

Consciousness and neurophysiology¹

KARL H. PRIBRAM

Department of Psychology, Stanford University, Stanford, California 94305

There are two major questions that must be addressed before any reasonable discourse on the relationship between brain function and consciousness can be undertaken. These questions are: 1) Is there any need at all for the concept of consciousness, and 2) If there is such a need, what specific issues does the concept subsume?

In order to answer the first question let us look at some patients who have suffered brain resections. The most recent group of such patients of interest to us are those who have been described as having "blind-sight" (31). Careful resection of occipital lobe tissue for hemangiomas or other tumors was limited to the striate cortex of one hemisphere. The patients experienced, as would be expected, a contralateral homonymous hemianopia. This was confirmed by the usual perimetry tests. When however, the patients were asked to identify the position of objects on a grid or to make discriminations between objects by making either instrumental or verbal responses, the patients performed remarkably well, reaching well above an 80% criterion. When asked to describe how they accomplished this, the patients expressed utter surprise, stating that they had "seen" nothing and were only guessing. This state continued for many months (6-8 at the latest inquiry).

These dissociations of the reports of subjective experience from performance are not unique. After section of the corpus callosum, the right hemisphere of right-hand persons gives (via the left hand) instrumental evidence of discrimination while failing to express itself verbally (30). Other examples come from resections of the limbic structures of the medial portion of the temporal lobe (14). While expressing *complete* unfamiliarity with situations experienced repeatedly for as long as 20 years, such

ABSTRACT

This paper presents the need for a concept such as "consciousness" and the specific issues that must be subsumed by any such concept. Evidence comes from patients with discrete cortical resections who continue to display intact instrumental responses with complete denial of subjective awareness of that which is responded to. This evidence demands dissociation between inferences derived from instrumental responses and those derived from reports of subjective awareness. Further analysis of clinical evidence suggests that mutually dissociable dispositions compose "states of consciousness." The hypothesis is proposed that each state is defined by a particular relatively stable configuration of chemically active corebrain systems, although to date the specification of such chemical configurations has not been accomplished. Data are reviewed to show that these neurochemical configurations then serve as attentional controls, i.e., controls on sensory input. It is suggested that these controls operate on the electronic processing of signals in the cerebral cortex and that the pattern of such signals comprises the matrix that determines the content of consciousness. Data are reviewed to support the view that these patterns encode neural signals into the frequency domain, thus composing a holographic-like representation from which image construction (or reconstruction) occurs. Finally, evidence is reviewed which shows that such image processing can be distinguished from information processing, dependent on feature extraction, which occurs by virtue of the operation of the association cortex. —Pribram, K. H. *Consciousness and neurophysiology. Federation Proc.* 37: 2271-2274, 1978.

patients can learn and retain instrumental skills to a remarkable extent (29).

Whatever the mechanism, these patients demonstrate a dissociation between reports of subject awareness and performance capabilities. Unless we wish to ignore reports of subjective experience or label them as outright lies (and some of my behavioristically inclined colleagues are doing just that) we need a concept that covers subjective experience which is not tied to the instrumental and verbal responsiveness from which we ordinarily infer that such experience is occurring.

The clinic furnishes us with such a concept. We say that a patient who is comatose or stuporous is unconscious (even though the stuporous patient may make some limited though appropriate responses to stimulation). We do not say that a patient who is sleeping and dreaming is unconscious—we say that he is in a different state of consciousness. We have

more difficulty in describing the patient suffering from seizures arising from abnormalities of the medial temporal lobe. Such patients act consciously, i.e., with complete awareness which they can report at the time of the seizures, though their behavior may be aberrant, as in the case of episodic violence. However, at some time subsequent to the seizure, such patients are unable to report any awareness of what had transpired. This inability to report in one state what transpired in another is also true of the difference between the dream state and ordinary wakefulness. Thus, the concept of a variety of "states" of consciousness has developed.

There, then, is ample reason to admit the concept of consciousness to scientific inquiry. Those of us interested in brain function and its rela-

¹ From the American Physiological Society Symposium on *Physiological Basis of Mental Functions* presented at the 28th Annual Fall Meeting, Hollywood, Florida, October 13, 1977.

tionship to experience simply cannot do without such a concept. Further, the evidence noted above suggests that consciousness comes in dissociable "states," dispositions to behave and experience in a particular mode for a sufficient span as to be reliably studied.

An initial question concerning the issues that compose the concept of consciousness can therefore be posed. What brain mechanisms specify one or another state of consciousness? The clinical evidence already cited suggests a role for structures of the limbic forebrain, structures that have a long history of being implicated in the determination of more adequately described states such as hunger and thirst (for review see, e.g., 10). From the time of Claude Bernard (2) and Walter Cannon (5) such states have been described as due to regulatory mechanisms, intrinsically involving homeostatic feedback control operations, that are sensitive to concentrations (or ratios of concentrations) of the chemical substances that are critical to that state. In nonmammalian vertebrates these states become to a considerable extent mutually exclusive (as in the famous example of the spawning salmon who does not eat during his entire trip to upstream spawning grounds). As a model for mutually exclusive and therefore dissociable states of consciousness, these more primitive regulations may serve us well.

The most fruitful hypotheses to guide inquiry into the relation between brain and consciousness should, according to this model, be derived from a search for the neural regulations of chemical substances to which the regulatory mechanisms are especially sensitive.

My own laboratory does not have the expertise to investigate neurochemical problems. The other writers in this symposium will cover this territory. Our research has, however, addressed the issue of control mechanisms and has discerned three major classes of forebrain systems that serve as regulators of conscious states. Two of these systems involve limbic structures, the other, the basal ganglia (see 24 for review).

The data that differentiate these systems from one another also provide the evidence as to what it is that these systems regulate: Control is be-

ing exercised on the processing of sensory input—in psychological language, these systems serve to regulate attention. One of the systems is concerned with brief phasic responses to input—the orienting reaction that rapidly habituates whenever the input becomes repetitive. The forebrain locus upon which this system converges is the amygdala.

A second system centers on the basal ganglia and deals with a tonic readiness to maintain responses already under way. This readiness is not limited to the motor mechanism, however. Sensory set and appetitive functions are encompassed by the readiness mechanism.

Orienting and readiness must be coordinated if behavior and experience is to proceed in a unified fashion. A third control system has been identified that effects this coordination. This system converges on the hippocampus.

The data on the control of attention from which the above generalizations are derived are of three sorts: neurobehavioral, psychophysiological, and neurophysiological. The neurobehavioral data were gathered from primates—both nonhuman experimental and human clinical—with a variety of forebrain lesions. Their behavioral responses were measured and compared with control subjects in situations that 1) produced the orienting reaction and its habituation, 2) tested reaction time of an ongoing response pattern in the face of distraction, 3) evaluated the ability to track a "randomly" moving spot, 4) compared the ability to choose one item from a pair with the ability to choose it from a larger set, and 5) measured the subject's responses to rewarded and to nonrewarded items and to items where the probabilities of reward were manipulated (e.g., 30-70%, 40-80%, etc.).

The psychophysiological data were gathered on similar groups of subjects. Again the orienting reaction and its habituation were measured, this time, however, by means of the galvanic skin response, changes in heart rate, changes in respiratory rate, and changes in the contingent negative variation of transcortically recorded electrical brain activity and in the blocking of the alpha rhythm of the scalp recorded electroencephalogram. These data were compared with those

gathered by others using identical techniques in a variety of task situations (especially the work of the Lacey (13) and of Paul Obrist (16, 17)).

The neurophysiological experiments investigated the actual possibility that these controls over input were exercised. Changes in the recovery functions (cycles) of the visual system were produced by electrical stimulations of the structures under consideration. Further, changes in some of the properties of visual receptive fields were also produced. Interestingly, such changes often showed a long latency (up to 1-2 seconds) and often took minutes (10-15 minutes) to reverse, suggesting a change of state—perhaps chemical—had been produced by the electrical brain stimulations.

To summarize these investigations on states of consciousness: states are conceived to result from some relatively stable configuration of neurochemical processes by the operation of controls not too different from those regulating other homeostatic mechanisms. With respect to consciousness, these states operate to regulate sensory input and are therefore involved in the organism's attention processes. Three such control systems have been identified: one that deals with orienting, a phasic response to novel input; a second that maintains readiness to continue ongoing processing; and a third that coordinates orienting with readiness. Three anatomically distinct forebrain loci have been related to these systems and there is considerable evidence that the systems differ neurochemically (see 23 for review).

In concluding, one other aspect of consciousness must be addressed. The attentional controls that determine a state of consciousness must operate on some content, there must be something to attend to. Attention addresses sensory input but input is primarily processed in the sensory projection systems, not in the limbic forebrain or in the basal ganglia. It is the sensory projection systems and their associated cortexes that transform the signals originating in sensory receptors into the perceived images and meaningful information that can be attended, to form the content of consciousness.

The neuroscience community has become more and more aware of the

importance of electrotonic processing of signals in these input systems (3, 6, 20, 21, 25–28). Observations such as the fact that the early stages of retinal processing (as well as those in most other receptor systems) are devoid of the generation of nerve impulses have provided convincing evidence of the critical role of graded potential interactions in sensory signal processing. Additionally, these observations have provided minimodels of some aspects of the functional organization of more central stations (especially of the cortical sheets that so closely resemble the layered retinal mosaic). The question that arises is whether the transfer functions that are being meticulously described for each stage of electrotonic input processing can together account for the constructions we experience as the content of consciousness. Two major views have emerged. One emphasizes the convergence of signals onto neurons that, at successive levels of processing, progressively extract the features encoded in the signals (12). The other emphasizes a more parallel process that, by virtue of lateral inhibition (a graded potential, electrotonic mechanism) functions linearly to encode signals in the frequency domain (4, 8, 19). In the auditory mode the idea that the sensory system may function as a frequency analyzer is a century old (11, 18) and Bekesy (1) has demonstrated with an elegant series of experiments that somatosensory (and perhaps gustatory, as well) experience is processed according to more or less identical rules. What is new are the experimental results that indicate that visual patterns are processed by a similar mechanism that is sensitive to spatial frequency—the frequency of occurrence of light and dark in the input to the retina.

The two views of the sensory processing mechanism—that of a hier-

archical nonlinear feature extraction process and that of a parallel processing linear frequency analyzer—are not mutually exclusive. The question is not which of these mechanisms is responsible for information and image processing but which is responsible for what aspect of the content of consciousness.

A fruitful hypothesis for guiding inquiry might be that feature extraction leads to information (discriminable alternatives in conscious content) while frequency analysis leads to images. There is a considerable body of evidence that the intrinsic cortex associated with the primary projection systems is critical to the discriminations that define information and its meaning (see 9, 15, and 22 for review).

There is also indirect (in vitro) evidence that the transfer functions that describe sensory processing in the frequency domain can be used to construct images. This evidence comes from holography. A hologram is the result of encoding the frequency of interfering wave fronts generated by signals (points) within a source being imaged. The invention of holograms was a mathematical one (7) whose purpose was to enhance the resolution of electron microscopy. The mathematics involved is identical to that which describes the transfer functions of visual processing of spatial frequencies. Holograms can be constructed in a variety of ways—by digital computers; by analog optical information processing devices using lasers, lenses, mirrors and refractive gratings; and perhaps, if the above hypotheses are confirmed, by the brain.

The holographic hypothesis of image processing has the virtue of explaining several hitherto difficult aspects of brain function and conscious experience. One of these is the distrib-

uted nature of the brain's memory store. The name hologram derives from the fact that information becomes "spread" as a result of encoding in the frequency domain so that every part of the hologram can be used to construct the whole image. Another is the projective nature of our conscious experience. Except for the somatic senses we do not ordinarily perceive and feel the contents of conscious experience either at the sensory surfaces where stimulation takes place or at brain locations where the experience is encoded and can be elicited by direct electrical stimulation. Even in the somatosensory modes, consciousness can be projected to the end of a writing or surgical instrument or into space by appropriate adjustments of the phase of stimulation (as in a stereophonic audio system (1)).

We began this essay with the questions of whether the concept of consciousness was necessary to scientific inquiry and if it were, what the issues might be that the concept subsumed. We found that clinical evidence made it difficult to proceed without the concept and we reviewed experimental evidence to the point that several mutually interacting control systems stabilize neurochemical processes into states that we experience as conscious. We further adduced evidence that these systems operate on sensory input systems that function to process the information and images that form the content of consciousness. The control of information and image processing is defined as the experience of attention. Finally, putative neural mechanisms involved in information and image processing are detailed and their explanatory power in relating brain function to consciousness was reviewed. This is a rich harvest from a field that even a decade ago had hardly begun to be plowed. □

REFERENCES

1. **Bekesy, G. V.** *Sensory Inhibition*. Princeton: Princeton Univ. Press, 1967.
2. **Bernard, C.** *Leçons sur la physiologie et la pathologie du système nerveux*. Paris: Ballière, 1858. Lecture 16, Vol. II.
3. **Bishop, G.** Natural history of the nerve impulse. *Physiol. Rev.* 36: 376–399, 1956.
4. **Campbell, F. W., and J. G. Robson.** Application of Fourier analysis to the visibility of gratings. *J. Physiol. (London)* 197: 551–556, 1968.
5. **Cannon, W. B.** *Bodily Changes in Pain, Hunger, Fear and Rage*. New York: Appleton, 1929.
6. **Freeman, W.** *Mass Action in the Nervous System*. New York: Academic, 1975.
7. **Gabor, D.** Information processing with coherent light. *Opt. Acta* 16: 519–533, 1969.
8. **Glezer, V. D., V. A. Ivanoff and T. A. Tscherbach.** Investigation of complex and hypercomplex receptive fields of visual cortex of the cat as spatial frequency filters. *Vision Res.* 13: 1875–1904, 1973.
9. **Gross, C. G.** Inferotemporal cortex and vision. In: *Progress in Physiological Psychology*, edited by E. Stellar and J. M. Sprague. New York: Academic, 1966.
10. **Grossman, S. P.** *A Textbook of Physiological Psychology*. New York: Wiley, 1967.
11. **Helmholtz, H. von.** *Die Lehre von den Ton-*

- empfindungen* (1st Ed.) Braunschweig: Vieweg, 1863.
12. **Hubel, D. H., and T. N. Wiesel.** Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160: 106-154, 1962.
 13. **Lacey, B. C., and J. I. Lacey.** Studies of heart rate and other bodily processes in sensorimotor behavior. In: *Cardiovascular Psychophysiology: Current Issues in Response Mechanisms, Biofeedback and Methodology*, edited by P. A. Obrist, A. Black, J. Bruner and L. DiCara. Chicago: Aldine-Atherton, 1974, p. 538-564.
 14. **Milner, B., and W. Penfield.** The effect of hippocampal lesions on recent memory. *Trans. Am. Neuro. Assoc.* 80: 42-48, 1955.
 15. **Mishkin, M.** Cortical visual areas and their interaction. In: *The Brain and Human Behavior*, edited by A. G. Karczmar and J. C. Eccles. Berlin: Springer-Verlag, 1972, p. 187-208.
 16. **Obrist, P. A., R. A. Webb, J. R. Sutterer and J. L. Howard.** Cardiac deceleration and reaction time: an evaluation of two hypotheses. *Psychophysiology* 6: 695-706, 1970.
 17. **Obrist, P. A., R. A. Webb, J. R. Sutterer and J. L. Howard.** The cardiac-somatic relationship: some reformulations. *Psychophysiology* 6: 569-587, 1970.
 18. **Ohm, G. S.** Über die Definition des Tones, nebst daran geknüpfter Theorie der Sirene und ähnlicher tonbildender Vorrichtungen. *Ann. Physik. Chem.* 59: 513-565, 1843.
 19. **Pollen, D. A., and S. F. Ronner.** Periodic excitability changes across the receptive fields of complex cells in the striate and parastriate cortex of the cat. *J. Physiol.* 245: 667-697, 1975.
 20. **Pribram, K. H.** A review of theory in physiological psychology. *Ann. Rev. Psychol.* 11: 1-40, 1960.
 21. **Pribram, K. H.** *Languages of the Brain: Experimental Paradoxes and Principles in Neuropsychology.* Englewood Cliffs, NJ: Prentice-Hall, 1971.
 22. **Pribram, K. H.** How is it that sensing so much we can do so little? In: *The Neurosciences Study Program, III*, edited by F. O. Schmitt and F. G. Worden. Cambridge, MA: MIT Press, 1974, p. 249-261.
 23. **Pribram, K. H.** Peptides and protocrine processes. In: *Neuropeptide Influences on the Brain and Behavior*, edited by L. H. Miller, C. A. Sandman, and A. J. Kastin. New York: Raven, 1977.
 24. **Pribram, K. H., and D. McGuinness.** Arousal, activation and effort in the control of attention. *Psychol. Rev.* 82 (2): 116-149, 1975.
 25. **Rakic, P.** *Local Circuit Neurons.* Cambridge, MA: MIT Press, 1976.
 26. **Rall, W.** Dendritic neuron theory and dendro-dendritic synapses in a simple cortical system. In: *The Neurosciences: Second Study Program*, edited by F. O. Schmitt. New York: Rockefeller Univ. Press, 1970, p. 552-565.
 27. **Schmitt, F. O., P. Dev and B. H. Smith.** Electronic processing of information by brain cells. *Science.* 193: 114-120, 1976.
 28. **Shepherd, G. M.** *The Synaptic Organization of the Brain—An Introduction.* New York: Oxford Univ. Press, 1974.
 29. **Sidman, M., L. T. Stoddard and J. P. Mohr.** Some additional quantitative observations of immediate memory in a patient with bilateral hippocampal lesions. *Neuropsychologia* 6: 245-254, 1968.
 30. **Sperry, R. W., M. S. Gazzaniga and J. E. Bogen.** Interhemispheric relationships: the neocortical commissures: syndromes of hemisphere deconnection. In: *Handbook of Clinical Neurology. Vol. 4*, edited by P. J. Vinken and G. W. Bruyn. Amsterdam: North Holland, 1969, p. 273-290.
 31. **Weiskrantz, L., E. K. Warrington, M. D. Sanders and J. Marshall.** Visual capacity in the hemianopic field following a restricted occipital ablation. *Brain* 97: 709-728, 1974.