AROUSAL AND ACTIVATION OF THE BRAIN

The brain is constantly active, generating nerve impulses that create a background of electrical activity which underlies the various stages of sleep and wakefulness. One of the initial discoveries illustrating this fact was made by Berger who pioneered the technique of the electroencephalograph (EEG) which monitors the electrical activity measured at the scalp. Berger noted that during changes in wakefulness, brain waves could range between fast, low voltage activity and the slow, high amplitude wave forms characteristic of deep sleep.

The mechanism regulating these shifts remained unknown until the discovery by Moruzzi and Magoun in 1949 that the reticular formation, a collection of short-fibered neurons in the brainstem, is critical for maintaining an alert organism. Lesions to portions of this system caused somnolence, coma, and death. Concurrent with this research were similar discoveries by Lindsley who found also that electrical stimulation to these same regions produced an alert organism with fast brain wave activity.

Yerkes-Dodson Law

These results, along with others, served to initiate a conceptualization of the brain as aroused or activated, terms which were, and often still are, used interchangeably. Allowing these discoveries to the behavioral data on performance during under- or overstimulation from the environment, researchers began to view both brain and behavior as complying with the Yerkes-Dodson law. This law postulates an inverted U-shaped function of efficiency depending upon the degree of "arousal" of the organism. Under-aroused subjects perform as poorly as over-aroused subjects, with optimal levels occurring in a moderately
AROUSAL AND ACTIVATION OF THE BRAIN

aroused state. The activity of the reticular formation was presumed to parallel these states. The notion of brain activation or arousal as existing on a continuum has led to a considerable amount of confusion in the light of subsequent investigations. This has been particularly evident from the substantial development of research on the response of the autonomic nervous system (ANS) to psychically “arousing” events.

Since the discovery by Féré in the nineteenth century that electrical activity of the skin is spontaneously generated during rest and changes in task-specific ways, investigations on the correlation between skin resistance (or conductance) and changes to events in the environment have been numerous. Subsequent research has implicated changes in cardiovascular systems, electrical activity in the muscle, and pupillary contractions, all of which have been found to bear lawful relationships to certain parameters of stimulus events and the control exercised by the subject in attending to these events.

Paradoxes soon became evident. The desynchronization of the EEG corresponded to many of these peripheral changes, yet gross EEG does not habituate readily to stimulus repetition, while autonomic responses do so reliably. Critical experiments by Lacey further challenged the notion of a unified “arousal” mechanism by demonstrating a fractionation in responding between physiological systems. When a subject looks or listens to external events, heart rate slows and skin resistance decreases. However, when a subject attempts to solve a difficult problem, heart rate accelerates rapidly, while skin resistance still decreases. The question arises: Which system is measuring “arousal”?

Cortical Arousal

Additional perturbations for a simplified theory were produced by the concurrent endeavors of Sharpless and Jasper in the United States and Sokolov in Russia. These researchers were the first to note that a change in activity of the ANS is produced by a novel event, and that habituation will ensue if the event is recurrent. However, the important aspect of their findings relate to the fact that changing any parameter of the stimulus causes a reappearance of the arousal response (Sokolov, 1960), or in the Russian term, the orienting reaction. This suggests that the arousal reaction is partly due to the previous production of a cortical model. Sharpless and Jasper also noticed that the ANS response separated into a phasic component which habituated readily and a tonic component which habituated much more slowly. Studies have now demonstrated that the phasic portion is almost always of the order of 1-3 seconds, depends upon the intensity of the stimulus, and is entirely a reflex response. The most common cause of its occurrence is a mismatch to a previously encoded input (a memory trace). Another way to express this is to suggest that the phasic portion of the orienting reflex is sensitive to stimulus information. The tonic portion, while initially part of the orienting reaction, can be brought under voluntary control and can be extended in time depending upon the interest or intentions of the individual. Thus arousal, from Sokolov’s demonstration, must be cortical, at least where information is involved, and not just due to reticular neurons.

As well, arousal seems to split into two parts, one of which is totally outside of the control of the subject, and one which is not.

Since these discoveries, further advances in the analysis of electrical brain waves have utilized averaging and D.C. recording techniques. When a series of evoked responses is averaged, the effects of stimulus onset produce early positive and negative shifts technically described as P1, N1, P2, N2. These correlate temporally with the phasic portion of ANS responses. In D.C. analysis slow negativity is found to accompany states of attention or expectancy. This response is called a contingent negative variation (CNV) and parallels HR deceleration remarkably (Lacey). Thus, not only are phasic and tonic changes found in ANS peripheral mechanisms but are also paralleled by phasic and tonic effects in CNS electrical activity.

A final complication for a unified arousal theory came as a result of lesion studies on monkeys (work by Pribram and colleagues). It was found, contrary to expectation, that the behavioral correlates of orienting (head turning, ear flicking, focusing, etc.) could be dissociated from the autonomic responses of skin resistance and heart rate. The critical finding was that if, due to specific lesions, the organism failed to produce autonomic responses to
stimuli, behavioral orienting occurred but failed to habituate. Pribram found that the critical brain structures involved in this dissociation were the frontal cortex and the amygdala (a system of nuclei found in the upper brainstem).

Despite these many contradictions, theorists have been reluctant to part with the concept of a unified arousal system largely dependent upon activation of the reticular formation. Recently a critical analysis of the literature on the disparate measures and findings in the study of arousal and habituation (Pribram and McGuinness, 1975) has established a new conceptual framework for the data, categorizing the various findings in terms of the types of attention and their respective control mechanisms. A source of inspiration for this endeavor comes from the analysis of attention processes by William James (1950) who suggested that attention could be both involuntary (reflex) and voluntary, reflecting the intentions or will of the individual. Such a framework has made it possible to reconcile the conflicting findings by postulating three major control systems.

Control Mechanisms

Arousal. The first control mechanism regulates arousal and centers on the amygdala. The amygdala acts to regulate both efferent and afferent information transmitted between the primary systems of the frontal lobe, the hypothalamus, and the reticular formation. Frontal lobe input to the amygdala determines the level of distractibility of the organism, while the integration of information to and from the hypothalamus in turn regulates a STOP mechanism that arrests ongoing behavior sufficiently to register a new event. The reticular formation generates sufficient neural activity to boost the signal to a level of awareness. In effect, the organism then asks, What is it?

Activation. The second control system takes over when the stimulus has been registered in awareness. Handling the next stage in processing, this system allows the organism to ask, What's to be done? This phase is called the activation or readiness phase and is centered on the basal ganglia, structures that regulate motor control. While this system predominates, in attending to the environment the organism's posture remains stable, muscle activity is reduced, heart rate slows, and a slow negative shift in D.C. potentials is recorded. An organism can extend this phase until a suitable decision is achieved: Take action, code input, or ignore.

Effort. A final control mechanism centering on the hippocampus allows for a precise integration between these two modes. This control system is postulated as requiring "effort." Effort is conceptualized in terms of the degree of control essential to take the organism out of a throughput or entirely reflex reaction, like the stimulus-response reflexes characteristic of lower organisms. Hippocampal function in conjunction with the reticular formation makes it possible for the organism to inhibit continuous distraction and to avoid perseverative responding to any stimulus. The effort mechanism acts upon both the arousal and the activation systems, regulating voluntary behavior in sufficient measure to allow for planned, coherent activity, but not to such an extent that meaningful or biologically relevant stimuli go undetected.

Attention

Thus far, the attention system has been characterized as reflexive and intentional without qualitative distinctions between processes. Two further operations are of interest to the study of brain mechanisms in attention. While the organism is functioning essentially in a voluntary mode, its attention can be directed in two ways. First, the organism may want to catalogue or selectively attend to stimulus events in the external environment. When taking in information, selecting or coding input, the organism has its attention broadly focused, that is, the arousal and activation modes are operating in a state of balance. When this balance is achieved, the critical brain structures involved in cataloguing or selectively attending to stimuli are the areas of the temporal cortex (the so-called association areas) for specific sensory modalities. In the absence of these structures the animal is "selectively" impaired in making correct choices of the appropriate channels for an individual mode.

Another attention process—one that has been characterized, behaviorally, as narrowly focused—is related to tasks that require reason-
ing, problem-solving, or difficult discriminations. In such tasks the role of "effort" can be most clearly discerned. The effort is conceptualized neurally by the amount of damping that hippocampal activity produces on the reticular formation—an electrical analogue of "Do not disturb." Effort is further demonstrated by the rapid rise of heart rate, which appears to be the result of an increase in the anaerobic metabolism in the muscles (Berdina et al., 1972).

In general, most effort is required in problem solving tasks, such as mental arithmetic, where external input is eliminated from awareness. The difficulty of maintaining this mode of attention varies according to the spontaneous activity levels of individuals. Young children, for example, find it impossible to concentrate on a problem for more than a few minutes. Individuals also have difficulty performing tasks where discrimination between two very similar inputs is required. A dramatic illustration of the effort required by such a task is found in Pavlov's classic demonstration of neurotic "breakdown" produced in dogs. The animals were trained to respond to a high tone and to ignore a low tone. As these tones were gradually made to sound alike, the effort to make the distinction became so great that their neural functioning began to deteriorate. The dogs howled and writhed at their harnesses.

The utilization of attention as a unifying principle determining what we are aroused to notice, or what we choose to be aware of, has a decided advantage over the view that we are either simply aroused or not aroused. Arousal as defined here emphasizes the reflexive aspects of the attention system. For the young infant it is the most characteristic mode of responding and it is slowly replaced by an ever increasing control over the mode of activation or readiness. In selective attention, arousal generally precedes activation. The organism notices something in his environment and distinguishes between stimuli. When the organism attends to internal events, as in reasoning or problem solving, activation precedes arousal. Here the solution to the problem provides the maximum information, and the arousal resulting from performing the task varies according to the degree of creativity or novelty provided by the solution. This account provides an explanation for the significance of the Aha experience, which so frequently culminates a long period of contemplation on a difficult problem.

BIBLIOGRAPHY


KIMBLE, D. P.; BAGSHAW, M. H.; and PRIBRAM, K. H. The GSR of monkeys during orienting and habituation after selective partial ablations of the cingulate and frontal cortex. Neuropsychologia, 1965, 3, 121-123.


KARL H. PRIBRAM
DIANE MCGUINNESS

AROUSAL MECHANISM
See Sexual Arousal Mechanism

AROUSAL SYSTEMS IN INFANTS: CONDITIONING

Historical Overview

Modern studies of infant conditioning originated in the 1920s and 1930s, based largely on Pavlov's formulations. Pavlov's view that conditioning was a higher cortical rather than a subcortical function suggested that infants lacking cortical maturity should fail to condition. On the other hand, the functional subcortical structures of the infant might be expected to mediate conditioning until inhibited by maturing higher cortical mechanisms. Infant