

THE NEW NEUROLOGY AND THE BIOLOGY OF EMOTION: A STRUCTURAL APPROACH¹

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THE recent past has seen the emergence of a new neurology. Where there had been a concentration of effort to clarify sensory mechanisms there is now an emphasis on information processing; where there had been a focus of research activity in the field of neuroendocrine mechanisms, there is now an interest in the process of control. Not that research in sensory and humoral mechanisms has lagged: Quite the contrary, these efforts have been multiplied. But at the same time, a wider awareness has been achieved: Detailed analyses of sensory and neuroendocrine processes now serve as models in miniature of a wider range of neural mechanisms. What I want to examine today is the impact which these data on neural information processing and control might have for our views of emotion.

EMOTION AND THE NEUROHUMORS

Historically, emotion was conceived to result from the action of circulating humors and other visceral functions. The historical view has been brought into the present by the attested effectiveness of psychotropic drugs and the role of brain amines in determining states of sleep, wakefulness, and alertness. True, crucial changes from the Jamesian position have been necessary: Circulating humors come up against the blood-brain barrier and so are often ineffective centrally. To be active humors must often be synthesized from substrate by the brain itself. But the brain's capacity to do this has been amply demonstrated: Norepinephrine, serotonin, histamine, dopamine and, γ -butyric acid (GABA) are assuming larger and more specific roles in our knowledge of the determinants of the predispositions to behavior (Schildkraut & Kety, 1967).

The amines do not exhaust the list of brain secretions which alter the psychological state and thus behavior. A group of as yet chemically unidentified

"releasers" is secreted into the venous portal system which bathes the brain's base where it joins the pituitary—the master endocrine gland which controls the secretions of the other endocrine glands by way of its own (Harris, 1960).

Neurosecretory activity of this sort is found spotted throughout the core structures of the diencephalon and the mesencephalon: from the infundibulum in the hypothalamic region to the locus ceruleus of the pons (e.g., Jouvett, 1967).

These core structures of the nervous system display an additional property: They are sensitive to a variety of chemical agents. From front to back, receptor sites have been identified as sensitive to estrogenic steroids; circulating glucose, amino acid, or a derivative; osmotic equilibrium of electrolytes; androgenic and adrenal steroids (Davidson, Jones, & Levine, 1965), acetylcholine, epinephrine, and the partial pressure of CO_2 (Pribram, 1960).

Through complex reciprocal interrelationships of hormones distributed by the circulation to and from target organs and possibly through central integrative effects of the cholinergic and adrenergic sensitivities, these neurosecretory and receptor mechanisms are equilibrated into physiological systems, each of which determines one or another psychological predisposition. These systems are the determiners of mood—Cannon's homeostats brought up-to-date. They constitute the seromechanisms of physiological drive, the background against which breathing, eating, drinking, sleeping, alerting, sexual, and maternal behaviors are initiated and consummated.

MEMORY AND THE HOMEOSTATS

In the days when neurophysiology was primarily concerned with sensory and with humoral mechanisms, it was easy to claim that perceptual processes stemmed from an elaboration of sensory mechanisms while the process of motivation and emotion were elaborations of humoral mechanisms. Were this possible today I would not need to make this presentation.

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The problem is this. Observers of, and experimenters with, the human scene repeatedly find as inadequate a neuroendocrine-based approach to motivation and emotion. The thrill of discovery, the disappointment of failure, the joy of sensing, the gloom of separation—these experiences seem distant from the core homeostats just described.

Schachter's (Schachter & Singer, 1962) experiments delineate the problem. Four groups of students are asked to take an examination. Two groups take it in a socially hostile, two in a socially friendly, environment. In each setting, one group receives an injection of epinephrine, the other a control injection of normal saline solution. The students relate their experience. The hostile setting bred hostility, the friendly setting produced friendly feelings, as expected. The effect of epinephrine was unexpected, however. The drug produced an enhancement of *both* friendly and hostile feelings. Whatever the physiological state produced by the injection, its label was determined by the setting—by the student's perceptions of his social environment.

Schachter's (in press) more recent experimental results support the earlier ones. The control of human eating behavior is now under scrutiny. Schachter found that two classes of variables determine when eating occurs: internal and external. Most eating takes place when both sets of variables coincide to produce drive and opportunity jointly. By his usual ingenious and sometimes somewhat fiendish techniques, Schachter has dissociated the occasions when neurohumoral stimuli are maximal from those when opportunity beckons. He has shown that the obese among us rarely fail to heed the call of opportunity, irrespective of humoral state—the more usual response of the average person is to forgo food “unless it's time to eat.”

“Unless it's time to eat.” This phrase encapsulates the first of the issues I want to emphasize here. One is prepared to eat, predisposed to eat, by the workings of the homeostatic mechanism. But this mechanism is tuned by experience; its bias is adjusted to operate around a set point established by previous experience much as the behavior of the home heating plant is constantly determined by the bias or setting of the thermostat. Experience, memory, is involved in the operation of the system—even when the system is humorally operated. For the obese, memory is also involved, but instead of humoral stimuli, gustatory and ol-

factory stimuli form the basis of the motivating remembrances. And lest you think the motivation of the obese is so completely different from that of the normal you and me, just forget the weight bit; go on a trip—preferably on an unlimited budget—say an ocean voyage, the Munich beer parlors, the Viennese coffee houses, and the Provencal restaurants, and weigh in on your return. Especially if you are over 35 years old.

Nor have animal studies been unconcerned with this problem: The multiplication of drive names of which curiosity is the most ubiquitous attests to the need for a wider base for motivation and emotion.

SENSORY SERVOMECHANISMS

“The time to . . .” provides this base. Essentially, experience builds within the organism a set of expectancies, neuronal models of the events experienced. Until recently a cognitive term such as “expectancy” had little to support it in the way of hard neurological fact. This has changed radically with Sharpless' and Jasper's (1956) and Sokolov's (1960) classical demonstrations that orienting and dishabituation occur whenever a repetitiously experienced configuration of input is changed along any of its parameters. Utilizing the behavioral (eye movements, ear flicks, and body orientation), the electroneural (EEG, low voltage fast activity in isocortex and theta activity in the hippocampus), and psychophysiological (GSR, change in heart and respiratory rates) responses, investigations of the neurology of novelty, the basis of “interest,” have confirmed and amplified the earlier conclusion. (Bagshaw, Kimble, & Pribram, 1965; Gruening, Kimble, Gruening, & Levine, 1965; Haider, Spong, & Lindsley, 1964; Kimble, Bagshaw, & Pribram, 1965; Thompson & Spencer, 1966.)

These studies are important here because they suggest that some form of “homeostatic” servoprocess is operative with regard to sensory, as well as with regard to humoral, mechanisms. The “expected” forms the background, the set point against which the novel is matched. Indeed, the retina provides a model which shows just how apt this extension of homeostat theory is.

The observation that a stabilized image fades rapidly has been attributed to retinal adaptation. Adaptation, in turn, was for many years attributed simply to the bleaching of photochemical substances in the receptors. More recently this view has been

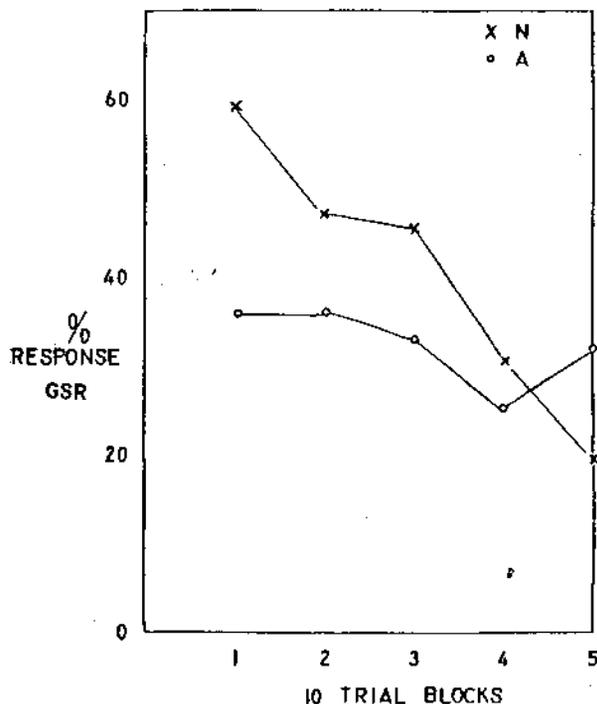


FIG. 1. This and the following figure are examples of the differential impairment of components of the orienting reaction following amygdalotomy in monkeys. (This figure shows the absence of the GSR component. Other studies have shown the GSR to be intact in other situations, e.g., threshold to shock—Bagshaw et al., 1965; Gruening et al., 1965; Kimbte et al., 1965.)

challenged and, on the basis of studies using microelectrodes, the electroretinogram, and the electron microscope, adaptation has been shown to depend as well on feedback between elements of a pool of retinal neurons—amacrine and bipolar cells (Dowling, 1967). The threshold of a part of the visual receptive field of a single ganglion cell (as determined with a microelectrode) becomes adapted when another part of the receptive field has been illuminated. Some kind of retinal interaction must be going on to account for this effect. Where it is that the interaction takes place has been narrowed by the use of electroretinograms made up of several waves—of which the B wave parallels psychophysical adaptation yet remains undisturbed when the optic nerve is cut and the retinal ganglion cells are allowed to degenerate.

Finally, electromicroscopy has revealed double contacts between bipolar and amacrine cells which could well function as the site of the feedback which makes of retinal adaptation a typical homeo-

stat or servomechanism. In fact, the experiments just described are usually put into the context of a "sensitivity" or "gain" control mechanism for the sensory process.

Retinal adaptation can be conceived of as a model in miniature of the process of habituation. The recent elegant studies of Richard Thompson and Spencer (1966) on habituation tend to support such a view: They found a response decrement to occur in afferent spinal channels only when multi-neuronal pathways were involved. Their studies demonstrated further that some form of semi-permanent memorylike depression or desensitization of the synaptic process is apparently involved, and that this depression cumulates when many synapses are concerned with the behavior which becomes habituated.

The point to be made, then, is that sensory as well as humoral mechanisms are organized along homeostatic lines—that expectation, based on the mechanism of habituation, serves as the stable background against which sensory stimuli are matched or appraised as familiar or novel. Thus, humoral and sensory mechanisms are found to be special cases of ubiquitous neural servoprocesses which any theory of emotions has to take into account.

EMOTION, AROUSAL, AND UNCERTAINTY

So far, the concern has been with an initiating, homeostaticlike process which is stimulus derived

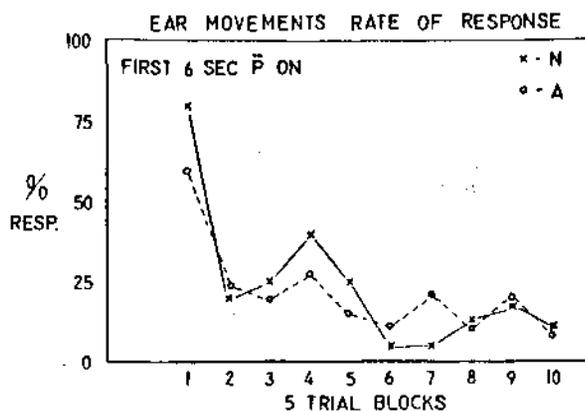


FIG. 2. This figure shows that ear movements display the normal orienting and habituation curves when monkeys are repeatedly exposed to tone beeps just as in the experiment which produced the GSR curves in Figure 1. (See text for other component dissociations in this situation.)

and memory based. There is a good deal of evidence that even this initiating process is not a simple one. Studies performed in any laboratory (Bagshaw et al., 1965; Grueninger et al., 1965; Kimble et al., 1965) using frontolimbic brain lesions, have succeeded in teasing apart at least two components of the orienting reaction: One component is an indicator of searching and sampling; the other component is manifest when a novelty is registered. Only after such registration does habituation occur. The indicators of registration are the presence of a GSR, shortened latency of onset of low voltage fast activity in the EEG, a disruption of the respiratory rhythm and a speeding of the heart rate. All of these indicators have been used to define arousal.

And so the argument comes around to an examination of the second major view of the emotional process, viz., that emotion depends on the mechanism of arousal. The experimental results just mentioned thus raise the question of when arousal leads to registration, habituation, and memory formation and when arousal leads to disruption. The classical answer has been (Hebb, 1955; Lindsley, 1951) that the *amount* of arousal determines its outcome. The evidence for this view has been marshalled so repeatedly that it need not be mentioned here. What can be added is that, on the basis of the evidence obtained in the studies of the orienting reaction, "amount" is shown to be dependent on experiential organization, on the configuration of the expectancies challenged by the novel input. "Amount" is thus viewed as amount of match and mismatch between configurations, not as an amount of excitation or energy available to the neurobehavioral system.

It is the *distribution* of excitation which is altered—and further: The amount of change can be measured as information. Habituation reflects redundancy; novelty indicates information and uncertainty. The expectancy-novelty process may thus be conceptualized as a mapping of intensity into a spatial neural dimension, an image out of which interest is engendered. But more of this later.

The "amount" referred to by arousal or activation theorists has, according to this analysis, been to some extent misidentified. Amount of arousal, amount of activation, is not to be conceived as some quantitative change in intensity, in energy level in the central nervous system, but as a change in the *uncertainty* (and thus the information) of the

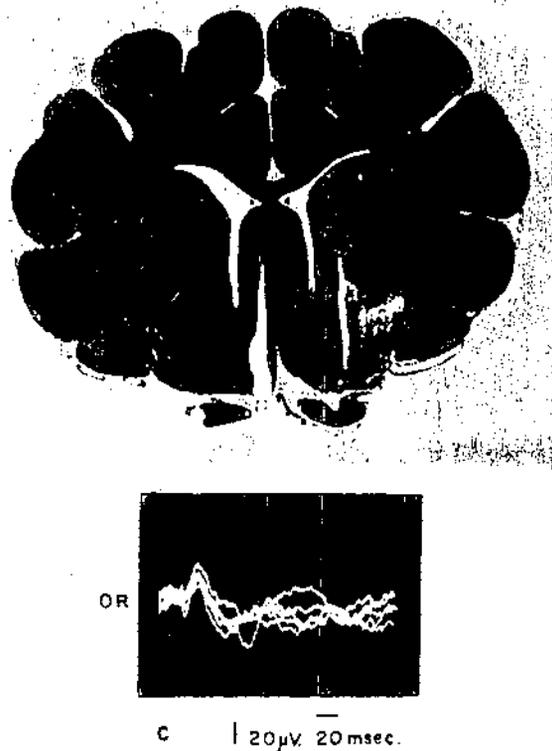


FIG. 3. Responses in the optic nerve (placement shown) obtained in the awake atropinized and curarized cat. (These responses disappear when the nerve is cut central to the electrode placement—Spinelli et al., 1965.)

system. As noted by Lindsley (1961) low voltage fast EEG activity indicates desynchronization; and desynchronization of neural activity suggests an increased capacity to handle information: Neural elements are independent of each other and thus available to function as separate information processing channels. Thus we might quip that the 1967 model of the arousal theory of emotion has built into it a measure of uncertainty.

This is as far as the arousal theories—or, as we might now better call them, the uncertainty theories—of emotion can take us. This does not mean that this is all there is to arousal. The concept of activation, so often coupled with that of arousal, suggests that disruption of control is also involved. But before the relationship between uncertainty and control can become clear we need to return to the expectancy-based servotheories. The Schachter results are not yet accounted for: The nonspecific aspects, the augmentation of this or that feeling, can be handled by uncertainty theory; the specificities of emotions continue to be elusive.

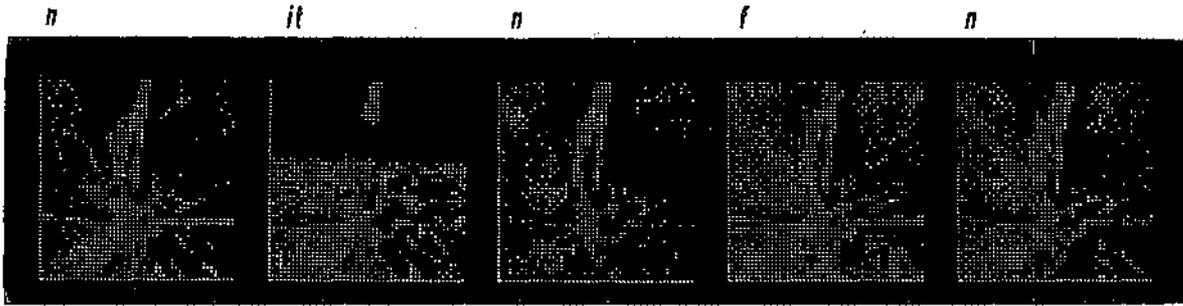


FIG. 4. Effects of stimulation of the posterior "association" cortex of a cat on a visual receptive field recorded from a neural unit in the optic tract. (These records are made by moving a spot with an X-Y plotter controlled by a small general purpose computer—PDP-8—which also records the number of impulses emitted by the unit at every location of the spot. The record shown is a section parallel to and $2 SD$ above the background firing level of the unit. Note the dramatic change in the configuration of the receptive field, especially after stimulation of the posterior "association" cortex—IT, inferotemporal.)

REQUISITE VARIETY AND SELF-CONTROL

These specificities suggest that there is more to emotion than quantitative disequilibrium and uncertainty, more than the disruption of the psychological process. The specifics of emotion suggest the operation of a variety of processes engaged in changing the states of equilibrium and in elaborating specific types of control to meet specific expectancies. Intensity begets temporal as well as spatial consequences in the nervous system.

One road open to the organism in his recourse to variety in control is to act on his environment. As I have indicated elsewhere (Pribram, 1963) whenever a homeostatic system becomes stabilized, new sensitivities develop and new techniques, new programs, are adduced to handle these new sensitivities. For example, when thermostats were initially introduced into homes, the occupants for the first time became aware of the chilling effect the cooling of the outside walls produce at sunset because of the radiation of body heat to those walls. Outside-wall thermostats were therefore introduced, adding variety to the control of heating in houses. This spiralling aspect of the functions of biological control mechanisms is neglected in the more usual formulations of the homeostatic process and in the arguments levied against biological servomechanism.

But action is not the only way in which an organism can achieve variety in control. The possibility exists that he may exert self-control, i.e., make internal adjustments with his neurological systems, adjustments that will lead to reequilibration without recourse to action. My thesis will be

that these internal adjustments are an important part of the experience of emotions.

There is now good neurophysiological evidence that such internal adjustments are possible and commonplace. A large number of experiments have been done to show that the organism's input channels and even the sensory receptors themselves, are subject to efferent control by the central nervous system. A recent series of studies performed in my laboratories demonstrated corticofugal influence as far peripherally as the cochlear nucleus and optic tract, originating in the so-called association areas (Dewson, Nobel, & Pribram, 1966; Noble & Dewson, 1966; Spinelli & Pribram, 1966, 1967; Spinelli, Pribram, & Weingarten, 1965; Spinelli & Weingarten, 1966; Weingarten & Spinelli, 1966). Changes in click- and flash-evoked recovery cycles were shown in these locations: Even the size and occasionally the shape of receptive fields of units in the visual system could be altered by stimulation of this cortex.

The recovery cycle data are of special interest here. When a double click or a double flash is used to evoke a neural response, the amplitude of the second of the pair of responses serves as an indicator of the duration over which a part of the system is occupied in processing the first of the pair of inputs. A depression in the amplitude of the second of the pair of responses thus indicates a longer recovery—a longer processing time for a signal within the channel. Such an increase in processing time effectively desynchronizes the channel to repetitive inputs: Fewer fibers are available for processing any given signal in the series.

Prolongation of recovery thus reduces redundancy in the channel. At any moment more information can be processed provided the system has sufficient reserve redundancy, and there is good evidence that this is so (Attneave, 1954; Barlow, 1961). Thus the rate of information processing is enhanced. What is interesting in our experiments is that stimulation of the so-called association cortex (the inferotemporal area) reduces redundancy, while stimulation of another area (the frontal) enhances

redundancy in the visual system. These opposing effects operate essentially either to "open" the organism to his environment, allowing more rapid information processing to go on; or, conversely, to "close down" the input channels so as to limit, to focus for a longer time, on fewer aspects of the available stimulus configuration.

The results of these experiments suggest that the organism has at least two ways in which he can internally adjust his uncertainty, neither of which

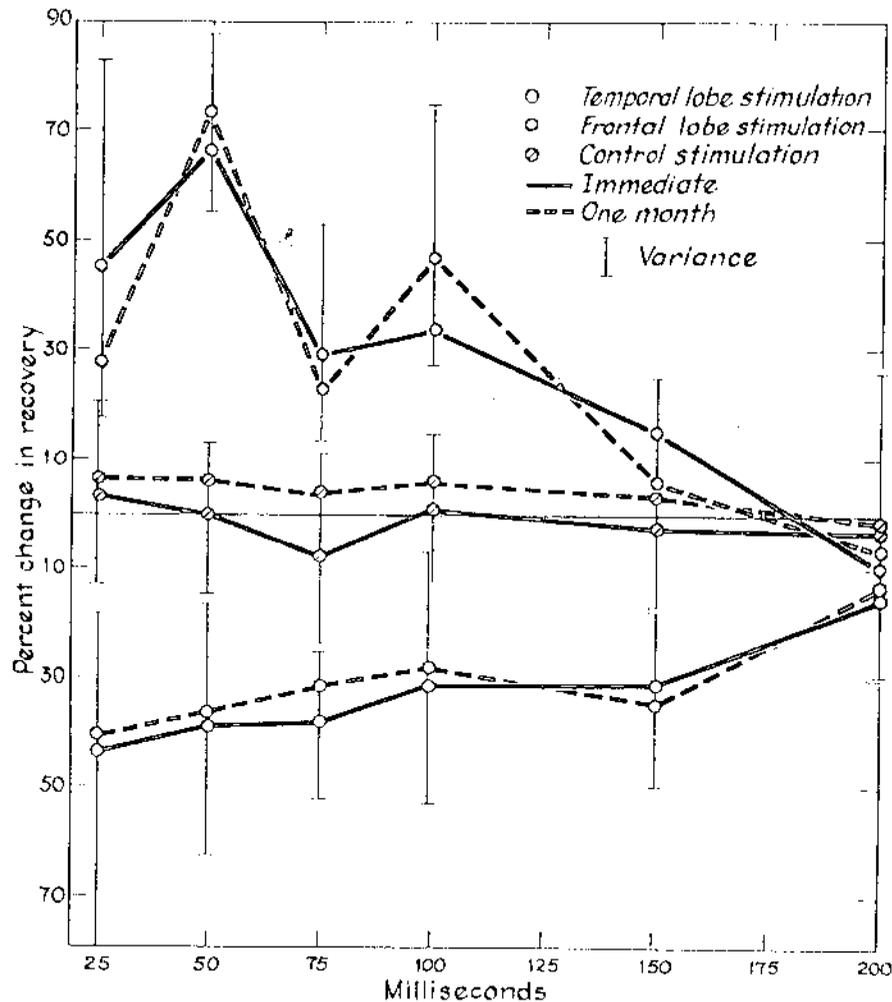


FIG. 5. This figure reports the percentage of change in the second of a pair of responses recorded with small macroelectrodes in the visual cortex of fully awake monkeys when exposed to pairs of flashes with and without electrical stimulation of the "association" cortex. (The records were made with a small special purpose computer—CAT—which allowed the summation of a large number of responses—50 for each data point for each subject, four subjects per group reported. Note the depression of the second of the pair of responses when the posterior—IT—cortex, and their enhancement when the frontal—F—cortex is stimulated. No change is observed when the electrical stimulation is made in the parietal region—Spinelli & Pribram, 1966, 1967.)

entails action. One way is to increase the rate with which he handles information, the other is to decrease that rate. One mechanism "opens" the organism to input, the other restricts input. Internal adjustment can thus be attempted either through closer coupling with the external environment or by minimizing the external and placing reliance on internal configurations.

Another way of stating this is to say that control may be manifested in one of two dispositions or attitudes: a participatory attitude which facilitates the rate of information processing; or a preparatory attitude which diminishes uncertainty by allowing the organism to repair to previous, acceptable states of organization.

In short, the specificities of emotion as viewed here are the result of a process called, in engineering, the "Law of Requisite Variety." The capacity of an organism to regulate, to control, can at best equal its capacity to process information. In biological systems the converse also holds: The capacity of an organism, whose channels are also capable of storage through the mechanism of habituation, to process information can at best equal its capacity to maintain control. A greater information processing demand on such a channel with storage characteristics can lead to greater uncertainty; as already noted, this can be biologically disruptive. Only by building up variety of control through habituation can the organism keep pace with the increasing complexity to which it becomes sensitive—the increase in interests aroused—whenever stability is achieved. Thus a reciprocal neurophysiological mechanism is needed.

The orienting-habituation studies provide evidence that such a reciprocal mechanism actually operates to alter almost simultaneously the organism's information handling capacity and his capacity for taking measures of self-control. Further, two modes of control have been experimentally identified—one functioning as a participatory, the other as a preparatory, attitude toward input.

THE EXPERIENCE AND THE EXPRESSION OF EMOTION

With these data in mind, I will now try to meet head-on the problem posed by this new neurology for our view of emotion. Perhaps the clearest approach is to resort to that old-fashioned trilogy and ask what the difference is between perception,

action, and emotion. There is now ample evidence, some of which I have reviewed here, that when an organism *perceives* he is forming an image, an internal representation of his environment. Miller, Galanter, and I in *Plans and the Structure of Behavior* (Miller, Galanter, & Pribram, 1960) argued that when an organism acts he is making an external representation of his plans, the neural programs in his head—his motives, intentions, and values. Tolman (1932) and also Skinner (1938) had earlier pointed out that an act is to be defined by its outcomes, that operant conditioner's "responses" were the marks of behavior left on the paper fed through the cumulative recorder. These marks can now be identified realistically as external representations of deprivation and other physiological states and the expectations of the organism set up by the schedules of cues and reinforcers. To social scientists and humanists, of course, the concept of act as a representation is certainly familiar.

To turn to emotion within this framework is to suggest the obvious statement that emotion expresses the relationship between perception and action. Another way of stating this is to say that emotion relates information processing and control mechanisms, image, and plan. As suggested in the previous section of this paper, this relationship depends on the Law of Requisite Variety. According to this view, whenever the organism is operating beyond the bounds of requisite variety he becomes motivated, emotional, or both. The relationships appear to be the following.

When the variety of perceptions exceeds to some considerable extent the repertory of action available to the organism he is motivated to, i.e., attempts to extend this repertory. Whenever this attempt fails, is nonreinforced, frustrated, or interrupted, the organism becomes of necessity emotional, i.e., he must resort to mechanisms of self-regulation, self-control. Further, on the basis of experience, emotion is likely when the probability of reinforcement from action is deemed low.

The converse situation produces a relatively "flat" motivationless and emotionless state. When the repertory of actions exceeds the variety of perceptions, the constructed external representation comprises a larger and larger share of the organism's perceptions until a means-ends reversal takes place: The medium becomes the message. This situation occurs only when the organism restricts his per-

ception to a limited, relatively "closed-system" part of his universe. To deal with this inversion he must "open" himself to variety—in today's language he must take a "trip."

The suggestion is, therefore, that motivation and emotion occur when the organism attempts to extend his control to the limits of what he perceives. To the extent that this attempt is appraised as feasible at any moment the organism is motivated; to the extent that the attempt is appraised infeasible at any moment, the organism—unless he is to "give up"—becomes of necessity emotional, i.e., he relies on self-regulatory mechanisms: either to participate in the uncontrollable or to prepare for another attempt. Motivation and emotion thus go hand in hand. But motive implies action, the formation of an external representation; e-motion, on the other hand, implies the opposite, i.e., to be out of, or away from, action. To be emotional is to be, to an extent, "possessed," i.e., to be controlled. Motivation and emotion, action and passion, to be effective and to be affective: These are the organism's polar mechanisms for accomplishing requisite variety when he perceives more than he can accomplish. As already noted: When he can accomplish more than he perceives, a whole new set of techniques must be brought to bear—the consciousness expanders so popular today, are, according to this view, a corollary of our technologically proficient society.

This conception of emotions as neural processes that structure *input*, i.e., moods, interests, and attitudes, allows the inclusion of "positive" as well as "negative" emotions. No longer is emotion just disruptive—though expected or actual disruption of action initiates the emotion. Nor is emotion, in this context, to be necessarily avoided. Excessively rapid action without due deliberation—whether painful or exhilarating—is viewed as extreme as is excessive passion and inaction.

Finally, a word about the expression of emotions. According to the above analysis, the expression of emotions indicates that an internal process of control, rather than action, is operative in the organism's attempt to accomplish requisite variety. In a social environment (or to the organism himself) such expressions serve as communicative signals which are usefully read and taken into account in further interactions. Such affective signals often signify the intentions of the organism as clearly as do his actions—they suggest, however,

that action at the moment, for one reason or another, is infeasible.

At this point the physiological psychologist can leave the field of emotion to his colleagues. The experimental psychologist knows well the manipulation of expectancy; the social scientist is thoroughly versed in uncertainty; the psychotherapist deals daily with the problem of control; the ethologist has detailed the social significance of emotional expression; and the psychoanalyst has been deeply concerned with the signal aspect of affect. The structural view of brain mechanisms presented here—an information processing servosystem set to operate within the law of requisite variety—it is hoped points up the pertinence of each of these aspects to each other and to a problem which so vitally concerns us all: emotion.

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