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Arousal, Activation, and Effort in the Control of Attention

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This review attempts to organize a range of neuropsychological and psychophysiological data on attention. Three separate, but interacting, neural systems are distinguished: One controls *arousal*, which is defined in terms of phasic physiological responses to input. The arousal control circuits center on the amygdala. A second system controls *activation*, which is defined in terms of tonic physiological readiness to respond. The readiness circuits center on the basal ganglia of the forebrain. A third system is discerned which coordinates arousal and activation. This coordinating activity is defined as demanding *effort*. Its circuitry centers on the hippocampus. When arousal, activation, and effort are involved in problem solving, at least two further distinctions can be made. During *categorizing*, arousal precedes activation; during *reasoning*, activation precedes arousal. Finally, the review addresses the question of whether effort in problem solving is to be attributed solely to peripheral muscular factors or whether, in fact, direct monitoring of changes in brain organization (changes in set, attitude, etc.) can be productive of measurable indicators of effort.

In the mid 1960s, R. J. Douglas and K. H. Pribram presented a series of experiments detailing the effects of hippocampal lesions on problem-solving behavior. The results of these experiments were accounted for by recourse to the concept of experiencing a change in awareness which was interpreted as indicating the involvement of "attention." A continuing interest in problems of attention has been reflected not only in the work reported from our laboratory (a dozen and a half papers) but also in that of many others (see reviews by Mostofsky, 1970; Horn and Hinde, 1970; and Kahneman, 1973). Research has largely been directed to two general paradigms defined by the following operations: (a) recording the occurrence of physiological or behavioral responses against a background of monotonous repetition of

sensory events (orienting, vigilance, and habituation) and (b) the invariant (categorizing), or the variable but computable (reasoning), pairing of the outcome of response (reinforcement) to sensory events. An assessment of the data derived from these paradigms (in approximately 200 experiments) has led us to identify three basic attentional control processes: One regulates *arousal* resulting from input; a second controls the preparatory *activation* of response mechanisms; and a third operates to coordinate arousal and activation, an operation that demands *effort*. The first two sections of this review will delineate these attentional control systems; the last section will deal primarily with higher order cortical attentional controls that operate during categorizing and reasoning.

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REFLEX ATTENTION, REPRESENTATION, AND THE CONTROL OF AROUSAL

Arousal is said to occur when an input change produces a measurable incrementing of a physiological (e.g., single unit recording of neural potentials; galvanic skin response) or behavioral (e.g., response amplitude of a spinal reflex; frequency of a locomotor response) indicator over a baseline. The types of input change that produce

arousal have been studied extensively and have been labeled by Berlyne (1969) as collative variables. These include sudden changes in intensity to which the organism is unaccustomed, changes in the timing of inputs, and changes in the ground in which a stimulus figure appears, in particular when input is scarce, surprising, complex, and novel. Such collative characteristics also define the concept "information" as it is used in the study of communication systems (see e.g., Brillouin, 1962); thus it is possible to treat organisms subject to arousal as "information processing systems," where input is matched against some residual in the organism of his past experience, or some competence (Miller, Galanter, & Pribram, 1960; Pribram, 1971). Without such matching, there could be no novelty or information nor even a measure of change in intensity.

This knowledge has led to behavioral research which has been addressed to such issues as adaptation level (Helson, 1964), expectancy (Bruner, 1957) and the development of "neuronal models" (Sokolov 1960, 1963), while neuroscientists were able to demonstrate the occurrence of a permanent or semipermanent modifiability of neural tissue (see Pribram and Broadbent, 1970; Horn and Hinde, 1970).

Neural Modifiability

Sharpless and Jasper's (1956) and Sokolov's (1963) classical studies paved the way for an analysis of the requisites for producing behavioral and physiological arousal responses. Especially significant was the implication of information processing systems by Sokolov's findings (1963) that *any* change in a repetitively presented stimulus configuration would elicit responses even when that change was a shortening of the sensory input or the lowering of its intensity. Sokolov concluded that the organism's sensitivity was not just a measure of its threshold but rather that sensitivity was a function of a match between input and some competence, a neuronal "model," or a patterned memory trace developed in the brain as a representation of the experienced stimulus configuration. Any mismatch produces orienting.

Many investigators concerned with modifi-

ability of neural tissue as a consequence of experience seized on the habituation of an initial neural or behavioral arousal reaction as an extremely simple test paradigm that suited this purpose. Although these efforts and results have been reviewed by Horn and Hinde (1970), we will highlight certain issues that are relevant to this presentation.

An approach initiated by Spencer and Thompson (see Groves and Thompson, 1970) involved recording from the spinal cord and illustrated that neither sensory afferents nor motor efferents accounted for habituation of spinal reflex behavior. Further, Thompson discerned two primary systems, two classes of neurons; those that responded more slowly and incremented for relatively long periods before decrementing, and those that rapidly decremented their activity with repetition of the stimulus. The incrementing "monitoring," "sameness," or "arousal" neurons lie more ventrally and medially in the region of the origin of the visceromotor outflow, while the decrementing neurons lie, for the most part, in the dorsal horn of the spinal cord. Convergence of these two systems of neurons was assumed to account for the activity of a third population of ("novelty") neurons whose response characteristics were identical to those demonstrated by the reflex: arousal reaction, habituation, and dishabituation.

Thompson's parallel processing model of arousal, habituation and dishabituation, shared by many other investigators (e.g., Horn, 1970; Segundo & Bell, 1970; Spencer & April, 1970) is simpler than Sokolov's as it depends only on spatial summation of arousal and decrementing. No "neuronal model" of the input is developed, only a decrementing to repetition and an "arousal" proportional to the strength of the input. The model does not account for Sokolov's findings that in the intact organism dishabituation occurs when stimulus duration is *shortened* or stimulus intensity is *diminished*. These phenomena imply a hierarchical process involving storage and subsequent matching of input to store. Horn (Horn & Hinde, 1970) has developed a scheme whereby such a hierarchical process can be realized without any unnecessary assumptions that go beyond

the data obtained by practically everyone; namely that the decrementing observed is due to self-generated synaptic depression and not to the development of inhibition (inhibitory postsynaptic potentials characterized in intracellular recordings by hyperpolarization).

This does not mean, of course, that inhibition fails to occur in many systems. The sensory and motor pathways are replete with circuits that lead to both lateral (i.e., neighborhood) and self-inhibition. As we shall see shortly, habituation becomes organized into patterns in these pathways whether by the mechanisms proposed by Horn or by the action of inhibitory circuits, or both.

Core Brain Arousal System

The rostral extension into the mesencephalic brain stem of a column of medially placed cells accounts for the well documented arousal effects of stimulations of the reticular formation (see Lindsley, 1961, and Magoun, 1958 for review). Less well known is the fact that such effects are obtained even more rostrally in the diencephalon in a continuation of this neuron system into the hypothalamus.

The contribution of hypothalamic visceromotoric mechanisms to the reflexive aspects of the orienting reaction has been noted by Feldman and Waller (1962). The episodes of fighting and fleeing that are produced by electrical or chemical stimulation to the so-called "defense" region of the hypothalamus can be related to the orienting reaction. Abrahams and Hilton (1958) and Abrahams, Hilton, and Zbrozyna (1964) found that, in attempting to produce a defense response by stimulation of the hypothalamus, at first, a much lower degree of arousal occurred, indicated by pupil dilatation and postural alerting. Only when the level of stimulation was increased and maintained for a few seconds did hissing, snarling, running, and piloerection occur. In the later study, alerting behaviors were measured in greater detail, and during mild stimulation the authors observed changes in pupil dilation, head movement, pricking the ears, respiration, and blood flow. These same changes were also recorded during responses to sim-

ple auditory, visual, or cutaneous stimuli in the absence of hypothalamic stimulation. Since these physiological changes are the same as those observed in all orienting responses, the defense reaction could therefore be considered in part as due to an increase of arousal.

Sensory Systems and the Neuronal Model

There is ample evidence that a host of other brain mechanisms are involved in the orienting reaction. Electrical brain recording, both with macro- and with microelectrodes, shows that initial desynchronization and increase in neuronal discharge occurs in a large number of neural systems. One of the characteristics of familiarization consequent on repetition of a stimulus is the progressive restriction of these sites (John, 1967; John & Killam, 1960). Paradoxically, however, this restriction involves primarily the sites where arousal neurons are located and does not encompass either sensory pathways or the primary sensory projection systems where responses continue to be recorded in the habituated organism. These, therefore, became prime candidates for the locus of comparison of the input stimulus configuration with the neuronal model registered earlier through habituation.

To determine where the detailed comparisons necessary to the Sokolovian model of habituation and orienting might occur, Grandstaff and Pribram (1972) studied the possibility that Thompson's results pertained only to spinal cord and perhaps lower brain stem mechanisms but that at more rostral stations of the sensory projection systems, *patterns* of change rather than simple decrementing were produced during habituation. Surprisingly, this study showed the Thompson model to hold at the collicular and thalamic levels: electrical responses recorded from the lateral geniculate nucleus as well as those from the retina and superior colliculus (also obtained with microelectrodes by Horn and Hill, 1966; and by Bures and Buresova, 1970) in intact monkeys subjected to repetitive visual stimulation uniformly decremented to repetitive monotonous stimulation, and enhanced responses occurred only when a change in stimulation was initiated. Soko-

lov's model was saved, however, by the results obtained from recordings of the activity of visual cortex. Here, habituation produced no uniform decrementing—some records invariably and reliably showed an incrementing of activity, while others decremented (over each of many days of recording) and still others showed no reliable changes. A *patterned habituation* response occurred, and dishabituation to a change in stimulation disrupted this pattern.

Patterned changes in cortical *rhythmicity* also occur. Thus patterning of electrical brain activity is not limited to abrupt potentials evoked by the stimulus. Earlier studies have been reviewed by J. Mackworth (1969). More recently it was shown that during habituation, changes occur in both latency (increase) and duration (decrease) of desynchronization when baseline activity is in the 10 Hz alpha frequency range (Bagshaw & Benzie, 1968; Grandstaff & Pribram, 1972). More complex frequency analysis of the ongoing cortical activity of limited areas of the visual cortex (Grandstaff & Pribram, 1972) has shown that a decrease in power with habituation in 8–10, 37–50, and 72–80 Hz frequency ranges occurs when the amplitude of the evoked potential decreases. By contrast, in those electrode placements where the amplitude of the evoked response increases, an increase in power in the alpha and other critical ranges is obtained. These patterns of change do not occur at subcortical loci (optic nerve and lateral geniculate nucleus) but are limited to recordings made from the visual cortex, supporting the conclusion that *patterning* of neuroelectric activity, an indication of the construction of a "neuronal model," is primarily the function of a cortical information processing competency.

The occurrence of a patterned response at the cortex suggests that each of the cortical sites can be considered separate information processing channels, which is consonant with the anatomy of these systems. Neisser (1967), Kahneman (1973), and Lindsay (1970) have thoroughly reviewed the behavioral evidence for considering the sensory channels to be primarily parallel processing systems, or at least some form of multiplex-

ing mechanism that relies on an initial simultaneous parallel processing stage, a problem which will be considered in the section on categorizing. Here we first outline the neural systems involved in the arousal and activation that leads to desynchronization of the patterned neuronal model.

Amygdala Circuits

There is evidence for the involvement of the amygdala and related frontal cortical structures in the attentional control of the core brain arousal systems. This evidence delineates two reciprocally acting circuits, one facilitatory and the other inhibitory, both converging on hypothalamic structures related to arousal. Such reciprocal innervation allows sensitive modulation (tuning) of the arousal mechanism.

In pursuing the question of which brain systems are involved in orienting and habituation, we first replicated and showed some of the limits over which the Sokolov results held (Koepke & Pribram, 1966, 1967). When adapting the techniques to the monkey

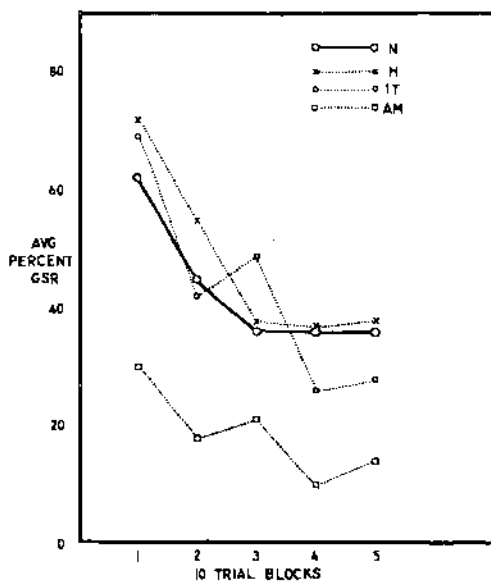


FIGURE 1. Curves for overall percentage of galvanic skin response (GSR) to the first 50 presentations of an irregularly presented 2-sec tone. (Abbreviations: N = unoperated group; H = hippocampectomized group; IT = control group; AM = amygdalectomized group.)

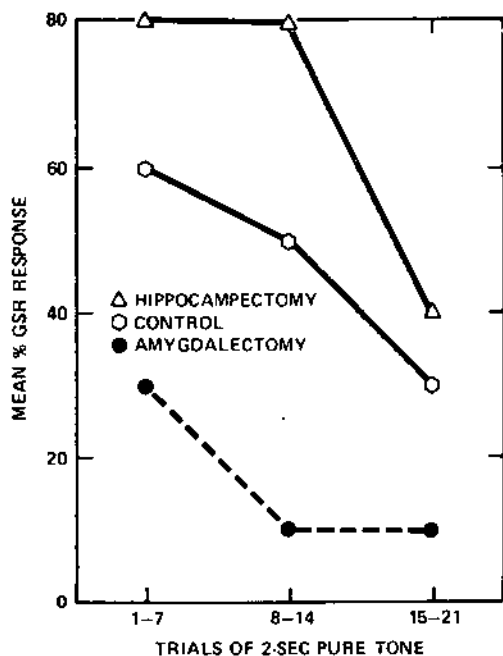


FIGURE 2. Curves for a more detailed analysis of the first 21 trials (split into 7-trial blocks) or percentage of galvanic skin response (GSR) to a 2-sec tone for the amygdectomized, hippocampectomized, and unoperated monkeys. (See also Table 1.)

we found, contrary to expectation, that lesions of the mediobasal, frontolimbic forebrain, and not of the convexity of the cerebral mantle, had a dramatic effect on measures of orienting (Bagshaw, Kimble, & Pribram, 1965; Kimble, Bagshaw, & Pribram, 1965).

Amygdectomy results in a failure of behavioral habituation, producing an ever-recurring locomotor orienting reaction (Bagshaw & Benzie, 1968; Schwartzbaum, Wilson, & Morrissette, 1961). Such hyperreactivity is also produced by lesions of the orbital surface of the frontal lobe (Mettler & McLardy, 1948; Ruch & Shenkin, 1943; Wall & Davis, 1951) which has been shown to be a part of a larger orbitofrontal-insular-temporal-polar-amygdala system (Kaada, Pribram, & Epstein, 1949). When an analysis of the viscerautonomic components of the orienting response was carried out on frontal and amygdectomized monkeys, it was expected that these components would

parallel behavioral orienting. In many instances the opposite was observed.

Resections of dorsolateral frontal cortex *always* abolish the viscerautonomic components of orienting (Kimble, Bagshaw, & Pribram, 1965; Luria & Homskaya, 1970; Luria, Pribram, & Homskaya, 1964), while amygdala resections produce a bimodal distribution. Electrodermal responses during orienting (Figures 1 and 2; Bagshaw & Benzie, 1968; Bagshaw, Kimble, & Pribram, 1965) are reduced in amplitude and amount for most subjects. However, certain subjects show an increased number and amplitude of response (see Figure 3 and Table 1). Tonic heart rate is paradoxically elevated (see below), but all phasic heart rate responses are abolished (Bagshaw & Benzie, 1968; Pribram, Reitz, McNeil, & Spevack, 1974).

Thus, reciprocal systems appear to be involved—one apparently relates to the dorsolateral frontal cortex since resections of this structure *invariably* eliminate visceral-autonomic orienting responses. The other, op-

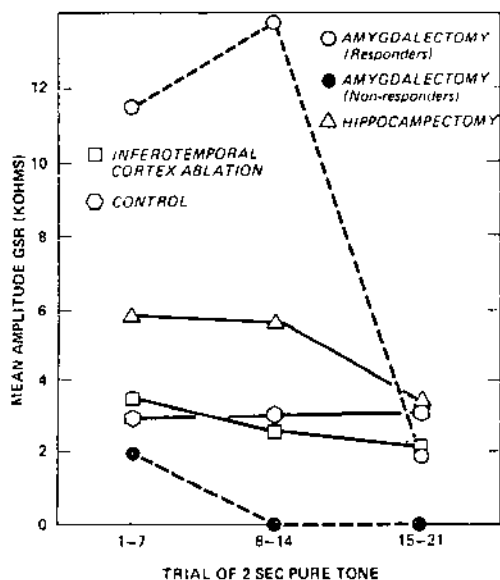


FIGURE 3. Group mean amplitude for galvanic skin response (GSR) to tone on the first 21 trials showing the bimodal distribution of the amygdectomized monkeys when compared with normal (control) and with two other brain-lesioned groups of monkeys: inferotemporal cortex resection and hippocampectomy.

TABLE 1
AMOUNT AND AMPLITUDE OF GALVANIC SKIN RESPONSES OVER TRIAL BLOCKS FOR SUBJECTS

Group	Response (%)			Amplitude (Ω)		
	Trials 1-7	Trials 8-14	Trials 15-21	Trials 1-7	Trials 8-14	Trials 15-21
Normal (14)	63	54	43	3.0	2.9	3.2
Hippampectomy (7)	71*	70*	62	5.9*	5.8*	3.5
Amygdalectomy (6)						
Hyperresponsive (2)	90*	50	40	11.4*	4.3*	1.9
Hypo-responsive (4)	15*	00*	00*	2.0	—	—

Note. Number of subjects in each group appear in parentheses following the group.
* $p < .05$.

posite in function, is most likely related to the orbitofrontal cortex which has been shown to be the rostral pole of an extensive inhibitory pathway (Kaada, Pribram, & Epstein, 1949; Pribram, 1961; Sauerland & Clemente, 1973; Skinner & Lindsley, 1973; Wall & Davis, 1951). These data relate to the early descriptions of the behavior of amygdalectomized animals (Pribram & Bagshaw, 1953) which focused on the fact that while the majority were tame, unresponsive to threat, and nonaggressive, the opposite finding was also occasionally observed (e.g., Rosvold, Mirsky, & Pribram, 1954), and more recent behavioral studies by Ursin and Kaada (1960) using restricted lesions and electrical stimulations have confirmed the suggestion that at least two more or less reciprocal systems can be identified in the amygdala.

Attentional Control of the Arousal System

The presence of reciprocal systems suggests the existence of a locus upon which they converge, a locus which, from anatomical considerations (Pribram & Kruger, 1954), is most likely to be found in the hypothalamic regions of the brain stem. This suggestion is supported by microelectrode evidence at the spinal cord level (Groves & Thompson, 1970) which indicates that the origin of the desynchronizing mechanism leading to orienting may be localized to the medial parts of the spinal cord where the visceromotor outflow originates. The neurons that respond during orienting are likely to have derived their

input from locations near the visceromotor regulating mechanisms. This is borne out both by the results of electrical stimulations of the hypothalamus (noted above), the amygdala (Gastaut, 1953, 1954), and related cortical areas (Wilcott, in press). Thus, not only can the visceromotor components of orienting be sharply distinguished from the somatomotor components, but their role in the orienting mechanism appears to be primary.

The fact that the two amygdala systems are reciprocal, one facilitating, the other inhibiting arousal, suggests a controlling, modulating mechanism and is in accord with evidence on other control functions of the amygdala and related structures. Injections of carbachol into the appropriate hypothalamic site will initiate drinking; such injections into the amygdala have no effect unless the animal is already drinking, in which case the amount of drinking becomes proportional to the amount of carbachol injected in an exquisitely accurate relationship (Russell, Singer, Flanagan, Stone, & Russell, 1968). The frontoamygdala influence can be conceived as a finely tuned determinant controlling visceromotor arousal initiated by the hypothalamic mechanism during orienting. It is as if in the absence of the frontoamygdala systems, the animal would fail to control his drinking behavior: Once started he would drink under circumstances in which others would stop. This is exactly what happens—and more. Both eating and drinking are controlled in this fashion—not only their cessation but also

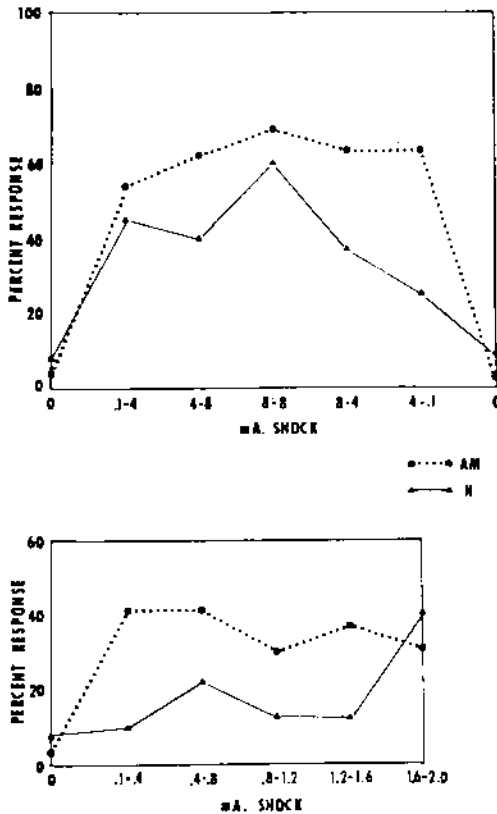


FIGURE 4. Top: Curves of percentage of galvanic skin response generated by three runs of stimuli in ascending and descending intensity (in map) by the amygdalotomized (AM) and control (N) groups. Bottom: A finer breakdown of stimulus values from .1 to 1.0 mA, pooled ascending and descending values. (From "Effect of Amygdalotomy on Stimulus Threshold of the Monkey" by M. H. Bagshaw and J. D. Pribram, *Experimental Neurology*, 1968, 29, 197-202. Copyright 1968 by Academic Press. Reprinted by permission.)

their initiation (Fuller, Rosvold, & Pribram, 1957).

Sensitivity and Registration

The question arises as to the significance for the orienting reaction of the visceromotoric components per se. The absence of visceromotoric reactivity during orienting could result simply from lowering the sensitivity of the organism to stimulation. However, resections of frontal cortex (Grueninger, Kimble, Grueninger, & Levine, 1965) or of the amygdala (Bagshaw and Coppock, 1968; McNeil, 1972) do not abolish galvanic skin

responses to movements or to shock. When threshold for shock was measured, frontal lobectomized (Grueninger & Grueninger, 1973) and nonresponsive amygdalotomized subjects were found to have, if anything, greater sensitivity (see Figure 4). Specifically, these monkeys frequently produced a maximal number and amplitude of responses to intensities that produced very little or no reaction in normal subjects.

This leaves no doubt that the peripheral response mechanism remains intact. Neither a change in sensory sensitivity nor an altered peripheral response mechanism can account for the effects of frontal and amygdala lesions on the orienting reaction. The critical influence exerted by these forebrain structures appears to relate to arousal induced registration of input effecting changes in the organization of central mechanisms.

Certain changes relate to the finding that despite reactivity to shock, the amygdalotomized and frontally lesioned subjects have fewer "spontaneous galvanic skin responses" during the shock sessions, suggesting an altered base level. So far, we have referred to phasic changes in the initial period of observation, which often reach asymptote within three to five stimulus presentations. However, while behavioral and some electrocortical responses appear to be normal during orienting, after frontal and amygdala lesions (Bagshaw & Benzie, 1968; Schwartzbaum et al., 1961) the background level of these responses is lower than for controls. For example, ear flicking is practically absent during interstimulus intervals (Bagshaw & Benzie, 1968), and while electromyographic responses occur with normal latency, the amplitude of these responses is considerably reduced (Pribram, Reitz, McNeil, & Spevack, 1974).

Accompanying the reduction in baseline of phasic responses, a striking tonic psychophysiological effect followed amygdalotomy. This was the finding of a paradoxically elevated basal heart rate (Bagshaw & Benzie, 1968; Pribram et al., 1974). The paradox has been clarified by experimental results obtained by Elliott (Elliott, Bankart, & Light, 1970) in which he found that novel input had little effect on tonic heart rate or

had an effect (deceleratory) opposite to expectations. However, response factors and incentive factors (reinforcing consequences) had strong accelerating effects. Thus, arousal, though it may produce a brief initial phasic acceleration (Obrist, Wood, & Perez-Reyes, 1965), leads more often to tonic heart rate *deceleration*, which is indicative of *activation*, a process detailed in the next section. In short, the monkeys with absent arousal reactions are consistent in showing an elevated tonic heart rate. As Elliott's data indicate, and as will be detailed in the last section of this article, elevated tonic heart rate is manifest when the situation demands "effort" on the part of the organism.

The effects of amygdectomy can be interpreted as follows: Because the specific controls on arousal are removed, behavioral arousal fails to lead to the registration of the situation by altering the neuronal model but results in nonspecific defensive "effort" to cope with the situation. This defense reaction is characterized by an attempt to shut off further input (see Pribram, 1969), and is reflected in an elevated heart rate and other changes indicative of a lack of readiness to respond meaningfully to the input. Thus "effort" is manifest in the absence of readiness. This interpretation is borne out by the results of an experiment in which infant kittens were raised in isolation. When examined at the age of 6 months their visceromotor and endocrine reactivity in orienting experiments was essentially similar to that of amygdectomized subjects: They had not learned to cope with situations and thus showed the "defensive" syndrome suggestive of considerable "effort" (Konrad & Bagshaw, 1970).

Summary

Studies relating brain function and the orienting reaction to sensory input have pointed to the presence of a system of neurons responding to the amount of input to them by maintaining or incrementing their activity. This core system of neurons extends from the spinal cord through the brainstem reticular formation, including hypothalamic sites, and lies in close proximity to those responsible for the engenderment of

visceromotor responses. By way of its diffuse connections, this system is responsible for the more ubiquitous "arousal" responses recorded throughout the brain concomitant with orienting. Forebrain control over this core brain arousal system is exerted by reciprocal facilitatory and inhibitory circuits centered on the amygdala. These circuits control the onset and duration of neural arousal much as they control the onset and duration of visceromotor and appetitive responses.

Our interpretation of the relationship between the lack of visceromotor responses to orienting and the failure to habituate behaviorally has been to suggest that a deficiency is produced in the more ubiquitous central mechanism by which organisms "register" input. When such failure in registration occurs, the organism's nervous system is temporarily swamped by the arousing input and reacts defensively to shut out all further input and thus leads to automatisms. This interpretation fits the clinical picture of the amnesic states (*deja vu* and *jamais vu*) and the automatisms occurring during psychomotor seizures produced by epileptic lesions in the region of the amygdala. There is also considerable congruity between this interpretation and those of Mednick and Schulsinger (1968) and of Venables (Gruzelier & Venables, 1972) in their report of two classes (galvanic skin responders and non-responders) of patients diagnosed as schizophrenic. However, the interpretation also suffers from the difficulties that plague understanding of these clinical syndromes: How do disturbances of registration in immediate awareness influence subsequent retrieval? This will be discussed further in the following sections.

VIGILANT ATTENTION, EFFORT, AND THE CONTROL OF ACTIVATION

The interaction between behaving organisms and their environment is not one-sided. The organism is not just a switchboard for incoming stimulation. Rather, the essence of behaving organisms is that they are spontaneously active, generating changes in the environment often by way of highly programmed, that is, serially ordered, responses

(Miller, Galanter, & Pribram, 1960; Pribram, 1960b, 1962, 1963, 1971). These organizations of behavior must involve the construction of neuronal models in at least two ways: (a) control of the somatomotor system which effects the responses and (b) feedback from the outcomes (reinforcing consequences) of the behavior. Sherrington (1955), in discussing central representations, framed the issue in terms of whether the organism is intending to *do* something about the stimulus variables in the situation. In a review of the evidence Germana (1968, 1969) suggested that any central representation or "neuronal model" must include such "demand" characteristics. Thus he proposes that Pavlov's "What is it?" reaction (which we have called "arousal," the registration of input in awareness) may not occur unless there is also a "What's to be done?" reaction. As we shall see, our analysis would suggest that both reactions occur and that they can be distinguished: registering input, indicating "What is it?", and vigilant readiness signaling "What's to be done?" Strictly behavioral analyses have led to a similar dissociation. The early studies of Lawrence (1949, 1950) and the more recent work of Broadbent and Gregory (reviewed by Broadbent, 1971) are perhaps the best known in terms of independent manipulations of stimulus set and of response set.

Contingent Negative Variation and Activation

The simplest situation which demands that responses become serially organized is one in which two successive input signals are separated by an interval. The first input signals the organism to become ready to make a response to the second which determines the outcome. A large body of data has been gathered in this situation, using slow changes in brain electrical activity such as the *contingent negative variation* (CNV) (Walter, Cooper, Aldridge, McCallum, & Winter, 1964) and tonic changes in heart rate. Lacey and Lacey (1970) have established a correlation between the amplitude of CNV and heart rate deceleration. (J. I. Lacey and B. C. Lacey, 1974, and Malmö and Bélanger, 1967, distinguish between their 1-

minute-long changes in heart rate and "enduring" changes in background level. We shall call both of these "tonic" in the present review, though it is possible that the shorter changes are related to activation while more enduring levels of heart rate reflect effort.)

The CNV was originally proposed to reflect an expectancy developed when a specific response was contingent on awaiting the second of two stimuli. This would suggest that the CNV reflects another central event indicating that an input is about to be matched to the organism's neuronal model. However, other workers suggested that the negative shift in potential reflects intended motor activity (e.g., Kornhuber & Deecke, 1965; Vaughan, Costa, & Ritter, 1968). Still others (Weinberg, 1972; Donchin, Gerbrandt, Leifer, & Tucker, 1972) demonstrated that a CNV occurs whether or not an overt motor or even a discriminative response is required, provided some set or expectancy is built into the situation. Such sets do, of course, demand postural motor readiness. Weinberg (1972), for instance, has shown that in man the CNV continues until feedback from the consequences of reinforcement of the response occurs, and similar evidence has been obtained in monkeys (Pribram, Spinelli, & Kamback, 1967). In a review of the CNV literature, Tecce (1972) suggests that three types of negative potentials interact depending upon the demands of the experiment: (a) CNV due to expectant attentional processes; (b) the motor readiness potential signaling intention to act; and (c) more or less "spontaneous" shifts whose occurrence cannot yet be attributed to specific task situations. This classification though consonant with results from a series of studies (Donchin, Otto, Gerbrandt, & Pribram, 1971, 1973) does not indicate the full diversity of the CNV. Recordings were made from several cortical locations under a variety of vigilance conditions. These studies showed that sites which produced transcortical negative variations (TNVs) depended upon the type of vigilance task. Thus, frontal TNVs are recorded only early in a task and when the task is changed; motor negative potentials are recorded only in anticipation of the necessity to make an

overt response; postcentral negative potentials are largest when the organism must hold a response (continuously depress a lever) until a signal to release it occurs; and special sensory systems respond to their specific inputs (Pribram, 1971). The TNV appears to be an indication of either arousal or activation of the brain tissue from which it is recorded.

Sustained, tonic changes in potential have also been noted in subcortical negative potential shifts recorded in animals by Rebert (1972, 1973, in press) and in man by Grey Walter (1967) and by Haider (1970). It is as yet too early to characterize the meaning of such shifts for every location, but in general, it appears that negativity develops whenever a portion of brain tissue is maintaining a readiness for processing. This conclusion is also reached by Hillyard (1973) in an analysis of the CNV and human behavior. Hillyard also notes, in line with our analysis, that brainstem controls on overall cerebral negativity exist. We therefore will distinguish between the term TNV (multiple local readiness of cerebral tissues) and CNV (controls on these local potential shifts).

At the end of the negativity, if and when the organism actually begins to *do* something, a sharp positive deflection is usually observed, and this positivity has been related to consummatory behavior (Clemente, Sterman, & Wyrwicke, 1964) and to a sharp increase in power both in the alpha (8–12 Hz) and theta (+8 Hz) ranges (Grandstaff, 1969) in the visual cortex. It remains to distinguish between the TNV that occurs as a function of arousal, and the *desynchronization* which produces a decrease of power in the alpha and theta frequency range while accompanied by the negativity shifts of activation.

Go and Stop Mechanisms

Preliminary evidence (Rebert, 1972; Walter, 1967) suggests that a source controlling CNVs indicative of activation may be located somewhere in the region of the dorsal thalamus and basal ganglia of the forebrain because the polarity of slow activity is similar in hypothalamic and cortical

leads but shows a reversal in the depths of the brain. This evidence fits that obtained from a host of studies concerning the role of hypothalamic and mesencephalic (reticular) mechanisms in initiating and terminating behavior. Miller, Galanter, and Pribram (1960) initially proposed, on the basis of clinical evidence, that corebrain mechanisms are primary in initiating and terminating behavior, reflecting fundamental behavioral systems. Mandler (1964) has extensively investigated the arousing consequences of the interruption of behavior obtaining psychophysiological evidence of arousal in humans interrupted while performing tasks. Pertinent neurobehavioral studies have been interpreted in terms of "go" and "stop" processes by Pribram (1971, chaps. 9, 10, 11).

At the brainstem level, reciprocal processes exist: a "stop" mechanism that, when stimulated, generates arousal (affect) and is dependent on satiety monitors in the more medial hypothalamic areas. This system, according to recent neurochemical evidence (reviewed by Pribram, 1971), is primarily serotonergic. In addition, there is a "go" mechanism which converges onto the far-lateral hypothalamic region which is not composed of cells but of fiber tracts such as the median forebrain bundle and others perpendicular to it. The data, from the studies recording deep-lying CNVs, suggest the hypothesis that we look for the control of the "go" process in the basal ganglia which give rise to many of the fiber tracts that make up the far lateral hypothalamic crossroads. Recently completed studies *substantially* support this hypothesis. Ungerstedt (1974) and Fibiger, Phillips, and Clouston (1973) have independently demonstrated effects identical to those obtained by Teitelbaum (Teitelbaum & Epstein, 1962) for lateral hypothalamic syndrome by interfering with the dopaminergic system of neurons connecting the substantia nigra with the basal ganglia.

Uncoupling of Stimulus and Response

Thus at both the cortical and the brainstem levels arousal and activation can be distinguished; arousal as a phasic reaction to input and activation as a tonic readiness

to respond. Yet, under many circumstances the two reactions appear to be yoked: at the cortex by the TNV and in the hypothalamic region by the reciprocity of the "stop" and "go" mechanisms. In such situations they share the function of reflexly coupling input to output, stimulus to response. In the absence of controlled arousal and activation, behaving organisms would be constantly aroused by their movements and moved by arousing inputs. There must be some process that involves both arousal and activation which allows the uncoupling to take place. This process is habituation, which we have seen to be critical in the development of the neuronal model. Action generated inputs (the outcomes of actions, their reinforcing consequences) appear to produce more complexly structured neuronal models than repetitions of simple inputs per se, and reflect the participation of the central motor

systems in generating input. It takes longer to form a habit in, than to habituate to, the same situation. Complex inputs such as repeated exposure to the same musical performances do not readily induce habituation but in such situations a good deal of motor readiness—listening—is also involved.

Having considered the effects of certain limbic lesions on arousal, we need now to review the effects of limbic lesions on habituation and to relate such effects to the activation of vigilant readiness.

Hippocampal (Papez) Circuits

Subjects with bilateral hippocampectomy tend to show a percentage of reactivity and amplitude of the galvanic skin response opposite to that observed in the nonresponding amygdalotomized monkeys (see Figures 2 and 3 and Table 1) in the ordinary orienting paradigm. In addition, the phasic skin response terminates considerably more rapidly in hippocampectomized subjects than in controls (see Table 2 and Figure 5). It appears from this that hippocampectomized monkeys (and amygdalotomized hyperresponders) re-equilibrate more rapidly than normal subjects whose slower galvanic skin response recovery may indicate a more prolonged processing time. As we shall see below, this is consistent with other data that show impaired processing of the disequilibrium produced by a mismatch of input to the neuronal model as a result of hippocampectomy.

A further change is that such subjects show delayed or absent orienting reactions when thoroughly occupied in performing some other task (Crowne & Riddell, 1969; Kimble, Bagshaw, & Pribram, 1965; Raphelson, Isaacson, & Douglas, 1965; Riddell, Rothblat, & Wilson, 1969; Wicklegren & Isaacson, 1963). In short, these animals appear to be abnormally intractable.

But in some situations this appearance of intractability is restricted to the overt responses of the organism, not to orienting per se. Douglas and Pribram (1969) used distractors in a task in which responses were required to each of two successive signals. Hippocampectomized monkeys initially responded much as controls did by overtly

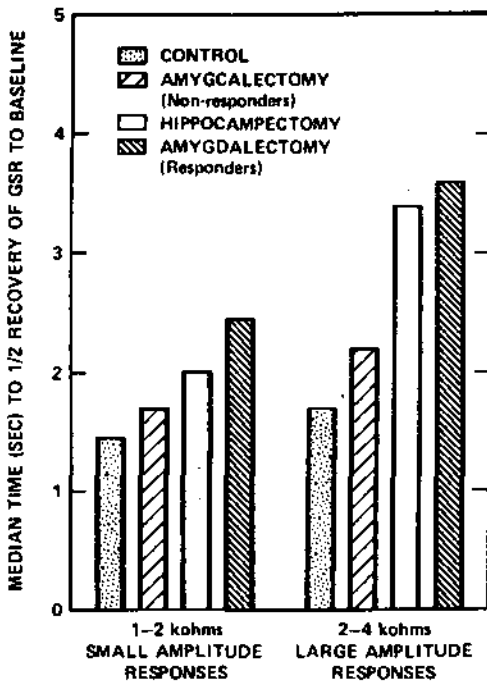


FIGURE 5. Bar graph showing the time taken to attain half recovery to baseline of the visceromotoric perturbation measured as an electrodermal response (galvanic skin response, GSR). (Small, 1-2 Kohms, and large, 2-4 Kohms, perturbations are treated separately since amplitude of response has an obvious effect on recovery time. See also Table 2.)

manipulating the distractors and thus increasing the time between the two required responses. However, in contrast to the behavior of the controls who simultaneously habituated overt manipulation of the distractors and the interresponse time, the hippocampectomized group showed decrementing only of the overt manipulations—their interresponse time failed to habituate at all. In this situation, hippocampectomized monkeys continue to be perceptually distractible while becoming behaviorally habituated and indistractable (Figure 6). This result is identical to that obtained in man with medial temporal lesions: Instrumental behavior can to some considerable extent be shaped by task experience, but verbal reports of the subjective aspects of experience fail to indicate prior acquaintance with the situation (Milner, 1958).

The dissociation between habituation of

TABLE 2
HALF-RECOVERY RATE OF GALVANIC SKIN RESPONSES FOR SUBJECTS

Group	Half-recovery rate for controlled amplitudes (kΩ/sec)	
	Small 1-2k	Large 2-4k
Normal (14)	.320	.460
Amygdalectomy (6)		
Hyperresponsive (2)	.730*	.730*
Hypo-responsive (4)	.250	.460
Hippocampectomy (7)	.580*	.620*

Note. Number of subjects in each group appear in parentheses following the group.
* $p < .05$.

perceptual responses and habituation involving somatomotor performance appears to be part of a more general effect of hippocampal lesions, as it is manifest in other situations

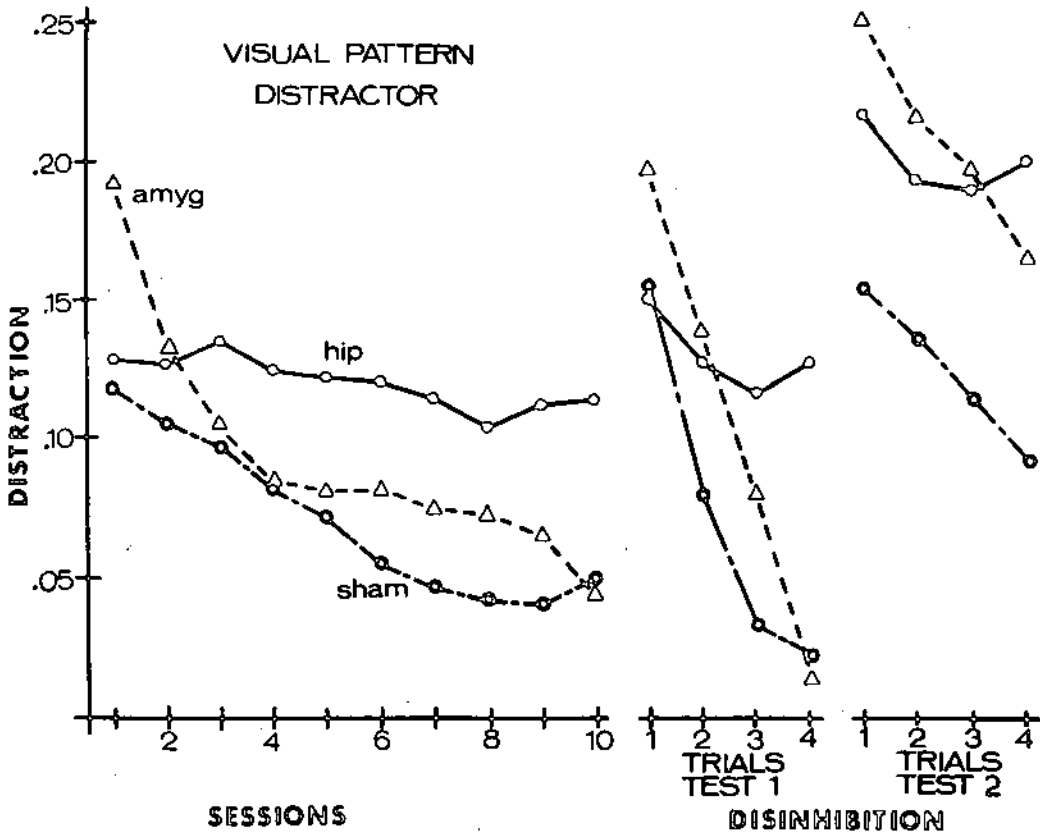


FIGURE 6. Distraction with visual pattern stimulus as distractor. (Abbreviations: sham = sham-operated subjects; amyg = amygdalectomized monkeys; hip = hippocampectomized animals.)

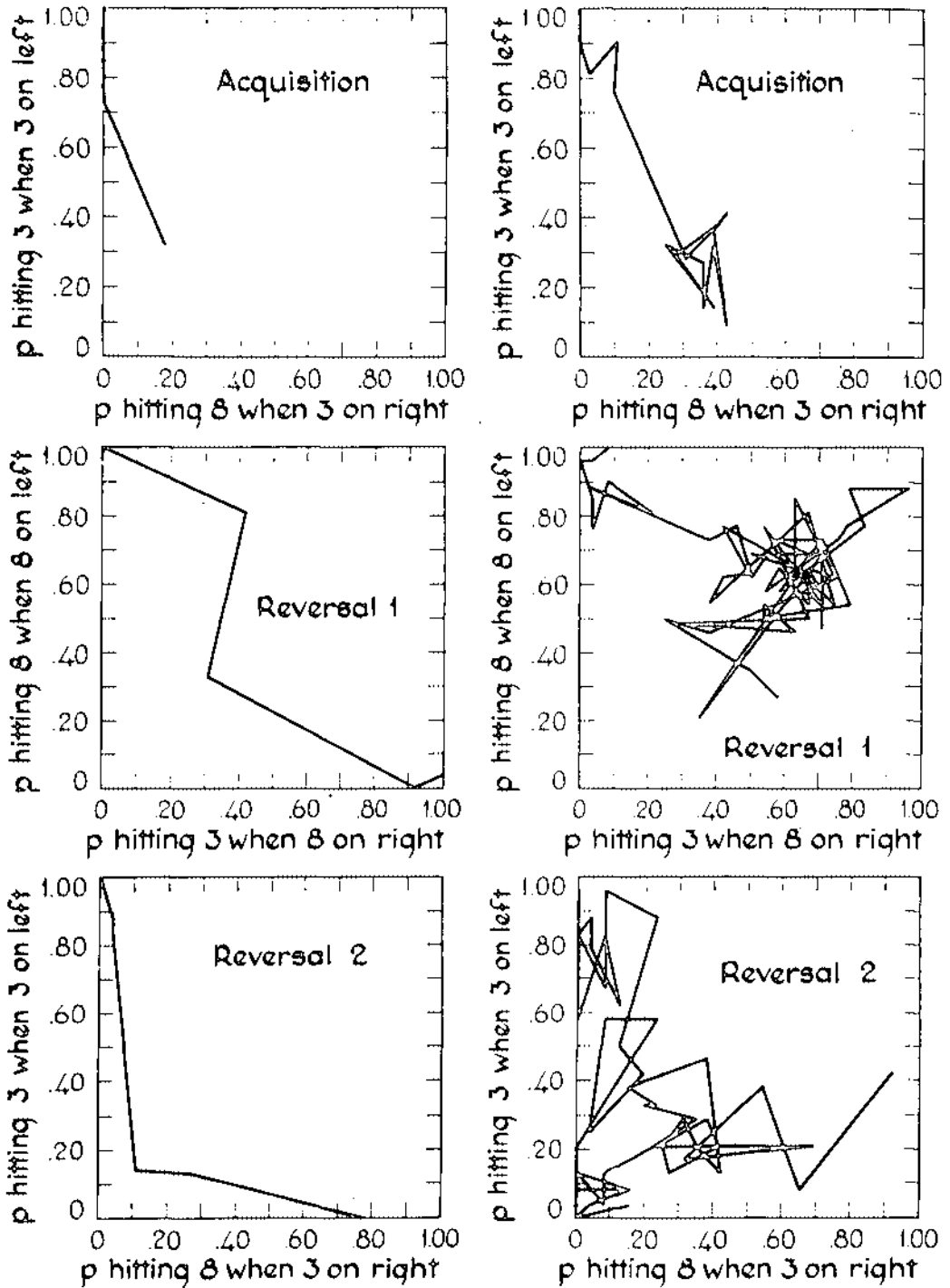


FIGURE 7. Individual curves for an intact (left) and a hippocampectomized (right) monkey during discrimination and the first two reversals. (The curves were constructed by joining in temporal sequence points summarizing pattern-discrimination and position preference of the "lesion" and "intact" monkeys for 50 trial sessions during pattern-discrimination and reversal training.) (From two figures in "A Decisional Analysis of the Effects of Limbic Lesions in Monkeys" by A. Spevack and K. H. Pribram, *Journal of Comparative and Physiological Psychology*, 1973, 82, 211-226. Copyright 1973 by the American Psychological Association. Reprinted by permission.)

in which hippocampectomized monkeys are tested. In a discrimination reversal situation, extinction of previously learned behavior and acquisition of newly correct responses were observed. However, in contrast to their controls, the monkeys with the hippocampal lesions remained at a chance level of performance for an inordinately long time (Pribram, Douglas, & Pribram, 1969). This effect was due to the "capture" of the behavior by a position bias to respond to the 50% schedule of reinforcement—a bias hardly manifest in unoperated monkeys (Figure 7; Spevack & Pribram, 1973). This result suggested that a hierarchy of response sets was operative in the situation such that "observing" responses (indicative of "attention") were relinquished when the probabilities of reinforcement of discriminative stimuli ranged around the chance level.

Taken together, these experimental results suggest that interference with the hippocampal circuit reduces the organism to a state in which the more effort demanding relationships between perception and action, between observing and instrumental responses, and between stimulus and response are relinquished for more primitive relationships in which either input or output captures an aspect of the behavior of the organism without the coordinating intervention of central control operations. The mechanism by which the hippocampal circuit accomplishes this relationship has been elucidated to some extent by recordings of electrical activity from the hippocampus both with micro- and macroelectrodes and by precise electrical stimulations of selected parts of the hippocampal circuit.

The Hippocampus—Arousal and Activation

The evidence that delineates the hippocampal mechanism accounts for the general observation that the *greatest* changes in gross electrical activity observed during habituation are recorded from the core brain (especially mesencephalic reticular and limbic control systems; John, 1967; John & Killam, 1960).

The hippocampus with its three-layered cortex provides the best opportunity for observing unit activity responsible for the

changes observed in gross electrical activity in repetitive situations. Vinogradova (1970) found that *all* neurons of the hippocampus habituate to repetition of a stimulus and dishabituate to any change in the stimulus configuration. But she distinguished two types of neurons, A and I: those activated (30–40%) and those inhibited (60%) by a stimulus, respectively. Habituation occurs by a progressively shortening response in the course of 16–20 repeated presentations. The averaged poststimulus histograms of the two classes are "mirror images of each other."

Some important characteristics of hippocampal units are that (a) the latencies of response to a stimulus do not change; (b) they are of the order of 100–1000 msec even initially; (c) in the ventral hippocampus (the only part present in primates, including man) stimuli must be of a minimum duration of from $\frac{1}{4}$ to 1 sec to produce any noticeable change in the background activity and (d) such facilitation persists up to 1 min after the cessation of the stimulus. These characteristics indicate a necessity for a long period of summation to precede hippocampal facilitation. Vinogradova (1970) interprets her findings as follows:

The duration of reactions in hippocampal neurones shows that the processes continue here long after the information processing is finished in all specific sensory structures, and in primary and secondary areas of the cortex as well. . . . As Gloor (1961) indicated, the quality of sensory information is almost erased in hippocampal neurones. (pp. 114–115)

These results are in accord with proposals previously put forward by Douglas and Pribram (1966). We suggested that the hippocampus constitutes part of an error (mismatch) evaluating mechanism which was conceived to process *only the perturbations* resulting from the mismatch among inputs (including those consequent on responses) (Pribram, 1971). Vinogradova is in agreement, therefore, in suggesting that precise sensory information is *not* involved. Further, she suggests a mechanism by which such processing can be achieved:

The hippocampus exerts a tonic inhibitory influence upon the reticular formation, blocking activatory processes through the tonic discharge of its I-neurones when novelty is absent and registration is

not needed. But when a stimulus which is not registered in the memory system appears, this inhibitory control is blocked (I-neurons become silent), arousal occurs, and the process of registration starts. (p. 114)

Lindsley has recently elaborated the mechanism by which the hippocampally controlled reticular formation can effect these changes in registration. Lindsley (Macadar, Chalupa, & Lindsley, 1974) in keeping with many other recent publications (e.g., Fibiger et al., 1973; Ungerstedt, 1974) has dissociated two systems of neurons that influence the hippocampal circuit. One system originates in the median raphé and associated structures of the mesencephalic reticular formation, the other originates more laterally in the locus ceruleus and other portions of the periaqueductal grey. We have come to know these two systems in the present review as a serotonergic (indole amine) "stop" mechanism associated with arousal, and a dopaminergic and norepinephrinergic catechol amine "go" mechanism associated with readiness and activation. Lindsley's findings were obtained by electrical stimulations of the appropriate structures in the mesencephalic reticular formation. Such stimulations of the stop mechanisms produced hippocampal desynchronization and at the same time a synchronization of the amygdala circuits. Taken together with Vinogradova's evidence, this suggests a reciprocal process by which the controls on arousal are maintained as long as hippocampal inhibition of the reticular formation is in progress—much as Vinogradova suggests. Only when a mismatch from the neuronal model is signaled to the reticular formation does this inhibitory control become loosened producing hippocampal desynchronization—and concomitant relaxation, synchronization, of the arousal functions of the amygdala circuits. Lindsley has found that often, though not always, such hippocampal desynchronization is accompanied by desynchronization of the sensorimotor projection systems, suggesting that "registration," an alteration of the neuronal model of the cortical representation, is occurring. Note that in this formulation the term "registration" refers to a change in the neuronal model, thus a "registration in memory," a

process that, as we shall see, requires effort. This use of the term registration must be distinguished from "registration in awareness" which, as noted earlier, is disrupted by interference with the amygdala circuits.

Theta Rhythms and Intent

The second mechanism discerned by the Lindsley studies is the catechol amine "go" system which has been the focus of this section. This mechanism makes possible the "What is to be done" reaction, the processing of response-produced inputs. When electrically stimulated, the mesencephalic portions of the "go" mechanism initiate hippocampal rhythmic activity in the theta range of frequencies. Early studies (Green & Arduini, 1954) had uncovered the paradox that the desynchronization of the electroencephalogram recorded from the brain's convexity during "activation" was accompanied by synchronization in the recordings obtained from the hippocampus. Though such synchronization is not as obvious in records obtained in monkey and man, computer analysis has shown it to occur and that it can also be studied in the primate (Crowne, Konow, Drake, & Pribram, 1972). This synchronous rhythm is in the theta range (4–8 Hz) and has become the focus of a long series of studies.

That theta frequencies are especially prominent in records made from the hippocampus was noted by Jung and Kornmüller (1938). Later a series of studies (Green & Arduini, 1954; Grastyan, 1959; Grastyan, Lissak, Madarasz, & Donhoffer, 1959) described the occurrence of hippocampal theta to the orienting stage in a conditioning situation. Still later, however, the occurrence of hippocampal theta was related instead to intended movement (Dalton & Black, 1968; Black & Young, 1972; Black, Young, & Batenchuk, 1970): intended rather than overt movement because the theta rhythm occurs in completely curarized preparations who have been trained in the uncurarized state to lever press. These conclusions were in part anticipated by another series of experiments conducted by Vanderwolf and his associates (Bland & Vanderwolf, 1972a, 1972b; Vanderwolf, 1969, 1971; Whishaw, Bland &

Vanderwolf, 1972). Rats were observed while moving freely in the test situation and hippocampal electrical activity was recorded continuously. Theta activity occurred almost exclusively when the rats were making "voluntary" movements, defined as acts or response sequences characterized by flexibility and modifiability.

Adey and his group (Adey, 1970; Adey, Dunlop, & Hendrix, 1960; Elazar & Adey, 1967; Radulovacki & Adey, 1965) took the investigation of behavioral effects on hippocampal theta rhythms a step further by showing that a shift (4-6 Hz) in power within the theta frequency range occurs in cats from the prestimulus period, through stimulus presentation, to the correct response. Bremner (1970) has further analyzed the changes in theta activity along three dimensions: (a) an increase or decrease in the total amount of power in the theta range; (b) a narrowing or broadening of the range of energy distribution around the peak frequency; (c) the location of that peak frequency in the electroencephalogram spectrum. Change in total power of theta depends on the visceromotor arousal (increase) versus somatomotor readiness (decrease) distinction delineated here, and the changes in contour and their distribution correspond to the categorizing-reasoning distinction to be pursued in the latter parts of this review.

Specifically, Bremner has used the habituated organism (rat and man) as a baseline preparation and then studied manipulations which gave rise to orienting, simple conditioning, discrimination, and discrimination reversal. He found that the power (amount of energy) of hippocampal theta increased as a function of the stimulus which produces orienting and arousal but decreased in the anticipatory interval preparatory to response in the conditioning situation. Narrowing reflects discrimination, and the location of the peak is shifted by discrimination reversal procedures, findings especially relevant to the results of the behavioral experiments reviewed above (Figure 8).

Thus Bremner finds that the power of theta produced by a distracting stimulus becomes attenuated when an organism is already preoccupied in the performance of a

task. Further, during discrimination reversal, despite the fact that the now positive stimulus elicits enhanced power in the theta frequency range within two or three trials, extinction of the prior correct stimulus shows a long time course and the dominant frequency may appear to shift in one direction or another (Gray, 1971). These data also suggest an explanation for the finding detailed above (Pribram et al., 1969) that hippocampotomized monkeys are little different from normal subjects in reversal learning except that they remain fixed at the chance level for an incredibly long period.

Summary

By way of review, we note that there exists evidence for the organization of a central representation of input, the construction of a (cortical) neuronal model. Changes in this neuronal model are controlled by two subcortical systems: One is located in core portions of the neuraxis and contains neurons that increment to or monitor input, while another more laterally placed, contains neurons which rapidly decrement when they are repeatedly stimulated. In addition, we have delineated three brain mechanisms in the rostral portions of these control systems: (a) The first centers on the amygdala, which regulates the monitoring or "arousal" neurons and becomes organized into a "stop" or reequilibrating mechanism. (b) A second is centered on the basal ganglia and involves the *activation* of "go" mechanisms—expectancies (perceptual) and readiness (motor). (c) Finally, a third mechanism comprising

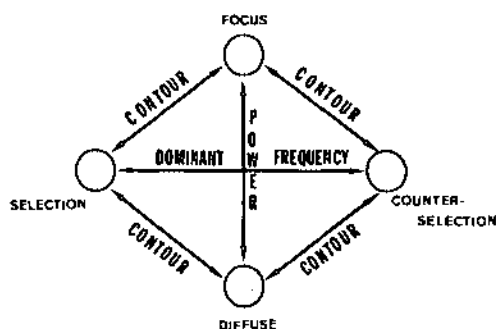


FIGURE 8. Diagram of the relationship among dimensions of hippocampal theta activity and behavior.

the hippocampal circuit has been identified, which uncouples the stimulus from the response by coordinating the amygdala and basal ganglia mechanisms so that appropriate changes in the central representation can occur, a process that entails *effort*.

As the amygdala is often considered to be one of the basal ganglia, albeit related specifically to the olfactory and visceral systems, brain structures similar in morphology, though different in their connections, control arousal and activation. Their coordination in effecting change in central representation, on the other hand, devolves on a circuit—the hippocampus—very different in morphology, and more akin to that characterizing the cerebellum, another mechanism notable for coordinating complex sequential processes.

Control by the amygdala is achieved by a reciprocal mechanism: a facilitatory lateral-frontal-amygdala-lateral-hypothalamic and an inhibitory orbito-frontal-amygdala-medial-hypothalamic circuit have been identified. Both circuits operate on the monitoring (e.g., satiety) neurons which in the brainstem appear to be serotonergic, that is, indole amine neurochemically. We suggest that the controls modulate the intensity and duration of the reaction initiated and thus modulate the organism's arousal, a "What is it?" reaction. This suggestion can be readily tested by electrically stimulating amygdala (and frontal) locations (much as was done by the Lindsley, 1961, and Clemente et al., 1964, groups) and recording with microelectrodes (as in Richard Thompson's experiments, cited in Groves and Thompson, 1970) to determine the effects on threshold and duration of the reaction initiated by the monitoring mechanism in the appropriate spinal or brainstem (reticular, hypothalamic) neurons.

Control over the "go" mechanisms responsible for the preparatory *activation* of brain systems appears to center on the basal ganglia. Activation of any particular part of the brain is signaled by the gradual development of a negative potential which becomes abruptly positive when the perceptual or motor response is executed. There is evidence that this slowly developing negativity per se is primarily of local origin. The mechanism and pathways involved in the

controlling function are apparently dopaminergic, part of a more extensive catecholamine system.

Hippocampal control over the organization of the relationship between arousal and activation leads to changes in central representations which may be conceived as changes of state, set, or "attitude." Such change, as illustrated in the final section of this review, demands "effort." Hippocampal function involves the notorious Papez circuit, largely invoked in discussions of brain function in emotion, conceived within a visceral theory framework (MacLean, 1949). It is an interesting historical note that Papez put forward his proposal within the context of Nina Bull's attitude theory of emotion (1951) and thus comes close to the views of the function of this circuit as proposed here.

What remains to be systematically investigated is the relationship between hippocampal electrical activity and the variety of electrical manifestations generated in the remainder of the brain. For instance, both the CNV with its concomitant cortical desynchronization and hippocampal theta rhythms have been involved in the intended execution of perceptual and motor responses. Usually study of dc shifts of the CNV type are prevented by the apparatus used to study the electroencephalogram frequencies, and the CNV has not been studied in relation to a frequency analysis of the tonic, ongoing electrical activity of the brain. One exception, already mentioned (Grandstaff & Pribram, 1972) showed that power in the theta range increases dramatically at the *end* of the CNV when a sharp positivity occurs. The remaining question concerns the correlations between the locations and conditions effecting decrease in power in the theta range in the hippocampus (as found by Bremner, 1970) and the buildup or terminal deflection of a CNV. The causal relation between the two types of electrical manifestation can be investigated by examining the CNV in subjects with hippocampal (and other Papez circuit) lesions.

The division of reflex and vigilant attention into arousal and activation components receives substantial support from an analysis

of the components of the event-related gross potentials evoked in the auditory system by Picton and Hillyard (1974). Their succinct summary speaks for itself:

In conclusion we should like to propose a tentative synthesis of all such data into an elementary model for the physiological basis of human auditory attention. The stability of the early [initial] components of the evoked response would seem to indicate that auditory information is analyzed in the lemniscal or primary auditory system in much the same manner regardless of whether it is attended or not. A secondary auditory system, imperfectly defined but probably comprising reticular formation, medial thalamus, and (frontal) association cortex, is involved when further evaluation of the significance of this auditory information is required. *Stimulus set* directs the preferential input to this secondary system from that part of the lemniscal system involved in processing the attended sensory channel. *Stimulus set* is evidenced, therefore, by the increased N_1-P_2 [large early components of the evoked potential] response of the frontal association cortex. The secondary system functions to compare input from the primary auditory system with memory models or templates of expected or significant stimulus alternatives. Once a relevant or significant signal has thereby been recognized, this decision is followed by appropriate *perceptomotor* sequelae. These sequelae, reflecting the contingencies of a *response set* mode of attention are associated with the generation of the widespread P_2 [late components of the evoked potential] complex recorded from the scalp. (p. 199)

In concluding this part of the review, we want to emphasize for behaviorally oriented psychologists the data we believe to be important to their interests.

Three neurally distinct and separate attentional systems—arousal, activation, and effort—operate upon the information processing mechanism. The presumed operation of these control systems is perhaps best illustrated as follows: The orienting reaction involves arousal but no activation; vigilant readiness involves activation but no arousal; the defense reaction involves both arousal and activation; when neither arousal nor activation is present, behavior is automatic, that is, stimulus-response contingencies are direct without the intervention of any of the control mechanisms of attention. Such automatisms, when they occur abnormally, are diagnostic of lesions affecting the medial surface of the temporal lobe, the site of two of the three control systems, and have also been

experimentally produced by extensive lesions of the basal ganglia (Mettler & Mettler, 1942).

Clearly, in the intact organism these control systems continuously interact with each other as well as with the information processing systems where the representational mechanisms become constituted. Figure 9 may help to summarize in highly oversimplified form the mechanisms detailed thus far, and it suggests the relationship to them of the various higher level cortical controls which are the focus of the discussion in the remaining parts of this review.

SELECTIVE AND VOLUNTARY ATTENTION

Whenever a problem demands a response to an invariant combination of input events (including those which are response produced) the task is usually referred to as a discrimination. The invariant combination must be detected, categorized, and selectively attended to make the appropriate response. This selective attending operates on the processing of information.

Another sort of problem solving occurs when the combination of input events is variable but computable. We will refer to these tasks as reasoning problems. In nonhuman primate experiments, the delayed response and delayed alternation are examples of such tasks: in human experimentation arithmetic calculations and other complex problem-solving exercises have been used.

Reasoning demands the uncoupling of attention from the immediate input variables—the attention involved is *voluntary*, therefore, in the sense that it is initiated by the organism rather than by some input event. Such intentional voluntary processes have recently been studied extensively and are no longer the complete mystery they once were (McFarland, 1971; Miller et al., 1960; Pribram, 1962).

The steadiness of the visual world during voluntary eye movement (as noted by Helmholtz, 1924) is not achieved through feedback from eye muscles but through a parallel processing feedforward biasing (Pribram, 1971, chap. 5) or open loop (McFarland, 1971) mechanism. Detailed experimental analyses by Merton of both eye movement

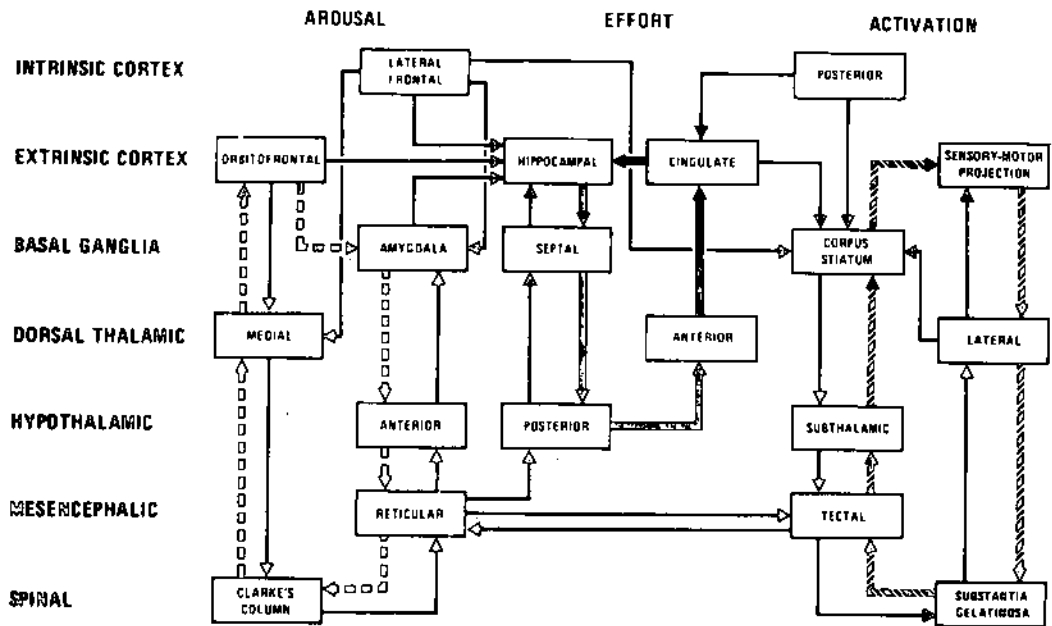


FIGURE 9. A highly oversimplified diagram of the connections involved in the arousal (amygdala), activation (basal ganglia), and effort (hippocampal) circuits.

(Brindley & Merton, 1960) and voluntary movement involving the pyramidal and gamma motoneurons (Merton, 1953) have been reviewed elsewhere (Pribram, 1971, chap. 13) and mark a beginning toward the scientific understanding of the term "voluntary."

An operational definition of selective and of voluntary attention, provided by the discrimination and reasoning tasks described above, will be used to illustrate how categorizing and reasoning involve the three attentional processes discussed earlier. However, we must begin with the delineation of two additional higher order (cortical) neural systems which control central competency by virtue of the organization imposed on incoming information.

Central Competency

In living systems, an arousing stimulus often *increases* the uncertainty of the organism by its novelty. This effect of input information is contrary to that obtained in nonliving communication systems where the information conveyed always *reduces* uncertainty. The difference between living and nonliving systems can be conceptualized in

terms of the channel over which the communication takes place. In nonliving communication systems the channel is akin to a sensorimotor channel which is fixed in capacity and does not alter with the communication. Living systems (and also computers) have the capability of memory which alters the *competence* with which they process information (Pribram, 1971, chaps. 14 & 16). This is produced by altering channel redundancy and superficially resembles a change in the number of channels with fixed capacity. The increase in competence is the result of increasing the complexity of the neuronal model, an encoding process described as "chunking" the information (Miller, 1956; Simon, 1974). This and similar mechanisms in human information processing effect a change in central processing very different from that produced by a simple increase in the number of fixed-capacity channels available.

The evidence that information processing competency can be changed in living organisms comes from a variety of problem-solving situations. Kahneman (1973), in reviewing several such studies from the psychophysiological literature, suggests that "arousal" is

in fact an indicator of a change in capacity—"the allocation of spare capacity"—much as this is changed in nonliving systems by increasing the number of channels available. He also goes on to equate "arousal" and "capacity" with "effort" and "attention" in a global fashion. We hope to have shown already that arousal is indicative of but one sort of attention, and we will now show that effort is involved only when the situation demands the regulation of arousal and activation to produce a change in information processing competency.

The way in which competency is controlled by brain systems in the living primate is demonstrated by the finding that removal of the area of the brain usually called sensory or posterior intrinsic or "association" cortex reduces the sampling of novel alternatives. The opposite effect is obtained when the lateral frontal cortex is resected. It was noted earlier that removal of this same frontal cortex led to an increase in behavioral orienting and an abolition of the viscerotonic components of orienting. There thus appear to be opposite effects (posterior and frontal) on the number of alternatives sampled in a situation. This was interpreted to indicate a dual control mechanism determining the ability to sample (Pribram, 1960a).

Supportive behavioral evidence came from an experiment by Butter (1968, 1969) in which he investigated the number of features usually attended by monkeys while discriminating between two cues. He did this by eliminating each feature in turn in various combinations. He found that resection of the same brain region (the posterior cortex) that produced a restriction in the number of alternatives sampled also produced a restriction in the number of features used to make the discrimination.

Electrophysiological evidence has been obtained that the posterior and frontal cortex contribute opposing controls on sensory channels. This evidence is based on changes produced in the recovery cycles of the system (the speed with which the system recovers to its full capacity after a sudden, intense stimulus) and the alterations produced

in the shape of visual receptive fields (Spinelli & Pribram, 1966, 1967).

These changes in sensory channels were, however, *not* attributed to a simple change in the *number* of channels of fixed capacity, as the effects of surgical resection have shown that as little as a few percent of an anatomically defined sensory channel is sufficient for ordinary discrimination learning, performance, and transfer (Chow, 1970; Galambos, Norton, & Frommer, 1967; Lashley, 1929). The remainder of any input channel appears to be redundant, spare channel capacity, under most circumstances. We therefore interpreted (Pribram, 1967) the results on the control of input channels by posterior and frontal cortex as influencing *redundancy, not sensory capacity* in the usual information theoretic sense. Specifically, we suggested that the input systems acted as channels in which spatial and temporal multiplexing could occur, a suggestion similar to that put forward by Lindsay (1970).

We would like to suggest, therefore, on the basis of the data reviewed above, that Kahneman's (1973) concept that arousal involves an increase in the number of sensory channels available be generalized to include constraints involving the redundancy characteristics, the competency, of that capacity. Kahneman's discussion approaches such a generalization when he speaks of changes in "structural connections between components." In technical language, such changes in competency would be reflected in changes in the equivocation of the channel (defined as the sum of noise and redundancy). Competency is the reciprocal of equivocation. Effort can then be defined as the measure of the attention "paid" to increase or maintain efficiency by reducing equivocation, that is, enhancing competency.

Internal and External Constraints

Garner (1962), in his analysis of the structure of redundancy, has shown that the total amount of constraint operating in any system of variables can be divided into internal and external components. Internal constraints refer to the relationships among the systems of variables under consideration, while external constraints refer to the rela-

relationship between these variables and some external referent system of variables. In our neurophysiological experiments we consider the constraints that describe the central operation of the channel as internal and the constraints that refer to operations on the environmental situation which control its sensory input as external. In addition, we have found it important to distinguish between temporal (repetition of the use of the channel or variable over time) and spatial (replication of the variable over space) redundancy for each of Garner's categories.

Specifically, we have suggested (Pribram, 1967) that when the frontal system becomes involved in the orienting reaction, the internal redundancy in the input channels is increased so that all of the information being simultaneously processed becomes chunked into one unit. By contrast, when the posterior cortex becomes involved in the attentional process, internal redundancy in the input channels is decreased, separating the bits of information in each channel from each other. This is concomitant with enhancement of external redundancy which, according to Garner's findings, enhances the ability to make discriminations, that is, to categorize input.

In short, we suggest that the controls on arousal and activation operate on the mechanisms of redundancy, on the constraints operating within and between channels rather than on the information being processed. These constraints involve the neuronal model and may be conceived of as operating on *memory* rather than on input information. Another way of stating this is to say that the controls operate on the context in which the informational content is processed.

A good deal of additional evidence can be cited to show that competency rather than sensory channel capacity per se is controlled by the attentional systems discussed here. For instance, the studies of Anderson and Fitts (1958) cited by Garner (1962) show that as much as 17 bits of sensory information can be simultaneously processed. The work of Lindsay (1970) which demonstrates the relationship between sensory discriminability (difficulty in distinguishing between inputs) and central processing competency

has already been mentioned. Pribram, Lim, Poppen, and Bagshaw (1966) and Mishkin and Pribram (1955), using various forms of the delayed alternation tasks, attributed the differential effects obtained after resections of the two reciprocal frontoamygdala systems as due to selective alterations in the structure of internal redundancy (spatial and temporal, respectively) of the remaining processing competency. Further, Pribram and Tubbs (1967) have shown that when the delayed alternation task, the nemesis of monkeys with frontal lobe resections, is externally parsed or chunked by making the intertrial intervals asymmetric, the deficit is completely overcome. Similarly, M. Wilson (1968) analyzed the trade-off between tasks involving external temporal and spatial redundancy in reciprocal mechanisms (anterior and posterior infero-temporal cortex) which have been delineated within the posterior system.

Thus, both Kahneman's (1973, pp. 8, 9, 15) analysis and ours attribute the control of arousal and selective attention to alterations in information processing channels, not the direct control on information and uncertainty per se. We differ in that Kahneman focuses on the problem of increasing the number of channels of fixed capacity—the "allocation of spare capacity"—while we emphasize the broader issue of competency, defined by any constraints operating on the structure of channel redundancy. We also differ in separating activation from arousal and in that we do not identify attention, arousal, activation, and effort as different names for the same process. Finally, we specify that effort accompanies only those attentional processes that result in a change in the representational organization of the information processing mechanism. Part of the mechanism detailing how and when effort is expended during attention has been revealed by studies measuring peripheral autonomic and somatic changes.

The Psychophysiology of Categorizing and Reasoning

The important viscerautonomic components in orienting have already been outlined. In studies in which perceptual and motor readiness are invoked, the involvement of the

autonomic nervous system becomes more specific due to activation (basal ganglia) of the central representation (sensorimotor cortex) of the somatomotor mechanism, where phasic and tonic mechanisms become separately involved. Further, the sympathetic system more often mirrors stimulus parameters such as novelty and complexity, whereas the parasympathetic division which controls heart rate reflects the parameters of the somatomotor readiness and response mechanism—for example, the incentives, response biases developed on the basis of reinforcing consequences of behavior. This distinction has been clearly demonstrated in a study by Elliott (1969; Elliott et al., 1970) as we have reviewed, by Dahl and Spence (1971), and by Hare (1972).

Experimenters, using autonomic measures during discrimination tasks in which input must be categorized in order to make an appropriate response, appear to use the term "arousal" as actually defined by the amount of categorizing required, and studies consistently have shown that sympathetically innervated phasic responses distinguish between variations in task largely on the basis of their collative, informational variables: their novelty, surprisingness, or complexity (Blaylock, 1972; Hare, 1972; Kilpatrick, 1972; Lacey & Lacey, 1970; McGuinness, 1973). A typical experiment showing this effect was that of Hare (1972) in which subjects viewing slides without making discriminations between them were less aroused (lower skin conductance) than those who had to categorize, and this was only an initial effect; phasic skin conductance responses rapidly returned to baseline (habituated) over trials. Difficulty due to changes required in response biases were reflected in tonic skin conductance but most precisely by tonic heart rate changes.

The absence of a precise relationship between galvanic skin response and response variables has not yet been demonstrated which may be because the galvanic skin response has no known metabolic function (Venables & Christie, 1973). Current data show that the involvement of somatomotor responses enabled by readiness, as well as tonic cardiovascular changes, provide the

clues to unraveling the controversial and apparently disparate views of the psychophysiological mechanism involved in attention.

Readiness and Execution

Two prevailing theories concerning the meaning of cardiovascular processes during attention appear diametrically opposed. On one hand there is the baroreceptor feedback theory of Lacey (Lacey, 1967; Lacey & Lacey, 1970) which, simplified, states that heart rate will directly affect stimulus intake or rejection through a process of feedback to the bulbar inhibitory centers in the brainstem, reducing arousal of the central nervous system (Bonvallet & Allen, 1963). On the other, Obrist and his colleagues (Obrist, Webb, Sutterer, & Howard, 1970a, 1970b) propose that heart rate is regulated by the motor demands of the organism and that these demands are controlled centrally. Findings by Jennings, Averill, Opton, and Lazarus (1971) have challenged the adequacy of either of these explanations and have produced results in line with an "amount of attention" hypothesis. They argue that as demands on attention increase, heart rate will *fall* in proportion to the complexity of the categorization demanded by the task, unless metabolic activity is engaged. This is somewhat in line with the view of this article, but their suggestions are still incomplete. As they note, this hypothesis does not explain the functional significance of cardiac deceleration during attention. Nor too, we might add, does it explain why heart rate always *increases* during reasoning.

To resolve these conceptual difficulties, the physiological processes will be examined in more detail. The assumption of the majority of theories is that there is a unitary relationship between cardiovascular and somatic processes whereas evidence shows that the situation is far more complex.

Any registered orienting response produces a dual sympathetic-parasympathetic effect. The cardiovascular reflex in orienting results in sympathetically controlled and cholinergically mediated gross blood flow shifts which are sometimes accompanied by an initial phasic heart rate acceleration. This will vary in magnitude with stimulus in-

tensity (Graham & Clifton, 1966) and an initial respiratory block will often combine to elevate the acceleratory effect (Jennings et al., 1971; Petro, Holland, & Bouman, 1970; Wood & Obrist, 1964), although the effect of intensity is not entirely predictable (Bull & Lang, 1972). We now know that this is due to parasympathetic inhibition and that all attentional (as opposed to movement-produced) heart rate changes are under vagal regulation (Eckberg, Fletcher, & Braunwald, 1972; Forsyth, 1970; Obrist, Howard, Lawler, Sutterer, Smithson, & Martin, 1972).

The initial phase is followed immediately by a heart rate change in the direction of deceleration, which is due to the vagus restabilizing the system. If the prepared somatic systems become mobilized to initiate an appropriate consummatory or defense pattern—eating, drinking, withdrawal, flight, or attack, (Abrahams et al., 1964)—heart rate will then come under the control of the somatomotor system and a tonic increase in rate occurs to meet the demands of the activity. The processes occur in fixed order: stimulus → blood flow shift → heart rate acceleration → heart rate deceleration, until the motor response determines more tonic heart rate acceleration and the system ultimately restabilizes.

During a vigilance or categorization task, the time course of the responses is somewhat different (Lacey & Lacey, 1970). Now the vagal restabilization phase is extended as part of a tonic activation—the vigilant readiness process. Lewis and Wilson (1970), for instance, examined cardiac responses to a picture-matching task in young children. In all children, a marked deceleration occurred which lasted until the choice was made. The most interesting finding was that the greatest deceleration was related to *correct* responses—if a subject was asked to “guess again,” heart rate did not return to baseline until the final choice. Correct responses occurred with longer response times and greater cardiac deceleration, which supports the suggestion that the vigilant readiness phase of the control processes has been extended.

Correlation to IQ demonstrated that there

was a relationship to both deceleration and error score for girls only. The sex difference finding could possibly be due to the greater amount of movement found in boys which would cause a heart rate acceleration and less attention to the task. This explanation is made more tenable by the recent finding of Obrist, Howard, Hennis, Murell (in press) that children's reaction times are slower in proportion to the amount of uncontrolled movement they produce. The relationship between motor control and reaction time was linear with age. As reaction times increased, motor responses and heart rate decreased. We therefore suggest, in line with Obrist et al. (1970a, 1970b), that when activation must be maintained, heart rate deceleration occurs as an accompaniment of somatomotor readiness.

This then partially accounts for the sequence of physiological events in a certain type of problem solving. When the organism prolongs attention to the complexity of input in a categorizing discrimination situation, he reduces extraneous noise by eliminating random movements. Heart rate then adjusts to the reduced demands of the system reflecting characteristics of the somatomotor system in which overt movements regularly precede blood flow changes and heart rate acceleration. Petro et al. (1970) found that after a voluntary contraction of the biceps muscle, heart rate increased with a latency of approximately 500 msec. However, when reasoning is initiated with its emphasis on which response to produce when, and the actual trial-and-error making of responses, the cardiovascular and somatomotor response relationship is the reverse.

Muscular Effort and Problem Solving

The locus of the demand for effort is different in categorizing and in reasoning, and this raises the question of the relationship between the various forms of attention and effort and also of the nature of effort itself. Could it be that the muscular contractions involved in making responses are totally responsible for the effort necessary to problem solving? A change in actual movement such as during categorizing and reasoning would obviously be accompanied by a decrease

(categorizing) or increase (reasoning) in isotonic contraction, but, in addition, activation of the readiness mechanism may also change a special sort of metabolism, usually thought to be largely anaerobic, which has been shown to be involved during concentration and problem solving and involves isometric contraction.

An understanding of this special metabolic process during attention has been provided by Berdina, Kolenko, Kotz, Kuzetzov, Rodinov, Savtchenko, & Thorevsky (1972). Until this study there was no functional explanation for the finding that sympathetically innervated blood flow shifts actually reduce oxygen uptake by the muscle while somatic activation increases it (Rosell & Uvnäs, 1962). The study of Berdina et al. suggests the possibility that this special sort of metabolism of muscle fibers is due to cholinergic mediators. Berdina et al. were interested in the effect of problem solving on blood flow and muscle contraction. Until their study, it had been extremely difficult to establish any precise relationship between electromyogram recording and problem solving due to the small amount of amplification produced by the technique, which often results in unreliable values (Jennings et al., 1971; Lader, 1965; Matthews & Lader, 1971). To avoid this difficulty they introduced a condition of partial muscular contraction: Subjects had to grip a hand dynamometer which they were pretrained to maintain at 30% of their maximum grip. Then, during the problem-solving experiment, subjects were asked to grip the dynamometer for as long as possible.

Both contraction alone and problem solving (arithmetic) alone caused significant blood flow changes. However, a combination of contraction plus arithmetic produced no greater changes in blood flow than either condition alone. On the other hand, the contraction *duration* was significantly increased by arithmetic from 181 to 235 seconds ($p < .001$). To disentangle voluntary effects from the purely reflex effects, they induced a forearm contraction by electrical stimulation. The results were the same even when the subject had no voluntary control over his muscles. An injection of atropine significantly decreased blood flow during arith-

metic and during contraction plus arithmetic but not during contraction alone. Atropine also reduced contraction duration during the combined task showing that the increased contraction during problem solving was *not* a somatic effect. Since small amounts of circulating atropine do not affect the neuromuscular junction, it was concluded that some form of sympathetically controlled metabolism was causing muscle force to increase, making muscles "work" under the special conditions of isometric contraction. Apart from other considerations, this experiment demonstrates conclusively that muscular effects do occur during problem-solving tasks and that they involve gross changes in tonicity which cannot always be observed by electromyogram recording. Equally relevant is the fact that as heart rate correlates so precisely with blood flow changes (Matthews & Lader, 1971), an increase in blood flow during problem solving automatically implies a corresponding increase in heart rate. The Berdina experiment thus explains the functional significance of the heart rate changes during categorizing and reasoning: Maintaining attention while problem solving is effortful and involves "hard work" and hard work is accompanied by metabolic changes. It does appear from this study that the outlines of the metabolic processes operating during intense concentration have been established.

In summary, the discovery that two types of muscle activation (isotonic and isometric) and two metabolic functions (aerobic and anaerobic) are involved in both voluntary attention and action makes it easier to understand why some confusion has arisen in the study of the psychophysiology of attention. Returning briefly to the Lacey hypothesis, physiological responding during stimulus intake will depend entirely upon how a task is constructed and whether it is primarily a categorizing or reasoning problem. We agree with Lacey that during a state of behavior characterized by heart rate deceleration, we are most open to environmental cues (Lacey & Lacey, 1970) but not necessarily for the reasons he suggests (see also critique by Hahn, 1973). Lacey's theory also requires acceleration when decisions are

made. How then could one interpret what is occurring in acquiring a categorizing or motor skill? When the coordination of arousal and activation is demanded, heart rate acceleration reflects the amount of effort involved in registering, adjusting, and changing the central representation to the requirements of the task. In accord with Lacey's assumptions, intake of information must alternate with concentration. A process ensues that must constantly shift between relevant stimuli in order to overcome the rapid decrementing of the system (just as continuous eye movements overcome the rapid adaptation of retinal receptors). When one plays tennis, for example, heart rate is elevated, but the player must flexibly attend (be aroused by) such cues as the angle and velocity of the approaching ball, the ground lines, the height of the net, and the position and angle of the opponent's body and his racket. As well, the intricacy of the series of highly refined changes in response and the transformational calculations based on this evidence could also elevate heart rate, even without the behavioral activity of playing tennis occurring (e.g., in a spectator). This is brought out clearly in a study by Johansson and Frankenhaeuser (1973) in which high heart rate accompanied the complex transformations required during an intake task.

By contrast, in reasoning tasks, activation precedes arousal. For instance, in playing a game of chess or engaging in any similar pursuit requiring a good deal of skill, transformational calculations must occur before the effective response is achieved. Once the "move" has been made, it may arouse an "aha" reaction: The move was successful, or, "Oh dear, why didn't I see that!" Again the physiological changes that occur are those that have been shown in the Berdina experiments, although the theories of Jennings et al. (1971) and Obrist et al. (1970) would predict the opposite.

Some of the task variables which affect arousal and activation and the effort required to overcome resistance to extinction of a prior set during categorizing and reasoning have also been investigated by Dahl and Spence (1971). They propose an activation

theory which adopts Bergum's (1966) technique of taxonomic analysis of performance, in which tasks are evaluated according to complexity and activation of response. Task demands were rated by independent judges, and the amount of heart rate change was correlated to each task. Heart rate increased with response demand, and all correlations were significant. A subsequent factor analysis revealed a major factor which they designated "density," or degree of concentration required; in other words, the total amount of cognitive effort involved in the task. The other factor which accounted for the greatest amount of variance in task performance was information content of relevant stimuli. Thus, again, collative variables are distinguished from the amount of transformational effort or "work" required in problem solution.

Cognitive Effort

Do these results mean that cognitive effort, the effort of thinking and problem solving, is due entirely to the activation of peripheral muscular mechanisms as reflected in changes of heart rate? We cannot answer this question conclusively at this time, and in fact, there may be no conclusive answer, at least not where normal intact problem-solving organisms are concerned. The neuromuscular apparatus works as a unit, brain and body inseparably yoked. Yet Malmö (Malmö & Belanger, 1967) and Lacey (B. C. Lacey & J. I. Lacey, 1974) have made an excellent case in their extensive, detailed, and perceptive reviews that there is good evidence to believe that the effort involved in cognitive work is not wholly due to changes observed in the muscular system. Further evidence comes from pathological situations such as complete cervical spinal transections which arise when partial separation between brain and body occur. We have already reviewed the fact that theta activity in the hippocampal formation, usually present when the animal moves about voluntarily, is also recorded under the same circumstances in curarized and therefore completely paralyzed subjects. A broken neck that completely severs the muscular system from control by the brain does not pre-

clude effortful problem solving. The competency to think remains.

We know from observations of sensory disturbances that processes which are initially localized peripherally become progressively neuralized. Thus phantom limb pain following an amputation can be successfully treated immediately by injections of an anaesthetic at the site of amputation. After a few months, however, such peripheral injections usually fail to have an effect, and spinal cordotomy (section of the spinothalamic tracts) must be done to relieve the disturbance. Should several years of intractible pain be experienced before treatment, even spinal cordotomy often proves useless. The brain itself must be operated upon: Frontal leukotomy or parietal lobectomy are now resorted to.

It is thus plausible that the neuromuscular processes demanding effort are to a large extent initially peripheral in their origin and manifestation. But as problem solving progresses and problem-solving skill develops, the effort becomes more and more a concomitant of the brain processes involved—apart from, or only *reflected in*, the peripheral manifestations—and thus becomes truly cognitive. How then are we to study and understand the brain processes that demand effort?

Studies of local differences in cerebral blood flow and metabolism provide the obvious answer (for review see Ingvar and Lassen, in press). However, it is also helpful to define the issues involved, especially since overall cerebral metabolism is augmented so little by even the most effortful problem-solving activities. Just as quantifiable definitions of information and uncertainty become useful in understanding information processing, so quantitative definitions of effort, work, and energy become useful in understanding control mechanisms. We have already noted that effort can be defined as the measure of attention "paid" to increase or maintain the efficiency of a communication channel by reducing its equivocation. As detailed, such reduction can be accomplished by reducing noise or changing the structure of the redundancy of the communication—chunking or parsing being

prime examples of such a process. McFarland (1971) has approached the problem from a control rather than an information theoretic stance and comes to the identical conclusion. In keeping with engineering tradition, he defines work (pp. 215–220) as the measure of the rate of changing the state of a system and energy as the capacity for doing work. Thus the changes in neuronal representational model, changes in information processing competency, in set, attitude or state, developed by the hippocampal circuit described in this review, demand work—by definition. Further, resistance to change may occur when changes take place in related systems and the changes are not independent of one another: For example, stimulus and response may originally be coupled as in a defense reaction—that is, internally constrained by a preexisting neuronal model. In such a situation, a change in state is produced only when the input and output systems become uncoupled by the hippocampal circuit. In a distraction situation, maintenance of state involves loosening an external constraint as we have seen, and the uncoupling of arousal and activation, thus increasing internal constraint. As an analogy, change in blood sugar level may be dependent upon, or constrained by, change in osmotic pressure and basal temperature and motor activity so that the behavior of an organism must be analyzed in relation to such constraints (see for example, McFarland, 1971).

The constraints operating in a system can often be expressed in terms of integrable differential or algebraic equations, in which case they are known as "holonomic constraints." Holonomically constrained systems allow description in terms of "the number of generalized coordinates required to describe the state of the system and this number is known as the 'degrees of freedom' of the system" (McFarland, 1971, p. 217). In systems showing holonomic constraints, it should therefore be possible, in principle, to measure resistance and therefore the effort necessary to overcome the resistance. For instance, in discrimination reversal and in delayed alternation, the rate of extinction of the hippocampal theta peak to the previously rewarded

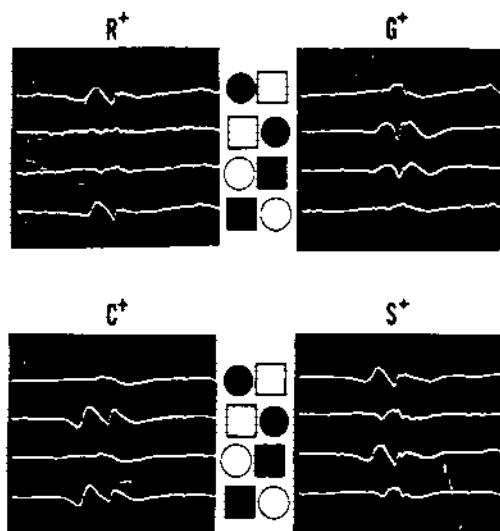


FIGURE 10. Comparison of *response-locked* activity evoked in temporal cortex when monkeys are performing (90% correct) color (top panels) and pattern (bottom panels) discrimination. The average evoked response (300 trials) was produced by the stimulus configuration shown in the diagrams between the panels. Each tracing = 250 msec prior to and 250 msec just after each response. Note that during the color discriminations the 1st and 4th (and the 2nd and 3rd) traces are similar, while during pattern discriminations the 1st and 3rd (and 2nd and 4th) traces are alike. These similarities reflect the position of the color cues in the color task and the position of the patterns in the pattern task. Position per se, however, is not encoded in these traces. Note that this difference occurs despite the fact that the retinal image formed by the flash stimulus is identical in the pattern and color problems. (Abbreviations: R⁺ = Red reinforced; G⁺ = Green reinforced; C⁺ = Circle reinforced; S⁺ = Square reinforced.)

stimulus might be used quantitatively in measuring the resistance involved in switching attention from one cue to another. In a selective attention experiment, where first one then another dimension of a multidimensional cue is reinforced (see Figure 10; Pribram, Day, & Johnston, in press; Rothblatt & Pribram, 1972), recording of hippocampal theta and mapping cortical CNV or desynchronization during the changeover from one dimension to the other might be similarly useful. Neurologically, this measure of resistance would reflect the rate of release from entrainment of rhythmic processes by a temporary dominant focus or

pacemaker. The problem is at the forefront of our capacity to conceptualize it; however, the direction in which conceptualization must proceed has been given: We must ascertain whether the constraints operating in a particular behavioral system are holonomically related and determine the number of coordinates that are required to describe it (the degrees of freedom involved). We can then perform rigorous quantitative experimental analyses of changes of state (transformations) of each of the coordinate subsystems and thus finally arrive at the resistance of the system as a whole and the effort involved in overcoming this resistance. E. Roy John (Bartlett & John, 1973; John, Bartlett, Shimokochi, & Kleinman, 1973), Adey (1967), Callaway and Harris (1974), and our laboratory (Pribram, Day & Glick, in press) have begun this type of analysis and initial results, at least, are promising.

This review has dealt with initial specification of the locus of resistance in the attention mechanism. We have outlined in a very preliminary way that at least two major subsystems, a visceromotor "arousal" and a somatomotor "activation" mechanism, must be considered. We have also reviewed the evidence for a control mechanism operating on each system (the amygdala circuits for arousal; basal ganglia for activation) and a mechanism (the hippocampal circuit) that operates to overcome the constraints which would ordinarily maintain a tight join between stimulus and response and thus keep these two control systems from functioning. We have suggested that overcoming these constraints may demand effort. Whether the constraints in attention operate holonomically or nonholonomically remains to be determined; but the techniques for determination are available. Should it turn out that constraints can be expressed or even approximated in terms of integrable differential equations, a measure on cognitive effort would be attainable.

Whether the attention comes by grace of genius or by dint of will, the longer one does attend to a topic the more mastery of it one has. And the faculty of voluntarily bringing back a wandering attention, over and over again, is the very root of judgment, character, and will (James, 1950, p. 424).

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