurobiology of the hippocampus*. New York: Academic Press.
- Petsche, H., Gogolak, G., & Van Zwieten, X. (1965). Rhythmicity of septal cell discharges at various levels of reticular excitation. *EEG Clinical Neurophysiology*, 19, 25-33.
- Pribram, K.H. (1954). Toward a science of neuropsychology (method and data). In R.A. Patton (Ed.), *Current trends in psychology and the behavioral sciences* (pp. 115-142). Pittsburgh, PA: University of Pittsburgh Press.
- Pribram, K.H. (1958). Neocortical function in behavior. In H.F. Harlow & C.N. Woolsey (Eds.), *Bio-*

- logical and biochemical bases of behavior* (pp. 151–172). Madison, WI: University of Wisconsin Press.
- Pribram, K.H. (1960). The intrinsic systems of the forebrain. In J. Field, H.W. Magoun, & V.E. Hall (Eds.), *Handbook of physiology, neurophysiology II* (pp. 1323–1324). Washington, DC: American Physiological Society.
- Pribram, K.H. (1966). Some dimensions of remembering: Steps toward a neuropsychological model of memory. In J. Gaito (Ed.), *Macromolecules and behavior* (pp. 165–187). New York: Academic Press.
- Pribram, K.H. (1971). *Languages of the brain: Experimental paradoxes and principles in neuropsychology*. Englewood Cliffs, NJ: Prentice-Hall. (Previous editions: Monterey, CA: Brooks/Cole, 1977; New York: Brandon House, 1982.)
- Pribram, K.H. (1974). How is it that sensing so much we can do so little? In K.H. Pribram (Contrib. Ed.), Central processing of sensory input. In F.O. Schmitt & F.G. Worden (Eds.), *The neurosciences third study program* (pp. 249–261). Cambridge, MA: MIT Press.
- Pribram, K.H. (1986). The role of cortico-cortical connections. In F. Lepore, M. Pitto, & H. Jasper (Eds.), *Two hemispheres—one brain; functions of the corpus callosum*. New York: Alan R. Liss.
- Pribram, K.H. (1991). *Brain and perception: Holonomy and structure in figural processing*. Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Pribram, K.H. (1994). Afterword to *Origins: Brain and self organization* (pp. 707–708). Hillsdale, NJ: Lawrence Erlbaum Associates Inc.
- Pribram, K.H., & Maclean, P.D. (1953). Neuronographic analysis of medial and basal cerebral cortex. II. Monkey. *Journal of Neurophysiology*, 16, 324–340.
- Prigogine, I. (1994). Mind and matter: Beyond the Cartesian dualism. In K.H. Pribram (Ed.), *Origins: Brain and self organization* (pp. 2–15). Mahwah, NJ: Lawrence Erlbaum Associates Inc.
- Psaltis, D., & Mok, F. (1995). Holographic memories. *Scientific American*, 273(5), 70–76.
- Singer, W. (1993). Synchronization of cortical activity and its putative role in information processing and learning. *Annual Review of Physiology*, 55, 349–374.
- Stumpf, C. (1965). Drug action on the electrical activity of the hippocampus. *International Review of Neurobiology*, 8, 77–138.
- Ukhtomski, A.A. (1927). Concerning the condition of excitation in dominance. *Novoe v refeksologii i fiziologii nervosistemny*, 2, 3–15.
- Verzeano, M., & Laufer, M. (1970). The activity of neuronal networks in the thalamus of the monkey. In K.H. Pribram & D. Broadbent (Eds.), *The biology of memory*. New York: Academic Press.
- Verzeano, M., & Negishi, K. (1960). Activity in cortical thalamic networks: A study with multiple microelectrodes. *Journal of Gen. Physiology*, 43, 177–195.