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BIOLOGY OF DRIVES

A Report of an NRP Work Session

chaired by

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A report of an NRP Work Session
held April 3-5, 1966

by

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NOTE: NRP Work Session summaries are reviewed and revised by participants prior to publication.

I. INTRODUCTION

A Work Session on the "Biology of Drives" was held on April 3 to 5, 1966. The purpose of this Work Session was to attempt to find some agreement, or at least to explore different views, on the concepts of drive and motivation. The term *drive* is closely related to biological needs and may apply to behavior ranging from eating to that characterized by some as exploration. The need for novel sensory input may be as physiologically based as the more obvious need for nutrients. As drives are viewed as representing physiological states, they may also serve as interoceptive stimuli to activate and direct behavior, and changes in "drive stimuli" may be critically involved in the learning process. It is useful in delineating the construct of drive as a central determinant of response variability to exclude the short-duration reversible changes in responsivity, such as those attributed to fatigue or habituation, and the long-duration changes, such as those considered to be learning.

It has been suggested that the term *drive* is similar to the word *force* as used by physicists, and it is worthwhile to note their illuminating similarities. In both cases, the terms represent conditions that impart movement, or have the potential to impart movement, to an object or an organism, and both are inferable from observable events. Neither the physicist nor the psychologist expects to see a *force* or a *drive,* but here the similarities seem to end. Force can be quantified and, whether it is measured in terms of pounds, newtons, or dynes, the reference is to the movement of some specified weight at a specified speed. Since *force* possesses a unitary dimension, one can make meaningful quantitative comparisons.

The situation is quite different with respect to the term *drive.* It is anything but a unitary concept as is explicitly elaborated in Hinde's presentation, "The Diversity of 'Motivational' Mechanisms." We use *drive* to refer to the state of the organism which produces activity although we are compelled to admit that there may be times when at least some would suggest the existence of a high *drive* level in the absence of any overt activity. Hinde sees the existence of "nonactive" behaviors, such as some fear responses and incubation in birds, as one of the objections to thinking of drive as an energy concept. Brady maintains that this lack of a specific referent for the terms drive and motivation indicates that there may be little, if any, scientific value in employing the concepts. Teitelbaum responds to the issue by suggesting an operational definition to distinguish between drive and motivation. According to Teitelbaum's view, one is justified in using the term motivation only when an animal can learn an arbitrary response to obtain an appropriate goal object. In this way it may be possible to separate the consummatory behavior related to drive states from motivation. A blowfly's responsiveness to sweet solutions may vary with periods of deprivation, but, since attempts to train this animal to perform an instrumental response in order to obtain a sweetened solution have failed, one can only speak of changes in drive level but not motivation. Lehrman and Hinde argue that, since the comparative literature is replete with examples of such diverse mechanisms underlying plasticity, it would be most difficult (if not impossible) to apply any operational definition of motivation to all animals. Animals can exhibit plasticity in one situation and not in others. In the absence of an exhaustive study of an animal's adjustive mechanisms in response to different environmental demands, it would be dangerous to conclude that a slight change in the testing situation would not result in the learning of an instrumental response.

In part precipitated by studies of the "reticular activating system," other terms have crept into our vocabulary which have much in common with drive as a nonspecific activator. We speak of "activation levels" and "arousal levels" and consider their relationship to learning, reinforcement, and ultimately performance. Berlyne's presentation elaborates on the usefulness of these concepts and the role of the environment-organism interaction in modulating "arousal," while Lacey, in stressing the difficulties in measuring any generalized "arousal," is forced to question the value of the concept.

It is a common observation that both nonspecific and some goal-directed behaviors go through periods of high and low activity, which it is only natural to presume are related to changes in the state of the organism. These changes in the state of the organism are not only determinants of fluctuations in activity, but also account for the fact that the effectiveness of a given stimulus in producing a response may be variable. The response-eliciting properties of stimuli and the relative figure-ground position of the various components of complex stimuli in perceptual and retentive processes vary with the state of the organism.

Drive and motivation are also used to imply a focussed as well as a nonspecific activity. We speak of hunger, thirst, sex drive, etc., and recognize that an animal may remain active until a specific goal is achieved. During the past ten years there have been a great number of reports of goal-directed behavior elicited by stimulation of the hypothalamus and this has led many to conclude that discrete neural areas in this part of the diencephalon underlie specific motivated behavior. Some recent work from Valenstein's laboratory which questions this interpretation is discussed in the "Epilogue" (see page 85). Analyses of the way neural and endocrine factors may bias behavior into certain channels are provided by the presentations of Goy, Grossman, Roberts, and Teitelbaum. Both Goy and Teitelbaum emphasize the developmental aspects of the problem.

Drives are, in part, focussed because of changes in specific response and perceptual thresholds, but they also gain direction through a learning process. As drives become goal-oriented we speak of motivational states. The precise nature of the relationship of changes in drive level to the learning process has been the subject of much dispute, but there are very few who would deny its importance. Elsewhere, Miller (1957) has said of the drive-reduction hypothesis of learning: "In its weak form, it states that the sudden reduction in strength of any strong motivational stimulus always serves as a reward, or, in other words, is a sufficient condition for reinforcement. In its strong form, it states that all reward is produced in this way, or, in other words, that drive reduction is the necessary and sufficient condition for reinforcement." Perhaps the weakest statement of the relationship of drive state to learning is that changes in drive level are accompanied by perceptual changes which increase the likelihood that certain associations will be formed. It is a real possibility, however, that some neural accompaniment of what is called drive state changes plays an active role in the physiological basis of learning and retention. The presentations of Bindra, Miller, and Pfaffmann deal with specific aspects of the relationships of drive to learning or reinforcement, while Stein presents some new data on the pharmacological organization of the neural system which may be basically involved in the reinforcement process.

II. THE DIVERSITY OF MOTIVATIONAL MECHANISMS AND THE DEFINITION OF DRIVE

The concept of drive has as many interpretations as there are investigators who are attempting to explore it. Rather than pursuing abstract discussion of its definitional aspects, often a sterile exercise, the speakers in this section have tried to clarify the nature of drive by examining the different ways in which the term is used in practice and by presenting some of the data collected in experiments involving drive. What becomes apparent from these discussions are the diversity and complexity of the issues involved in the biological mechanisms underlying the concepts of drive. To shed some light on this problem, drive concepts and the related behavioral phenomena are considered within the contexts of ethology, of the physiology, anatomy, and biochemistry of the brain, and of the evolutionary stages of development of certain behavioral aspects.

Hinde's introductory paper presents a broad interpretation of the role of drive in modern ethology and in it he stresses that generalizations about drive involving different types of behavior in a variety of species can be a distinct disadvantage to those trying to understand the field. Lehrman, amplifying Hinde's ethological overview, discusses the interaction of peripheral and central mechanisms in the differing behavioral responses of various species. He also points out the limitations of the concepts considered by investigators in their study of animal behavior. Brady emphasizes the difficulties with hypothetical inferred mechanisms in psychology and biology and is primarily concerned with a critique of the concept of drive as it is often used by psychologists and ethologists. He views the problem, i.e., behavior, as being amenable to investigation as part of a black box system.

A. THE DIVERSITY OF "MOTIVATIONAL" MECHANISMS: R. A. HINDE

In order to delimit the problem under discussion at the Work Session, Hinde defined the problem of motivation as that of *changes in responsiveness to a constant stimulus situation,* including only those changes in responsiveness which are reversible, but excluding changes lasting less than a second or two. Changes in responsiveness attributable to sense organs or effectors and near-permanent changes, such as those we ascribe to learning, were also excluded, although Hinde conceded that the distinction between these changes and short-term learning is not clear.

Drive Concepts

Hinde then addressed himself to the relative merits of using drive concepts. Following Miller (1959), he found them to be useful, provided that (1) the number of relationships needing definition is reduced by using intervening variables, and (2) an adequate degree of correlation exists among the dependent variables. He noted, however, that several dangers attend the use of drive concepts besides those stemming from their diverse (hence possibly confusing) applications. They may be misused as a blanket variable to provide unitary explanations of diverse characteristics of behavior which may well depend upon diverse mechanisms. In addition, it is not always clear at what analytical level such concepts should be used. For example, the nest-building behavior of canaries involves various types of behavior, such as gathering and carrying material, sitting, and building the material into a nest, that are highly correlated with one another. These are, themselves, comprised of many different activities. But at what level is a drive concept useful? At the overall level of a nest-building drive? Or at the level of the constituent activities?

If drive is used as an energy concept, several additional problems may arise: (1) the nature of intervening variables may be misunderstood and thus the investigator is tempted to look to the CNS for something providing the postulated energy; (2) the causes of an animal's choice of one behavior pattern over another may be confused with the causes of its general activity; (3) the concept of general activity is not always useful in explaining "nonactive" behaviors such as some fear responses or incubation in birds (Hinde, 1956, 1959, 1960).

Specific vs. General Drive

In those contexts in which it is useful to use the drive concept, the problem arises of whether a number of specific drives or a general drive can most profitably be postulated. Hinde mentioned several experiments relevant to the problem of the interrelations between hunger, thirst, fear, and sexual behavior (see review by Brown, 1961). According to Hinde (1966), some of the experiments which show an augmenting effect on several categories of behavior can be understood either in terms of peripheral effects or in terms of drive generalization. Further, the choice of dependent variables for measurement may determine whether one finds these effects in any particular experiment. For example, in Tugendhat's (1960) study of feeding behavior of the three-spined stickleback, those fish that had been intermittently shocked in the feeding section of their aquarium later exhibited feeding behavior characteristic of food-deprived sticklebacks, i.e., the number of completed feeding responses per unit time rose. Nevertheless, the animals fed less frequently and the total time spent feeding decreased; hence, according to whether one measured (1) the rate of feeding responses during each feeding period, or (2) the total amount of food consumed, or (3) the time spent feeding, different answers might be obtained as to whether shock caused an increase or a decrease in the feeding drive. Hinde found Meryman's (see Brown, 1961) experiment, showing that both hunger and fear increase the startle response of rats, less easy to account for. He did, however, suggest that experiments involving fear, and therefore acutely involving the autonomic nervous system, may not serve as a good general model for all behavior.

Other studies relevant to the issue of specific vs. general drives are those concerned with the effect of input through one sensory system on responses mediated by another sensory system. Such studies have demonstrated that multisensory convergence exists in single units in the reticular formation, hypothalamus, and elsewhere (London, 1954; Horn, 1963).

Arousal Concepts

A third group of studies are those concerned with level of activation or arousal. Duffy (1962) and others (Bindra, 1959; Lindsley, 1960) have suggested that physiological variables such as muscular tension, heart rate, skin tension, etc., can be used as measures of level of activation. Hinde noted that the concept of arousal, or activation, like that of drive, is useful only so long as the various physiological indices are highly correlated, and this is often not the case. (See pp. 25 and 28 for a discussion of this problem by Berlyne and Lacey.) He gave the further caveat that difficulties arise if sensory input is varied beyond the normal experimental limits; i.e., with very low sensory input, the level of activation may be increased, but normal behavior may disintegrate (Solomon et al., 1961). Such evidence suggests to Hinde that an optimum level of general input or drive might exist for efficient behavior. Other studies supporting this notion are those on the control of illumination by an operant response: rats will work both to turn a light on or off, the amount of light sought by the animal being dependent upon the conditions under which they have been kept. Furthermore, studies of hunger drive and preferred illumination show that (within limits) the two vary together, rather than exhibit the inverse compensatory relationship which would be expected if a constant general level of input were to be maintained. Therefore, Hinde offered an alternative hypothesis; namely, that the longer the food deprivation or the greater the "sex drive," the higher is the level of general input towards which an animal will work. In harmony with this view, he cited Kavanau's (1963) experiment with deer mice in running wheels worked by motors under their control or the experimenter's. After having their chosen setting reversed by the experimenter, the mice would work to restore it, whether the motor was on or off.

Summarizing his views on the problem of specific vs. general drives, Hinde suggested that: (1) there is relatively little evidence that, within the wide limits of normal input, the intensity or frequency of occurrence of a particular type of behavior can be increased by increasing input in general; rather, each type of behavior depends on the factors that are more or less specific to it; (2) behavior as a whole becomes inefficient when input exceeds certain limits, but the dysfunction that accompanies low input is not necessarily caused by low "activation," but perhaps by a change in the accustomed correlations between the different types of input; and (3) the level of general input sought varies with the motivational state. Regarding drive concepts as a whole, Hinde views them as useful so long as one is talking about the behavior of the whole animal—for instance, in the study of conflict and in the analysis of threat and courtship behavior. Clearly, also, drive concepts have been enormously fertile to learning theorists (e.g. Miller, 1959). But when one proceeds with physiological analysis, the usefulness of the drive concept gradually disappears.

Effect of Independent Variables

To illustrate the variety of ways in which independent variables can affect behavior, Hinde discussed the various effects of sex hormones and stimuli on behavior. First, each hormone affects many responses and aspects of behavior, from the initial development of the nervous system (Young et al., 1964) to the specific and general behavior of the maturing and adult animal. Secondly, each hormone may affect behavior by several different mechanisms: (1) by affecting the growth of morphological structures actually used in behavior, (2) by affecting specific sites in the CNS (e.g. Harris et al., 1958), or (3) by affecting the growth of peripheral structures whose feedback to the CNS influences the behavior in question (e.g. Lehrman, 1955). The effect of external stimuli on behavior may similarly come about in one of several ways: (1) by eliciting responses or increasing motivation, (2) by orienting responses without actually eliciting them, and (3) by bringing specific behavior to an end (i.e., "consummatory stimuli," as in feeding behavior, where stimuli to the stomach, perhaps acting through a humoral mechanism, bring feeding to an end) (see Miller, 1957)). Regarding the latter effect of stimuli on behavior, particularly feeding, Hinde noted that, when behavior is brought to an end by stimulation resulting from that behavior (i.e., by negative feedback), its end often takes place without the elimination of the eliciting factors. Furthermore, such consummatory factors operate in many ways. In some cases, they elicit a further response and end the behavior in question probably by an inhibitory connection between the two types of behavior. In other cases, they seem to have a direct inhibitory effect on the behavior without eliciting another response. As an example of the former type of consummatory stimuli effects, Hinde cited Sevenster-Bol's (1962) study of the stimuli that terminate courtship of the three-spined stickleback. The presence of eggs in the nest appears to increase aggressiveness in the males, so that when subsequent females enter their territory, they are attacked rather than courted.

Effect of Motivational Factors on Response

Turning to the manner in which motivational factors affect responsiveness (see Pfaffmann, page 62), Hinde mentioned five possible ways: (1) level of general input may change with motivation, as perhaps shown by the Kavanau experiments cited earlier (page 12); (2) motivation may increase activity, as in the traditional view; (3) increase in motivation may increase responsiveness to stimuli, as in Teghtsoonian and Campbell's (1960) work showing that food-deprived rats in a stimulus-controlled environment are far less active than similarly deprived rats exposed to the "hurly-burly" of laboratory life; (4) motivational factors may influence selective responsiveness to stimuli by involving a central effect as, for example, in the studies of courtship in the guppy by Barends and his co-workers, (1955) showing that size in the female and the internal state of the male as indicated by color determine the intensity of the courtship behavior; (5) motivational factors may influence the orientation of movements, as in Collias and Collias' (1962) studies of weaver birds which show them to form perfect stitches and build perfect nests only when motivation (i.e., hormone level) is sufficiently high.

Hinde then considered the question of whether a central state must be postulated to mediate the motivational factors under discussion. He suggested two main arguments for doing so: (1) when the extraneuronal factors are constant, the intensity of behavior may nonetheless fluctuate from moment to moment; and (2) the behavior may be switched off independently of the elimination of eliciting factors. On the basis of these arguments, Sherrington's term "central excitatory states" (coined to refer to states lasting a few milliseconds) has been used by others, such as Morgan (1943) and Beach (1947), to describe more enduring states in the CNS presumably responsible for these behavioral fluctuations. Despite evidence from physiological experiments suggesting the existence (especially in the hypothalamus) of mechanisms apparently of great importance in the control of functional sequences of behavior like those involved in eating, drinking, and sexual behavior, Hinde cautioned that Neal Miller's advice should be heeded: "In investigating the motivating effects of central stimulation of the brain, it is unsafe to take anything for granted."

Response to Constant Stimulus

Hinde then addressed himself to a related topic, the changes in responsiveness of an animal to a constant stimulus situation in the absence of consummatory stimuli. Using examples from his own laboratory, he described the response of chaffinches to predators such as an owl, stoat, or dog. Each predator elicits a "mobbing response," which rises to a peak and gradually wanes with time; this waning is not due to sensory adaptation or to muscular fatigue. Since analysis of the waning process in invertebrate organisms like the earthworm demonstrates that the process takes place at a number of different loci in the CNS (Roberts, 1962), an even more complex process is likely in higher organisms such as birds. There are, indeed, multiple and interacting consequences of merely responding to a constant stimulus; in the case of the chaffinch's response to predators, these can be characterized according to whether they lead to an increase or a decrease in response strength, the degree of their stimulus specificity, and their time constants of decay (Hinde, 1960b). Hinde emphasized that these effects cannot be explained away simply by using one or two intervening variables such as I_R and $_SI_R$* (Hull, 1943). He

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*In Hull's notational system, I_R (reactive inhibition) is generated whenever a response occurs. It acts as a barrier to repetition, directly inhibiting reaction potential. It may act as a drive, strengthening any activity associated with its reduction. $_SI_R$ (conditioned inhibition or conditioned nonactivity) reduces I_R.

reiterated that changes in responsiveness can be ascribed, perhaps, to changes in the central nervous state which are not necessarily unitary, and which are themselves influenced (but not necessarily immediately) by longer-acting extraneuronal factors, by the eliciting stimuli, and either positively or negatively by the consequences of the activity itself. These states may show some degree of independence of extraneuronal factors and may influence behavior in a number of different ways, e.g., by influencing activity and by changing responsiveness to stimuli.

CNS and Response

To illustrate the type of complexity of CNS states and the consequences of performance which he believes must be postulated, Hinde referred to the work of Beach and his collaborators (e.g. Beach and Whalen, 1959a,b) on the sexual behavior of rodents. These studies show that the sex hormone has both central effects on the CNS and peripheral effects on the structure of the penis; performance affects at least two central mechanisms in both positive and negative fashions. In addition, there are other decremental effects consequent upon the performance that are specific to the particular female with which a rat has been copulating.

As a further illustration, Hinde described his own studies of the effect of sex hormones on the nest-building of passerine birds, particularly the canary (Hinde, 1965; Hinde and Steel, 1966). These hormones have not only presumed central effects, but also affect a peripheral structure, the brood patch, which becomes swollen and sensitive to tactile stimulation. Through this ventral surface, the female receives stimulation from the nest she has built, and this has multiple effects upon her further nest-building behavior. With increased stimulation from the nest, the following occur: (1) nest-building movements become more rapid; (2) feathers to line the nest, rather than material for the outside of the nest, are more likely to be sought on subsequent gathering trips; (3) nest-building behavior as a whole is reduced; and (4) a long-term acceleration of reproductive development occurs, giving rise to a new hormonal situation not conducive to building.

Response to Novelty

Hinde then discussed responses to novelty such as the orientation reflex and exploration behavior. Agreeing with Sokolov (1960) that the orientation reflex can best be described as "a response to a discrepancy between the neural activity induced by the present stimulus situation and a neuronal model acquired as a result of experience," Hinde observed that, unlike many other types of behavior, the orientation reflex (and perhaps exploration) comes to an end as a result of a change in the internal state rather than a change in the external stimulus situation which stays constant.

According to the internal state of the organism, a strange stimulus may elicit curiosity or exploration, on the one hand, or fear and avoidance, on the other. However, there are some strange-stimulus situations that are apparently more effective than others in eliciting fear responses from all members of a species. In his studies of chaffinch mobbing to an owl stimulus, Hinde found that naive chaffinches responded somewhat to simple owl-shaped models, but were particularly responsive to models with owl-shaped eyes. Thus to Hinde it appears that fear responses can be elicited either by discrepancy from a neuronal model of the familiar or by concordance with a model of certain particular stimulus characters, a response which may have been acquired independently of experience of those stimulus situations.

In conclusion, Hinde proposed, first, that the usefulness of simple unitary drive concepts decreases as analysis proceeds. Secondly, he stated that generalizations about problems of motivation relevant for all types of behavior and for all species cannot be made! As a corollary of the second conclusion he suggested that generalizations based merely on the paradigm of feeding behavior are not necessarily of universal applicability.

B. COMPARATIVE AND DEVELOPMENTAL CONSIDERATIONS IN THE STUDY OF MOTIVATION: D. S. LEHRMAN

In the introduction to his presentation, Lehrman elaborated Hinde's formulation that some kind of concept related to motivation is needed to explain variations in response to a constant stimulus. He noted that the response variations can be of several kinds:

1. *Variations in response patterning.* In this kind of response, animals deprived of species-specific highly motivated acts for varying lengths of time show that act in varying degrees of "completeness" of pattern (e.g., a goose which has repeatedly been made to fly may—when you try to make it fly—make only a little head movement which only an experienced goose observer can recognize as the beginning of movement of the total pattern of flying (Lorenz, 1952)).

2. *Variations in threshold level.* This type is characterized by the degree to which various stimuli that resemble "ethologically" significant stimuli can elicit differing responses (e.g., chaffinch mobbing elicited by an owl-like stimuli as described by Hinde (see page 13)).

3. *Variations in orientation to the incentive.* This kind is typified by the following: (*a*) variations in speed of learning that can be related to organic states; (*b*) variations in the selection of learned responses from groups of such responses; (*c*) variations in the goal directedness until a given goal is reach; (*d*) variations in responsiveness to stimuli, i.e., selecting certain stimuli to respond to rather than others.

Lehrman then proceeded to discuss some comparative approaches to motivation. He noted that many of the well-known concepts of motivation are noncomparative (i.e., intended to be applied without modification except for changes in constants to all kinds of motivated behavior regardless of the differences among kinds of animals). As examples, he cited the energy models of Lorenz and Freud, the goal-directedness and energy model of McDougall, physiological models such as Stellar's, and the stimulus-response (S-R) and learning models.

Level-Specific Capabilities

In considering what a comparative approach to such problems would require, Lehrman suggested that the notion of "level-specific" capabilities would be useful. This term would be more inclusive than the term "species-specific," which refers to behavior patterns found in particular species that owe very few formal characteristics to individual experience and that seem to be of use to the species in its natural environment. The term "level-specific" would refer, instead, to those aspects of behavior or morphology or physiology that are specific to a particular level of either development or evolution. Implied in such a concept would be the differences, for example, between a coelenterate and an insect, or between a bird and a mammal. At different levels of the evolutionary scale there are fundamental differences in the level of organization at which similar functions are carried out. For example, sexual, feeding, and migratory behavior occur in many kinds of animals because of environmental requirements; however, the means by which these requirements are met might be so different that no conceivable theory of motivation could be applied to them all unless some statement of their differences is made an integral part of the theory. In Lehrman's opinion, such a theory must consider *both* the level-specific morphology and physiology of an animal and the kinds of effects of experience and learning that are characteristic for animals at that level and developmental stage.

Level-Specific Situations

Lehrman next gave some examples of level-specific situations by comparing the feeding behavior of a jellyfish, a blowfly, and a rat. In all three cases, if the animal has been recently fed, its reaction to a feeding stimulus is very sluggish and its general activity level is likely to be lower than if it has not been recently fed. For all three types of animals, food intake is decreased by satiation and increased by deprivation. However, the mechanisms underlying such behavioral similarities differ considerably. For example, the jellyfish (a coelenterate) has a relatively undifferentiated central nervous system: a diffuse syncytium-like nerve network extends throughout its eight-tentacled contractile tissue (although it also has a nerve ring). Excitation from any point of stimulation spreads in all directions with a sharp measurable decrement. The cells contract at the point where the nerve fibers are active, causing the tentacles to bend up. Thus *some* of the motor organization represented by the combined movement of food toward the mouth and of the mouth toward food is created not by a central organization sending instructions in a coordinated way to different parts of the animal, but rather by the sheer geometry of the animal. Variability in response to a food stimulus results from a generalized change in reactivity owing to the pervasion of nutrient materials into the jellyfish tissues. The net effect is that the coordination of feeding movements is more intense and more efficient when the animal has not been fed than when it has.

By contrast, the blowfly has a much higher and more complex level of central organization. It has a central nervous system and a brain into and out of which peripheral information must pass. As Dethier (1963) has shown, chemical stimulation (with sucrose) of particular neurons of the legs causes the head to turn toward the side of stimulation, the mouth parts to be extended, and sucking movements to take place until the animal is sated. Regulation is accomplished by feedback via the recurrent nerve, which sends the brain information regarding the degree of distention of the crop, where most of the food is stored. With sufficient crop distention, a central command causes feeding to be discontinued. Severance of the recurrent nerve causes a total loss of regulation.

The rat, too, uses information from its stomach in regulating its food intake, but this factor is integrated with many other peripheral factors through central organization and integration unthinkable in the blowfly. To consider another difference between, say, an insect and a mammal, a rat can be trained to run a maze when it is hungry and also to run it when it is thirsty; in other words, it can generalize. An ant can be trained as rapidly as a rat to run a maze; however, it is unable to generalize and run the maze for a reward different from the original one. That is, the sensorimotor connections of the ant are particulate and short-arc in character, rather than being generalized and integrated as in mammals.

Limitations of Concepts

Lehrman then addressed himself to some of the questions that underlie both the phenomena studied by scientists and the criteria they apply to them. He noted that concepts not only of motivation but also of learning and perception have been based on a relatively small part of the total range of animal behavior and animal forms. The laws for all of these behaviors may vary considerably at qualitatively different levels of animal evolution. Scientists who explain animal behavior differ in their values regarding the appropriate material for study. For example, (1) some scientists believe that a description of behavior which has been obtained under stimulus control is sufficient for a meaningful behavioral science, whereas others use intervention for the purpose of understanding behavior when it is *not* being externally controlled. (2) Some scientists study animal behavior for its own sake without regard for any relevance to human behavior, whereas others would restrict their concern to those aspects of nature that are obviously relevant to human behavior. According to Lehrman, such values affect whether one considers a theory of motivation as being complete that describes how rats feed, or whether one regards it simply as a contribution to the understanding of a relatively small part of the natural world.

In his final remarks, Lehrman challenged one aspect of Teitelbaum's operant criterion of motivation (see page 46). Teitelbaum suggested that one should be able to attach any arbitrary response to any stimulus.* To Lehrman this criterion refers to a limited range of

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*Teitelbaum points out that an operant from the animal's natural behavior repertoire must obviously be selected. A rat cannot be required to fly in the air or a pigeon to swim under water; but, within the natural repertoire of responses that the animal possesses, one can be arbitrarily selected to reinforce. Otherwise, one is stuck with the possibility that a response is a fixed response to stimulus. [P. Teitelbaum] phenomena in a limited range of animals. He noted that bees can be trained to feed from artificial flowers of any hue, but not of any shape, despite their natural preference for certain shapes (which indicates the presence of some form perception). Also, one can train a bee to fly out of a round rather than a square hole in the hive; but it cannot be trained to leave through holes illumined by different colored lights. Thus, the bee can learn different tasks in different motivational contexts. Lehrman gave two other examples of motivated behavior that remain to be explained by current theory: (1) There is a fish which lives on a coral reef, that jumps in the correct direction from one tide pool to the next at low tide to reach the sea. It can learn to make these jumps in the correct direction *solely* by swimming out of the pools at high tide! (2) Part of the song repertoire of certain finches is learned by young birds on hearing their fathers sing during the spring in which they are born—before they can themselves practice the pattern. They can reproduce the songs when hormonally ready, a year after hearing the song.

C. POTENTIATING OPERATIONS: J. V. BRADY

Brady addressed himself to the problem of identifying the behavioral phenomena associated with drive and motivation, and to redefining the relationship of these phenomena to the anatomy, physiology, and biochemistry of the brain. Discussing first the behavioral side, Brady finds that the terms "drive" and "motivation" have too much surplus meaning to be very useful. There is the implication of unobservable subjective and physiological states, such as arousal, central excitatory states, activation, etc. Further, the surplus meanings imply the impossibility of control over motivational phenomena. This latter implication has been shown to be untrue by a number of experimental manipulations (e.g., "you can lead a horse to water, but you can't make him drink").

To Brady, the operations involved in drive and motivational phenomena have in common an influence on the effectiveness of the consequences of behavior. He views phenomena usually subsumed under drive and motivation as *potentiating* operations that determine the potency of the consequence that functionally defines the behavioral process. Such consequence-potentiating operations can obviously occur in any temporal relationship to the behavioral response process, i.e., either before or after the response. Several aspects of this potentiation conceptualization have been traditionally considered within the framework of drive and motivation:

1. *The deprivation-satiation continuum.* Deprivation obviously makes a consequence more effective, whereas satiation makes it less effective. This is equally true of negative consequences; hence, the effect of shock upon a consequence resembles that of satiation.

2. *Functional physiological equivalents of deprivation and satiation.* Functional equivalents of deprivation and satiation exist; thus, not only will a water-deprived animal drink increased amounts of water, but also will an animal fed salt, or left in the sun, or one whose brain has been surgically altered. To Brady, the advantage of conceptualizing these as potentiating operations is that no reference is made to subjective unobservables or to inferred physiological states. One simply specifies the functional equivalent or the operation that produced the behavioral phenomena.

3. *Acquired potentiation.* Conditioned and generalized potentiating effects are established so that a previously ineffective behavioral consequence acquires potentiating qualities. Brady views "acquired drives" simply as those operations that change the effectiveness of a consequence in order to maintain behavior.

4. *Temporal and quantitative aspects of consequence potentiation.* Delays and amounts of consequence obviously change the effectiveness of the consequence to maintain behavior. Reward that is too little or too late has little effect, and the same is true of punishment. The series of parameters emerging from brain stimulation operate in a similar way. All these operations have in common their influence on the effectiveness that maintains or attenuates behavior.

Regarding research on the central nervous system, Brady sees the task as not that of finding the centers or causes of drives, but rather as that of ferreting out the way in which tissue masses, distinguishable by independent anatomical, physiological, and biochemical criteria, participate in the interaction process between organism and environment, i.e., behavior. He sees no need to posit processes like arousal, central excitatory state, activation, etc. Rather, he visualizes the whole process as being amenable to rather straightforward investigation as part of a closed system (a black box) analyzable into input, transfer, and output processes. Inputs arrive at the brain from three sources: proprioceptors, exteroceptors, and interoceptors. Outputs leave through the autonomic, endocrine, and skeletal systems. The central transfer mechanism is admittedly somewhat complex. Nonetheless, Brady sees no reason for positing any special properties to that central black box until the possibilities of this sort of input-output analysis have been exhausted. Although a complete analysis of the input-output system is still a long way off, some progress has been made. Teitelbaum (see page 45) and Grossman (see page 50), for example, have been concerned with the problem of input and output and the function of the manipulations performed inside the black box. Lacey (see page 27), on the other hand, has been primarily concerned with one part of the output system, namely the autonomic, and Brady and his colleagues (see Mason and Brady, 1964) at Walter Reed have been developing endocrine measures to determine the nature of that output system.

III. DRIVE AS A GENERAL ACTIVATING FACTOR

A number of theoreticians who have used the concept of drive regard it as a type of generalized force or energy which in some way provides the biological pressure behind all ongoing behavior of the organism. This concept has been very difficult to maintain in the face of criticisms of more behavioristically oriented individuals. In recent years, therefore, the general energy concept of drive has been modified, particularly by those people who have investigated the ascending reticular activating system and its relationship to other aspects of behavior. It is obvious that the "arousal" that can be brought about by stimulating the ascending reticular formation may provide just the type of influence on behavior which was formerly thought of as drive in the form of "a general energy concept." Berlyne has represented this point of view. In his presentation, he explores the concept of arousal and how it may relate to a concept of generalized drive, whose existence does not exclude that of specific drives. He suggests an analogy with the general intelligence factor that Spearman posited over half a century ago as a variable that interacts with specific abilities in determining the proficiency with which an individual performs a particular task.

One of the ways of criticizing the notion of arousal as a general energy concept is to show that there is no such thing as generalized arousal. If arousal is differentiated, in other words, if it varies with changes in stimulus conditions or perhaps differs in different individuals under identical stimulus conditions, then the idea tends to break down. Lacey has done extensive studies of the autonomic reactions of the body to different stimulus conditions and of individual differences to the same stimulus conditions. His conclusion is that there is no such thing as generalized arousal.

If we abandon the notion of drive as a generalized energy concept, one alternative is to turn to the concept of drive as a focussed energy concept. This means that we do not think of any generalized system that imposes either goal directedness or pressure for activity, but rather propose that there are a number of relatively independent systems such as sex, hunger, thirst, aggression, and so on, each of which has a number of biological mechanisms which determine both the intensity and the direction of the system and yet can be studied relatively independently of one another. One of these systems, the sexual drive system, has been well studied by Goy in a long series of investigations carried out with W. C. Young and others. These studies have shown that sexual performance as measured objectively is under the influence of many classes of determinants, including hormones, genes, and environment through learning. In his presentation, Goy puts most of his emphasis on the role of hormones in early life in determining masculine, feminine, and hermaphroditic structural and behavioral patterns.

A. DRIVE AND AROUSAL: D. E. BERLYNE

The question of whether the concept of drive, for years the focus of motivation theory, can be identified with the newer concept of "arousal" was discussed by Berlyne. Aspects of both phenomena are suggestively similar. For example, the description of an animal in a state of high arousal resembles closely that of an animal in a high state of drive. A prepotent response (whether learned or unlearned) seems to be stronger than usual when either arousal or drive is unusually high. In the absence of a prepotent response, both high arousal and high drive produce restlessness and diffuse activity. Furthermore, many of the recognized drive conditions, including food and water deprivation, pain, and sexual receptivity, are also capable of raising arousal, as shown directly by electrical probes of the reticular formation and indirectly by measures of the galvanic skin response (GSR), EEG, heart rate, etc.

If arousal can be identified with drive, then psychophysiological measures of arousal can be used to measure drive instead of, or in conjunction with, the older measures of drive through consummatory or instrumental motor behavior. Furthermore, the concept of drive can be broadened to include known effects of arousal not normally included, such as the heightening of receptor acuity and sensitivity (one aspect of the orientation reaction) and the facilitation of CNS functions as seen in increased discriminative ability, decision-making capacity, and "lability." Factors that induce arousal could then be assumed to induce drive. Thus, what Berlyne (1960, 1963, 1965) calls the "collative variables" (i.e., novelty, complexity, ambiguity, surprisingness, all of which seem to depend on the occurrence of mutually incompatible or disharmonious processes in the nervous system) would be counted as drive conditions. Novelty, surprisingness, and complexity variables have been found to affect such indices of increased arousal (components of the orientation reaction) as the incidence and magnitude of the GSR and the duration of the EEG desynchronization. So do conflict and subjective uncertainty, which seem to be the factors that underlie the motivational effects of the collative variables (Berlyne, 1961; Berlyne et al., 1963; Berlyne and McDonnell, 1965; Berlyne and Borsa, 1968). A broad new class of conditions that may impel activity and learning and a corresponding new class of reinforcing conditions are thus brought up for consideration.

Is Drive a Unitary Concept?

Berlyne discussed some reservations that are called for in making the identification of arousal with drive, however tempting it might be. First, the question arises whether the concepts of drive and of arousal are themselves unitary. In commenting on drive first, Berlyne cited the following three concepts that share the same name but are logically distinct (Berlyne, 1960).

1. *Generalized drive as an activating or energizing factor.* (This is the concept of drive identified with Hull's (1943) "D".) Woodworth first used the term "drive" in 1918 in the singular, apparently thinking of its use in engineering to designate the means by which power is conveyed to the moving parts of a mechanism.

2. *Specific drive as a factor that brings particular kinds of behavior to the fore and makes them prepotent over others.* In this usage, the word is often used in the plural ("drives") after Moss (1924). It is etymologically related to the German *Trieb,* which was the word that Freud's early translators rendered as "instinct" but is perhaps better translated as "urge."

3. *Drive as a vital factor in reinforcement.* Used in this way, it has two different roles: (*a*) *drive as a factor that makes certain events reinforcing,* as in the experiment by DeBold and his co-workers (1965) showing that swallowing water will reinforce a classically conditioned response only when an animal is thirsty, and (*b*) *drive as a factor that produces reinforcement by undergoing a change,* as in the notions of reinforcement as drive reduction or drive increase.

On comparing the notions of drive as outlined above with that of arousal, Berlyne found that several problems arise, depending upon the concept of drive under comparison. One of the safest equations is that between arousal and drive as a general energizing or activating factor. Both drive and arousal bear a curvilinear, inverted U-shape in relation to performance. That is, measures of intensity and quality of performance increase with drive up to a point, but, under excessively high drive, performance is apt to decline.

The equation between arousal and specific drive is more troublesome. Anokhin (1955) has suggested that within the reticular formation there are a number of different structures corresponding to different biological activities which can be excited separately. However, the centers for specific drives appear to be in structures other than the reticular formation, notably the hypothalamus and the limbic system. It seems likely that states of high arousal with different origins and different accompaniments will all heighten activity in general but predispose the organism towards different kinds of activity.

The relation between arousal and drive as a factor in reinforcement is as yet unclear. Arousal obviously has a great deal to do with reinforcement, but the extent to which the latter involves increase or decrease of arousal remains to be determined. A review of relevant findings in such diverse areas as neurophysiology, animal learning, psychopharmacology, personality theory, human verbal learning, and experimental aesthetics suggests that reinforcement of instrumental conditioned responses (reward) can, in fact, result from either of two mechanisms (Berlyne, 1967). When arousal (drive) is at an excessively high level, a decrease will be rewarding, but a moderate rise in arousal (drive) may be rewarding regardless of whether it is soon followed by a drop.

Is Arousal a Unitary Concept?

To what degree arousal is a unitary concept was next considered. Berlyne acknowledged that neurophysiological studies of arousal have made it increasingly clear that arousal is not just a matter of what goes on in the reticular formation. As already mentioned, there is evidence that the reticular formation is structurally and functionally differentiated. Moreover, "arousal" clearly depends on interaction between it and other structures, notably the neocortex, the limbic system, the lemniscal pathways, and, most important of all, the hypothalamus. In fact, Feldman and Waller (1962) and Gellhorn (1961) have suggested that the hypothalamus is the main center for arousal. On neurophysiological grounds, then, arousal appears to be a far more complex and diverse process than it first seemed.

An additional obstacle to viewing arousal as a unitary concept is the large number of measurable variables that are regarded as manifestations of it. These measures seem to be correlated with one another to some extent in at least some situations, but their intercorrelations are far from perfect. (See Lacey's discussion on page 28.) Berlyne commented that this problem is analogous to one that has long been faced by psychologists interested in human individual differences, particularly abilities. Early in this century Spearman (1904) recognized that all human abilities seem to be correlated to some extent; thus a person who excels over another in one task is likely to excel at least slightly in another task. This observation led to his notion of a general intelligence or "g" factor. In a variant of this notion, Thomson suggested that the same data could be explained by assuming the existence of a number of overlapping factors such as spatial ability, verbal ability, etc. (Brown and Thomson, 1925). Later, Thurstone (1931) replaced the general factor with several bipolar factors, which were subjected to rotations determined by considerations of psychological meaningfulness.

General and Other Factors

Berlyne suggested that arousal is obviously a general factor, but there is reason to suspect that bipolar factors may also exist, i.e., a sympathetic-parasympathetic factor and an unpleasantness-pleasantness factor. Although these may be separated from the general factor of arousal, they may be oblique to it and to one another. Thus, high arousal may have an unpleasant or predominantly sympathetic quality, whereas more moderate levels of arousal may have more of a pleasant or parasympathetic flavor. In addition, specific factors evidently exist. They correspond to specific biological needs or drives, such as hunger, pain, and sexual excitement.

Thus, several different systems of factors or dimensions can be used to sum up the same data. Some will contain a general factor, and others will not. Different systems may be useful for different purposes. Ultimately, consideration of physiological or psychological meaningfulness may favor one of these descriptive systems over others. For example, we might eventually arrive at a system of dimensions, each of which may be identified with the activity of a particular neural structure. But our knowledge is surely not yet sufficiently advanced for us to feel that one classificatory scheme need be imposed on us.

In conclusion, Berlyne suggested another potentially fruitful analogy—that between motivational phenomena and the stock market. Stocks, like the responses or activities of animal organisms, are susceptible to powerful factors that tend to drive them all up or down together. But both groups of stocks and individual stocks are affected by influences that are peculiar to themselves. For these reasons, prices of different stocks tend to move with the market as a whole, but their fluctuations also show some independence and some may rise while others may fall. So, arousal may be viewed as a Dow-Jones index, with GSR as a bellwether stock. Then heart rate and EEG could be rails and utilities, with hunger, thirst, and sex as selected growth-industry groups. Unfortunately, Berlyne had neither the time nor the capital to develop this promising approach further.

B. FRACTIONATION AND DIFFERENTIATION OF "AROUSAL" PROCESSES: J. I. LACEY

Lacey began his presentation by stating that he is extremely suspicious of the reliability of the concept of "general arousal" and hopes to see it supplanted by a description of a series of specific mechanisms and their interactions. He distinguished three types of arousal on the basis of the operations used to measure them: (1) *behavioral arousal*—from coma and deep sleep through relaxed wakefulness, excited behavior, to panic; (2) *somatic arousal*—from no sympathetic-like activity to the maximum observable sympathetic activity; (3) *electrocortical arousal*—change of electrocorticogram from high-voltage slow activity through low-voltage fast activity.

None of these types can be viewed simply as a unidimensional continuum since each form of "arousal" is itself complex. Lacey contends that the widely held notion that one continuum indexes another is incorrect. Rather, he views each of the three "arousals" as a complex set of phenomena mediated by demonstrably different neurological pathways. Moreover, each of the autonomic components of somatic arousal may have a different role to play in the transactions of the organism with its environment. To Lacey, then, it is precisely in the verified exceptions to the rule of covariance that most information can be gained regarding the function of automatic-somatic mechanisms of behavior.

Among the exceptions noted by Lacey are the independent findings in the 1950's by Bradley (1958) and by Wikler (1952) that cats or dogs given atropine can exhibit an electrocortical pattern characteristic of sleep (high-voltage slow activity) while being behaviorally excitable and capable of well-coordinated motor behavior. Conversely, with physostigmine administration, an EEG characteristic of a highly alerted, activated cortex (low-voltage fast activity) can be produced in a behaviorally drowsy and quiet cat or dog. Along the same lines, Feldman and Waller (1962) have recently dissociated the neural pathways mediating maintenance of behavioral arousal from those mediating electrocortical arousal in chronic animals. Animals with massive bilateral lesions in the posterior hypothalamus are somnolent and totally unresponsive behaviorally to sensory stimulation; however, the same stimuli that evoke no behavioral response elicit electrocortical arousal. In the same study, Feldman and Waller made bilateral lesions in the midbrain reticular formations of cats. The lesioned animals could track a moving object quite well (for 24 seconds) in their visual environment while their EEG for the same period was synchronized, an EEG pattern usually indicative of sleep.

Interrelations Among Three Forms of Arousal

Lacey then described some work in his own laboratory directed toward specifying the precise conditions interrelating the three types of arousal mentioned earlier. He addressed himself particularly to the nature and neural mechanisms underlying a discontinuity among measures of autonomic arousal.

According to Lacey, although the autonomic patterns said to constitute arousal covary at best to only a disappointingly low extent, for many individuals the total pattern of autonomic response is quite reliable over a period of time. That is, response-specificity or response-stereotypy does exist. Lacey and Lacey (1962) tested a group of 40 children (ranging in age from 8 to 14 years) twice, with a 4-year interval between the tests, to measure their autonomic pattern of response to the cold pressor test (i.e., immersion of the foot in 4°C water). The following autonomic measures were used: systolic and diastolic blood pressure, heart rate, palmar conductance, and heart-rate variability. The results suggested that a biological continuum exists ranging from individuals with rigidly reproducible somatic response patterns to those with relatively random responses.

Some response patterns appear to be the anlage for the later development of psychosomatic disorders. However, most of the evidence is merely anecdotal; for example, the individual with very large cardiac responses year after year may be a likely candidate to develop paroxysmal tachycardia later in life. Also, the occurrence of large pressor responses is predictive, to a modest extent, of later essential hypertension.

Lacey and his collaborators (1953, 1958) found that the individual response patterns are reproducible regardless of the nature of the stressor, i.e., in the face of hyperventilation, mental arithmetic, etc. In addition, they found (Lacey et al., 1963) that, if one radically increases the scope of the kinds of activities in which the subject is engaged, one sees evidence of striking bidirectional fractionation of the response pattern. In other words, it is possible that, to a given stimulus, sympathetic-like changes will be seen in some response variables whereas parasympathetic-like changes will be seen in others. For example, Lacey and his co-workers (1963) have studied autonomic activity in a variety of stimulus situations, arranged along a hypothetical continuum from tasks such as mental arithmetic, which requires internal elaboration of already stored information, to vigilance activities in which the organism must attentively observe the external environment. They found that palmar conductance rises in all activities, but that heart rate rises only in those activities involving cognitive elaboration. When the subject is attentively observing the external environment, the heart rate falls to levels below those seen in a quietly resting individual who has been lying down for about one-half hour. The same thing happens to blood pressure. However, this differentiation between the two kinds of tasks is not made by skin resistance, respiration, or digital blood flow.

In explanation of this phenomenon, Lacey pointed out that the cardiovascular system has a rather unique role in corticodynamics: it is the source of the only known sensory input that will inhibit the activity of the cortex. That is to say, increases in blood pressure and in heart rate are fed back to the CNS via a well-defined, visceral afferent feedback pathway in a negative pattern. Increments of pressure affecting the pressure-sensitive or stretch-sensitive receptors in the aortic arch and in the carotid sinus are reflected in increments of activity of impulse frequency along Hering's nerve from the carotid sinus, and the aortic depressor nerve from the aortic arch. The effect of this increase in impulse traffic is to inhibit cortical activity and corticospinal activity. The neurophysiological literature is replete with demonstrations that increases in intrasinusal pressure produce such phenomena as slowing of the EEG elevation of the thresholds for evocation of motor reflexes and quicker termination of stimulus-evoked or "spontaneously" occurring episodes of autonomic, motor, or electrocortical activity. The names of Bonvallet, Dell, and Zanchetti figure prominently in this literature which Lacey (1967) has extensively reviewed and interpreted in a psychophysiological context.

There may be at least two pathways for the dissemination of sensory input: one to the ponto-mesencephalic reticular system and another, possibly a different one, directly to the head of the nucleus of the solitary tract, where indirect control is exerted on the excitatory activity of the ascending, reticular activating system. Bonvallet and Allen

(1963) and Bonvallet and Block (1961) have shown that, if minute lesions are made at the head of the nucleus of the solitary tract (carefully avoiding the ventromedial, descending, inhibitory reticular system and the vasodepressor neuron systems lying somewhat posterior and medial to this region) and the animal is excited either by reticular formation stimulation or by exteroreceptive inputs, the ongoing activity precipitated by this sensory input is relatively chaotic and long lasting.

The cardiovascular sympathetic-like activity may then be said to initiate an inhibitory homeostatic control by means of which cortical excitation is held within limits. By the same token, then, decrements in cardiovascular activity should indicate instances in which inhibition is not being employed. Lacey and his associates found that such instances occurred almost entirely when the organism was engaged in passive but attentive observation of the external environment.

Lacey and his group then studied the cardiac responses of human subjects in a reaction-time experiment to see whether they could produce depressor and bradycardiac responses that would correlate with better performance and thus confirm that the visceral afferent feedback pathway was, indeed, acting as described above. Upon presentation of a visual ready-signal, the subject was to press a key and to release it only when the stimulus signal appeared. His reaction time for the key release was measured. The subjects were tested in both fixed and variable foreperiod (the period of time between the point at which a given trial starts and the onset of the stimulus requiring a key-releasing response) experiments, and an averaged curve recorded. Lacey found that a steady massive deceleration occurs during the preparatory interval until the stimulus comes on; then the heart rate accelerates. Blood pressure, however, barely changes. The changes which do occur are in the direction of sporadically occurring modest increases. Preliminary evidence suggests that the two fractions (blood pressure and heart rate) have contrary effects on reaction time. The greater the change in blood pressure, the slower the reaction time, and the greater the heart rate deceleration, the faster the reaction time.

Confirmatory, but preliminary, evidence supporting the notion of facilitating effects of bradycardia and hypotension has been obtained by Lacey in evoked potential and alpha block experiments, particularly the latter. Lacey believes that the cardiac response may facilitate both the motor readiness aspect of performance and immediate information processing, judging by the subjects' performance on variable foreperiod tests. But more subtle aspects of information processing, such as responsivity to contextual but immediately relevant cues, are inhibited by immediate sensorimotor readiness. Individuals with massive deceleration are unresponsive to current and preceding foreperiod effects, whereas individuals with small decelerations are not only slow but are slowed trial-by-trial by the program of foreperiod intervals. Cats respond in the same way. Lacey has now a group of cats that behave like automata, doing reaction-time experiments on fixed or variable foreperiods and maintaining this performance on foreperiods from 150 milliseconds up to 10 seconds.

The relation of cardiac response to attention processes has been studied by Lewis and his co-workers (1966) in infants. Four separate groups of 24-week-old infants were exposed to different patterns of visual stimulation. Fixation times and heart rates of the subjects were recorded and the cardiac responses were subsequently grouped according to the duration of visual fixations. When the fixation time was 9 seconds or below, there was modest cardiac acceleration during the stimulus presentation. During a fixation lasting 10 to 19 seconds, a deceleration occurred; whereas with fixations lasting 20 to 30 seconds, there was a rather massive deceleration. Thus there is a correlation between the magnitude of the cardiac deceleration and the length of time in which the organism is presumably oriented to and scanning a stimulus.

Cardiac deceleration during the foreperiod of a reaction-time experiment also occurs in cats.* Apparently this response tendency is neither species-specific nor heavily dependent on early developmental processes but is built into a wide variety of organisms.

In summary, Lacey noted that the autonomic arousal system is fractionated; individual fractions may have separate roles in the control of electrocortical activity and of behavior. He believes that, as more is learned about these mechanisms and as they are increasingly subject to manipulation, the "big-A" of arousal will no longer be invoked.

C. NEUROENDOCRINE SETTING OF BEHAVIORAL PROPENSITIES: R. W. GOY

As recently as 20 years ago, when Beach published *Hormones and Behavior,* it appeared as though the products of the early gonadal hormones were not at all important in influencing the kinds of behavior seen in the adult. However, with the advent of a new technique pioneered

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* Unpublished experiments by D. Galin and J. I. Lacey.

by Young collaborating with Phoenix, Goy, and Gerall (1959), the notion that early hormones participate in the establishment of masculinity and femininity became an acceptable hypothesis. Experimental embryologists (see the review by Burns (1961)) had found that, for all of the mammalian species studied, androgen in some form is the critical morphogenic substance that determines the external expression of morphological sex in mammals. When androgen is present at the correct time and in sufficient quantities in embryological development, the external genital structures develop in the masculine form regardless of the individual's genetic sex. Conversely, in the absence of androgen, every individual develops the feminine form of external genitalia. If androgen is present in individuals of either genotype in insufficient quantities or at nonoptimal times, the resulting external genitalia are of mixed sexual types.

Influence of Androgen on Diverse Neural Mechanisms

Goy noted that relatively recently it has been found that many of the sexual characteristics of mammals other than those that pertain to external genitalia also appear to differentiate or to be established in a manner exactly parallel to that in which the genital structures themselves develop. This has led to the hypothesis that the developing nervous system differentiates in the masculine and feminine forms. From work during the past 5 years it appears that the developing nervous system undergoes psychosexual differentiation strictly in accordance with the amount and principle of androgenic guidance or stimulation. Thus both ovulatory capacity and female sexual behavior have been shown (Barraclough, 1961; Harris, 1964) to be dependent upon the absence of androgen for their normal development. The effect of early androgen is neither on the gonad itself nor on the pituitary gland of an androgenized female. Rather, it appears to affect primarily the brain centers that regulate the release of pituitary gonadotropins, causing the treated female to secrete gonadotropins acyclically and/or in deficient amounts. Goy suggested that the presence of androgen during the critical period might be viewed as masculinizing the brain-pituitary regulatory mechanism of the genetic female so that after puberty the pituitary secretes gonadotropin in a fashion corresponding closely to that in the normal male.

Among the early studies of the effects of early androgenic treatment on the sexual behavior subsequently displayed in adulthood are those done in the 1930's by Dantchakoff (1938a,b). She noticed that, if genetically female guinea pigs were exposed to androgen between the 20th and 27th days of embryonic development, they showed rather pronounced masculine traits in adulthood. For example, they pursued and mounted normal females that came into estrus, as normal males would. Although Dantchakoff was unaware that normal females may also exhibit this behavior, her observations stimulated other research. Using a modification of Dantchakoff's technique, Phoenix and his associates (1959) found that adult females treated during embryonic development not only showed more masculine behavior than normal females, but also failed to display feminine sexual behavior. Such an impairment was not due to ovarian dysfunction since all the animals studied were spayed and given a replacement therapy that is normally extremely effective. The hermaphrodites' behavior resembled more that of males castrated soon after the completion of sexual differentiation than it did that of normal females.

Discrete Developmental Period for Androgen's Masculinizing Actions

A period exists in early embryonic development when the developing nervous system is expecially sensitive to the masculinizing effects of androgen (Goy et al., 1964). In the guinea pigs, this period extends from the 30th to the 50th day of prenatal growth (gestation period is 68 days). In the rat, the sensitive period appears to be early postnatally after a 22-day gestation period. The extent to which female estrous behavior is suppressed is directly related to the total amount of androgen administered on a daily basis during the sensitive period (Table I) in both the rat and the guinea pig. Female estrous behavior can be completely suppressed in this fashion and male behavioral tendencies can be markedly augmented.

Effect of Deprivation of Androgen on Development of Genetic Male

Having shown that androgen will suppress feminine characteristics while augmenting masculine characteristics in genotypic females, the Young group also demonstrated that, in the genotypic male, an androgen deficiency during the period of psychosexual differentiation will permit the development of feminine characteristics and produce a deficiency in masculine ones. Grady and his co-workers (1965) have reported a study comparing the development of sex behavior in male rats castrated on the day of birth, and on the 5th, 10th, 50th, and later days, postnatally. If

TABLE I

RELATIONSHIP BETWEEN AMOUNT OF TESTOSTERONE PROPIONATE ADMINISTERED DURING THE SENSITIVE PERIOD AND SUPPRESSION OF ESTROUS BEHAVIOR IN ADULTHOOD [Goy, 1966]

Total amount of testosterone propionate,* mg.	Number of females tested	Number of tests	Proportion of tests in which estrous behavior was not displayed
0 (Controls)	20	52	0.02
1-5	17	51	0
11-15	41	123	0.31
21	68	112	0.53
40	16	48	0.58
45	23	69	0.89

* Androgen was administered daily by subcutaneous injections into the mother during pregnancy. The amount reported represents the cumulative total for androgen given from day 30 to 50 of the 68-day gestation period.

castrated at 5 days of age or earlier, the males were able to display markedly female sex behavior in adulthood when given female hormone replacement therapy; the extent of this ability was strictly proportional to the age at the time of castration. (Female behavior was scored according to the copulatory quotient, i.e., the number of times an animal displays the female lordosis pattern in response to mounting by a vigorous male.) The castrated males were tested also for their ability to display masculine behavior, i.e., intromission and ejaculation, when given androgen replacement therapy in adulthood. Those castrated from 1 to 5 days after birth, i.e., during the critical period, showed the greatest insensitivity to androgen, being markedly deficient in male sexual behavior as adults. Those castrated at 10 days of age or later, however, were relatively normal. Castration following the completion of the critical period of sexual differentiation does not have these same effects. Male guinea pigs castrated at birth show normal male sexual behavior when given androgen in adulthood, and male rhesus monkeys castrated at 3 months of age show no deficiency in the display of masculine behavioral patterns. Goldfoot and Goy* have recently shown that chemical antiandrogens, such as cyproterone acetate, administered during the critical period in the guinea pig, have effects similar to those of early castration in the rat.

*Unpublished studies.

Influence of Androgen on Development of Sex-Related Social Behavior

The studies so far described have been of the influence of early androgens on later, adult, hormone-dependent behavior. Goy (1966) has also studied the effects of early androgen on relatively hormone-independent behavior such as the nonreproductive social interaction of monkeys, whose social habit hierarchy normally differs significantly between the sexes (Harlow, 1965). Goy studied pseudohermaphrodite rhesus monkeys, i.e., genetic females given varying doses of androgen from 39 to 90 days prenatally which caused complete remodeling of all external genital structures into the male form while the internal genitalia remained female. He found that many of their behavioral patterns are critically dependent upon the specific duration and dosage of the administered androgen. For example, in one set of experiments, the animals were left with their mothers for the first 4 months of life, then were placed in individual cages and allowed contact with other animals only during a limited daily observation period. At that time, the animals would be grouped in peer groups of from four to six, similar in age and size. Daily observations were made of their social behavior for about 5 months, particularly of four behavioral patterns characteristically displayed more by males than females: (1) social threat or gape, (2) play initiation, (3) rough-and-tumble play, and (4) pursuit play. The behavior of pseudohermaphrodites given either high or low doses of prenatal androgen was compared with that of normal males, normal females, and genetic males also exposed to prenatal androgen. For all four behavioral patterns, pseudohermaphrodites which had received high and intermediate dosages behaved like normal males, whereas those which had received low dosages behaved like normal females (see Figure 1 on the following page). Androgen-pretreated males were not super males; rather, their behavior was like that of normal males. In all cases, for any given individual, frequency scores for all four behavioral patterns were highly correlated.

To Goy and his associates, behavioral masculinity or femininity of an individual can be thought of as a constellation of highly diversified behavioral characteristics, all of which are subject to the influence of androgenic stimulation very early in development, at a time when there is no possibility of displaying that behavior.

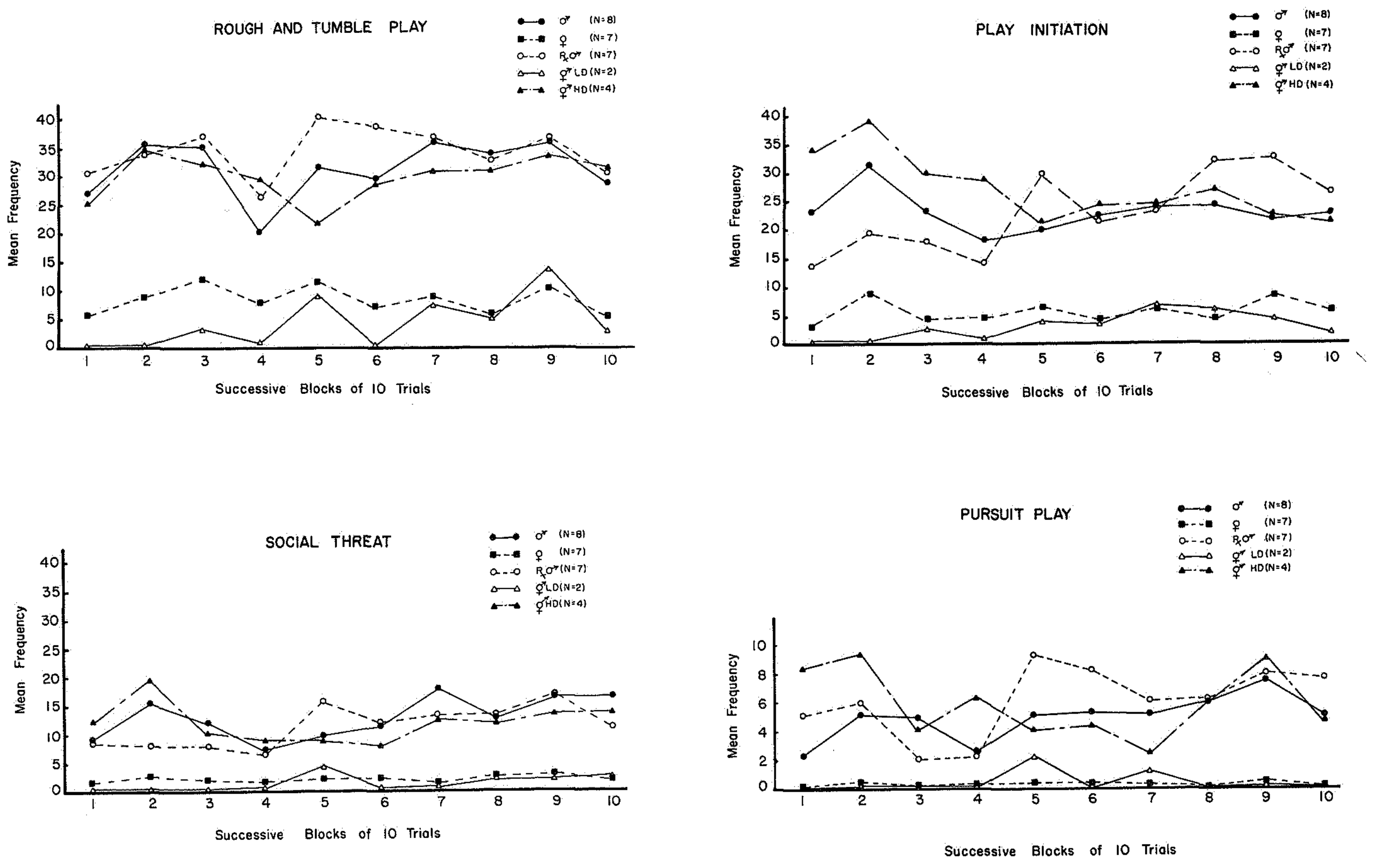

Figure 1. Frequency of performance of four types of juvenile social behavior (rough and tumble play, play initiation, social threat, and pursuit play) by rhesus monkeys: control males (♂), control females (♀), and pseudohermaphroditic females (⚥) given high (HD) or low (LD) dosages of testosterone prenatally, and males treated with comparable amounts of testosterone (Rx♂). [Goy]

IV. DRIVE AND BRAIN MECHANISMS

Any theory of drive as a force behind the generation of focussed behavior must involve an understanding of the degree to which the different drives can be separated from one another in their biological mechanisms. Thus this section on drive and brain mechanisms can be considered not only as a further elaboration of the preceding section but also as an exploration into the specific mechanisms underlying behavior directed toward different goals and the satisfaction of different need systems.

Roberts is primarily concerned with the motivational and species-typical behavior patterns that can be elicited from different parts of the hypothalamus and preoptic region. He emphasizes that many of these behavior patterns are not automatic motor responses, but possess many of the properties of normal motivational behavior. He presents evidence that the hypothalamus has an integrating role, i.e., it sends a divergent output to separate mechanisms for different elements of response patterns. Teitelbaum emphasizes the importance of understanding the neurophysiological basis of feeding behavior as well as its relationship to learning and reinforcement since it is often used as a model for drive. He thinks that there is a tendency to oversimplify some of the basic processes underlying the regulation of feeding and states that the problem must be regarded with an appropriate level of complexity before a proper analysis can be made. Grossman continues the discussion of the role of feeding and drinking centers in the brain but emphasizes those centers involved in feeding and drinking that are outside the hypothalamus which serve as a distributing center for sensory information. Thus he argues against the notion of a single center for any basic drive and proposes that we think in terms of distributed mechanisms.

A. CENTRAL NERVOUS SYSTEM: SPECIES-SPECIFIC BEHAVIOR AND DRIVE: W. W. ROBERTS

Roberts and his colleagues (1967) have been studying hypothalamic mechanisms controlling the motivational behavior of the opossum (*Didelphis virginiana*) utilizing electrical stimulation techniques. The opossum was chosen for study because its phylogenetic position as an extremely unspecialized primitive mammal suggested that its hypothalamic mechanisms might be more clear-cut and less dependent upon complex cortical functions than those of higher species.

Behavioral Patterns Elicited by Stimulation

In each of 53 animals, three multiple electrodes of four wires each were implanted, permitting stimulation of 12 different points in each animal. (Details of the stimulus parameters and electrode sites have been published (Roberts et al., 1967).) The animals were tested in an observation box containing different goal objects; for example, food, water, a stuffed toy dog that served as an acceptable female surrogate for the male-type mating response, a live rat, a log, simulated nesting materials, wood to gnaw, and, occasionally, receptive live females, opossum pups, and a variety of inanimate objects. When unstimulated, the animals usually ignored the test objects, but, when stimulated in the hypothalamus at suprathreshold voltages of 2 to 7 v, they interacted in a variety of behavioral patterns, depending upon the specific area stimulated. The responses included male mating, biting attack, defensive threat, eating, grooming, yawning, and several types of escape-like or exploratory locomotion. Each response pattern consisted of three to seven separable but correlated response elements. Whereas only 20 percent of the points evoked complete response syndromes with all elements, 80 percent elicited subsets that varied in completeness and in the individual elements included. For an example, see Figure 2 which shows the different combinations of the elements of the defensive threat pattern that were evoked by different electrodes. Despite this variation in completeness, Roberts concluded on the basis of a statistical analysis that the patterns are genuine clusters since the correlations between elements assigned to a given response pattern are high whereas those between elements of different patterns are low. He showed the following elicited response patterns in a film (Roberts, 1968).

1. *Male mating behavior* from both male and female opossums was elicited by stimulation of the medial preoptic area. The male mating pattern consisted of the following elements: (*a*) mounting, (*b*) rubbing the muzzle in the partner's fur, (*c*) relaxing on the partner, (*d*) giving the mating bite, (*e*) pulling the partner over on its side, (*f*) penile erection (in males), and (*g*) mating click. Stimulated male opossums given a toy stuffed dog as a surrogate sexual partner behaved in a manner almost identical to those given spayed females artificially brought into heat with hormones. Penile erection was relatively rare, elicited by only five

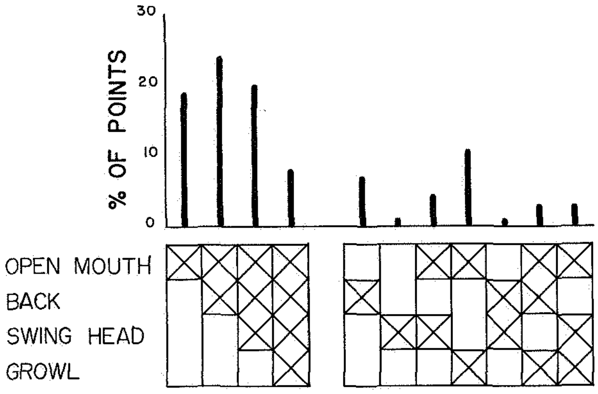

Figure 2. Combinations of threat elements. [Roberts]

electrodes, and then only at the beginning of the test session. Although erection could be elicited repeatedly on different days, it did not have the automatic quality of the other components. Intromission was never observed in the tests with live females. When presented with a fur mat instead of the stuffed dog, opossums posed, rubbed, and relaxed on it, indicating that the three-dimensional humped shape of the dog was not essential, but that the soft tactile stimulus of the fur was probably the critical factor. If the mat was then drawn away from the animal, it would attempt to pursue and cling to it. It would react similarly if the stuffed dog was withdrawn. If placed in a maze with the dog out of sight in one arm, it would learn to make the correct turn toward the dog over a series of trials.

2. *Biting attack* of a live rat could be elicited by stimulation of an elongated zone in the dorsal hypothalamus, extending from the posterior hypothalamus to the paramedial preoptic area. The speed, intensity, and effectiveness of this overt aggressive behavior, which was never displayed spontaneously without stimulation in the testing box, were dependent upon the intensity of stimulation, although Roberts stressed that no evidence was found for the close correlation that von Holst and von Saint Paul (1963) reported between the current thresholds and normal temporal

order of the different elements of centrally elicited response patterns in chickens. The biting attack pattern consisted of the following four elements: (*a*) *Seizing*—upon presentation of a rat, the opossum first bites its most accessible part. (*b*) The opossum then engages in *head tossing*, rapidly swinging its head and the prey in a figure eight. This rather complex species-specific behavior continues only as long as the prey struggles, and is omitted from the pattern if the prey is anesthetized or dead at the start of the attack. (*c*) *Kill-biting* occurs between bursts of head tossing as long as the prey continues to move. It consists of repeated brief bites that are shifted over the body. (*d*) When the prey stops struggling, the opossum begins *crunching-biting*, changing its grip to the head and biting it repeatedly and rhythmically. The response is not evoked by shock to the feet, which makes it unlikely that it is a secondary response to a centrally elicited pain sensation. Similar behavior can be elicited in cats stimulated in a similar area. In fact, stimulated cats will even learn a maze to obtain a rat they then can attack (Roberts and Kiess, 1964).

3. *Defensive threat* was elicited by stimulation of the ventral and medial hypothalamus. It was not obtainable from the preoptic area. The response consisted of (*a*) opening the mouth, (*b*) growling, (*c*) swinging the head from side to side, and (*d*) backing up.

4. *Eating behavior* was elicited from two zones, the preoptic region, where Andersson and Larsson (1961) have produced eating by local cooling, and a more posterior medial-lateral position between the fornix and the mammillothalamic tract. The latter region corresponds closely to the eating region in the cat and the rat (Brugger, 1943; Miller, 1960). The eating behavior resembled normal eating, and the opossum used its paws to push into its mouth food that had fallen out.

5. *Grooming behavior* was obtained in the medial preoptic region and anterior hypothalamus. The pattern was made up of (*a*) licking the forepaws, (*b*) using the wetted forepaws to wash the face, (*c*) licking the hindpaws, and (*d*) using the wet hindpaws to comb the cheek, scratch the ear, and comb the shoulder. Occasionally, the tail and anogenital region were licked, but the first four responses were the most common. Yawning was sometimes seen in association with grooming, although grooming occurred more often without it. Localized warming of the same area elicited washing without yawning (Roberts et al., in press). Roberts therefore considered the electrical stimulation to be acting as a non-specific excitant.

6. *Locomotor behavior, sniffing, and looking around* were elicited throughout most of the hypothalamus, except in the ventromedial region where the backing and crouching components of the defensive threat interfered with forward locomotion. Locomotion took various forms: exploratory behavior, sheer rapid locomotion, and escape behavior. Of the last form, two subtypes were distinguishable: (*a*) upward head orientation at low voltages and climbing upwards at higher voltages; (*b*) after general exploration, escape activity focussed toward the one transparent side of the box. The upward climbing was obtained with posterior stimulation while the transparent-window orientation was obtained by stimulation further forward.

On the basis of histologic studies of the stimulated points, Roberts concluded that: (1) The response patterns were elicited from relatively specific and differentiated zones that overlap partially in some regions (Figures 3 and 4). (2) The most complete and the most persistent responses were elicited near the center of the effective zones, with greater fragmentation when the points were near the periphery. (3) The anatomical locations of the effective zones for several response patterns were similar to those in higher species, suggesting phylogenetic continuity in the mechanisms from early mammals to modern carnivores and rodents. This was especially marked for biting attack, defensive threat, and the eating zone (Roberts and Kiess, 1964; Brugger, 1943; Miller, 1960). (4) There was no evidence to support a division of the behavior mechanisms into Hess's (1957) anterior trophotropic and posterior ergotropic zones.

Resemblance to Normal Motivational Behavior

These centrally aroused behaviors (see above) differ from stereotyped motor responses and, instead, resemble normal motivational behavior in the following respects (Roberts et al., 1967; Roberts and Kiess, 1964; Roberts and Carey, 1965).

1. They are complex combinations of three to seven response elements that form adaptive response patterns similar to those observed in spontaneous behavior.

2. The responses that involve environmental goal objects (mating, attack, and eating) are not performed in the absence of their objects, indicating that the stimulation was not eliciting the overt behavior directly or automatically, but was enhancing the capacity of the goal object stimuli to elicit the responses. Thus, these centrally elicited response

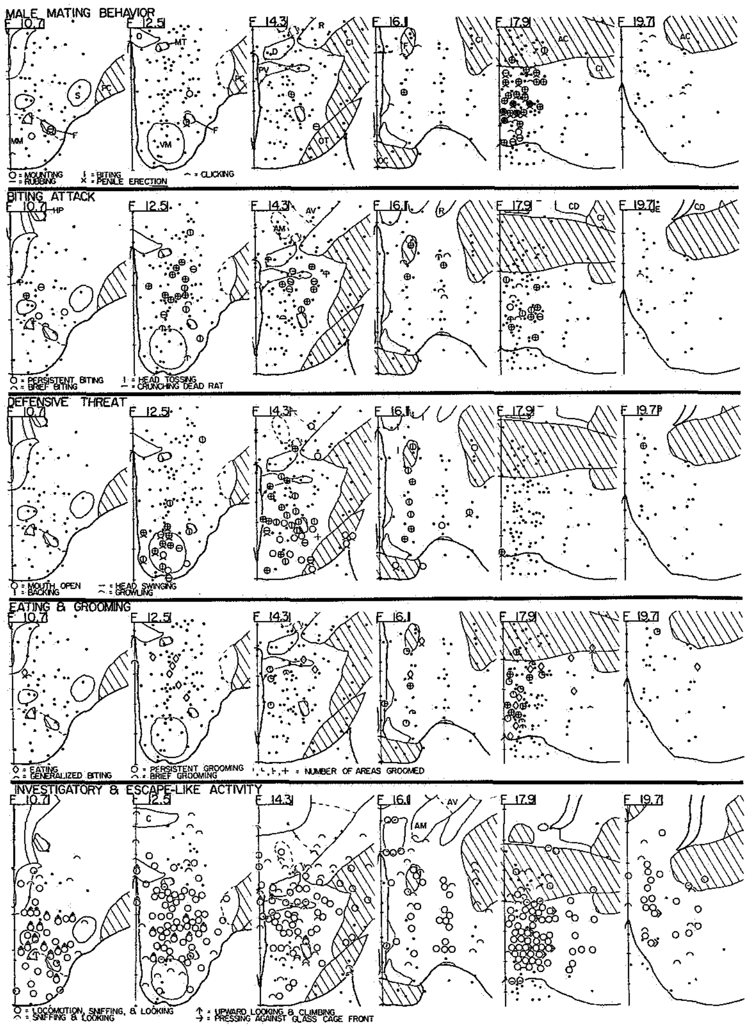

Figure 3. Locations of positive and negative points for motivational and species-typical responses plotted on frontal plane diagrams of the hypothalamus and preoptic area located 10.7-19.7 mm anterior to the interaural axis. Negative points are indicated by small solid circles. Plane F 10.7 corresponds to Bodian's (1939) Figure 10; F 12.5 is slightly anterior to Figure 8; F 14.3 corresponds to Figure 5; and F 16.1 is slightly anterior to Figure 3. AC, commissura anterior; AM, nucleus anterior medialis thalami; AV, nucleus anterior ventralis thalami; C, nucleus centralis; CD, nucleus caudatus; CI, capsula interna; D, nucleus dorsalis hypothalami; F, columna fornicis; H, hippocampus; HA, nucleus habenularis; HC, commissura hippocampi; HP, tractus habenulopeduncularis; LH, nucleus lateralis hypothalami; MM, corpus mammillare; MT, tractus mammillothalamicus; OC, chiasma opticum; OT, tractus opticus; PC, pedunculus cerebri; PV, nucleus filiformis pars paraventricularis; R, nucleus reticularis; S, nucleus subthalamicus; SE, area septalis; SM, stria medullaris; TH, thalamus; VM, nucleus ventromedialis hypothalami. [Roberts et al., 1967]

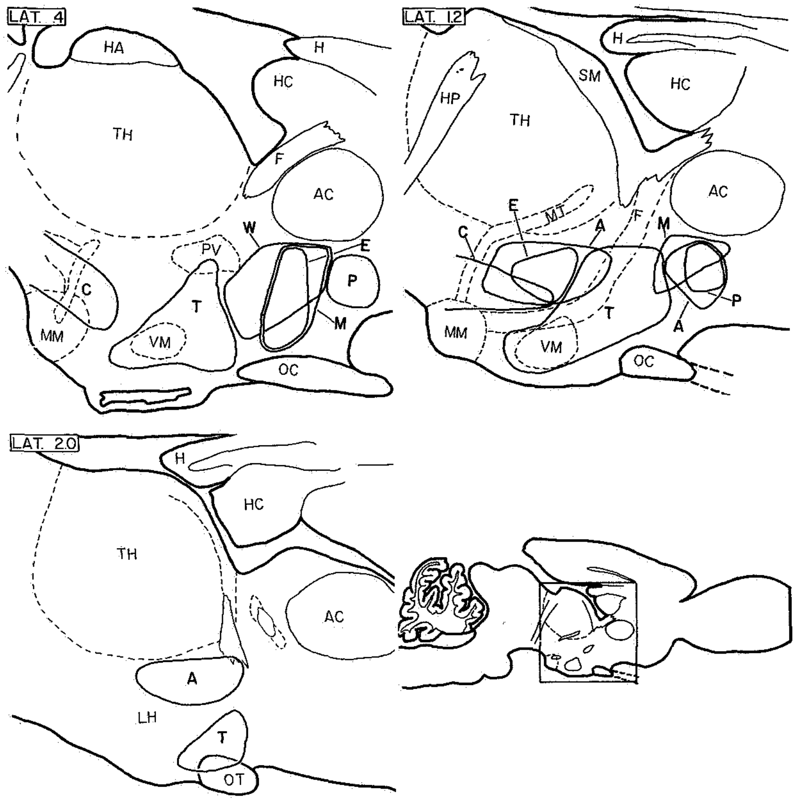

Figure 4. The principal zones from which the motivational responses were elicited projected onto sagittal diagrams located 0.4, 1.2, and 2.0 mm lateral to the midline. Lower right diagram shows a complete section 1.2 mm from the midline with a square indicating the portion enlarged in the other diagrams. Plane Lat. 0.4 corresponds to Bodian's (1939) Figure 17; Lat. 1.2 is slightly medial to Figure 15; and Lat. 2.0 corresponds to Figure 13. Response-zone abbreviations: A, biting attack; C, upward looking and climbing; E, eating; W, grooming; M, male mating behavior; P, pressing against glass side of cage; T, defensive threat. For structure abbreviations, see Figure 2. [Roberts et al., 1967]

tendencies meet Hinde's definition of "drive states" as "changes in responsiveness to a constant stimulus situation" in regard to species-typical consummatory responses.

3. When the goal objects are present, the animals respond to them in adaptive ways. Different response elements are elicited or directed by different stimulus aspects of the objects. When the stimuli of the goal object also elicit natural behavior tendencies, these are integrated with the centrally aroused tendencies, as when the fear aroused by an aggressive rat or a female produces hesitation and delay in the attack and mating.

4. The opportunity to perform many of these centrally aroused responses is positively reinforcing, and thus capable of producing learning of new habits. This has been demonstrated for several different responses in several species (Roberts and Kiess, 1964; Roberts and Carey, 1965; Roberts et al., 1967). This property meets Teitelbaum's reinforcement criterion of "drive states."

Roberts drew certain inferences concerning the nature of the underlying neural mechanisms from the work described above.

1. In the cases of the responses that were not performed if their goal objects were absent (mating, attack, and eating), it can be concluded that the effective hypothalamic zones are not part of the motor pathways, nor of the sensory paths normally excited by the goal objects. Instead, the hypothalamic cells directly excited by the electrical current appear to exert a facilitatory influence on sensorimotor mechanisms located elsewhere. A similar facilitatory action may characterize some of the other centrally aroused responses, but with the critical environmental stimuli provided by the animal's own body, as in grooming, or by the general environment, as in the exploratory and escape-like activity.

2. The output of the hypothalamus does not pass through a general integrating mechanism for complete response patterns, since most of the electrodes elicited incomplete patterns. Instead, it appears to send divergent projections to separate sensorimotor or reflex-like mechanisms for different response elements.

3. Thus, there appear to be relatively few, if any, individual cells in the hypothalamus that make general decisions concerning complete response patterns. However, the complete bilateral areas, which contain at least 6 to 8 times as many cells as the maximum directly excited by the stimulative current, may exert such a general modulating or controlling function when acted upon as a whole by humoral or neural input.

4. The male mating pattern was elicited in both males and females with indistinguishable threshold, completeness, frequency, intensity, and anatomical localization, indicating that both sexes possess fairly complete brain mechanisms for the male sexual pattern. Hence, infantile androgens are unnecessary for the gross ontogenetic formation of the cells and connections that constitute the response mechanism, but must exert their critical influence (see the presentation, page 31, and references of Goy) on more subtle or specific aspects, such as the sensitivity of the mechanisms to hormones or the development of neural input.

B. CAN STUDIES OF FEEDING CENTERS PROVIDE A MODEL FOR DRIVE?: P. TEITELBAUM

Since feeding behavior and its regulation are often used as a model of drive in general, it is particularly important that its neurophysiological basis be well understood. To Teitelbaum, "understanding" implies the Cartesian process of breaking a phenomenon into simpler units, then reconstructing it. In his opinion, the neurophysiological conceptualization of feeding behavior has tended to overdo the process of simplification by assuming the existence of simple reflex automatisms involved in food intake (in a manner analogous to the homeostatic regulation of acid-base properties of blood or of blood sugar) without considering that the behavioral regulation of food intake involves integration of these automatisms with other variables that make them less automatic (Teitelbaum, 1967a).

From Sherrington to Skinner

As Teitelbaum put the problem: "How does the nervous system get from Sherrington to Skinner?" Reflex mechanisms do exist that are sufficient to control food intake. For example, infant mammals suck reflexively and ingest enough food to gain weight and grow. But is this simple form of behavior the appropriate model to account for the regulation of food intake in the adult mammal? How can one evaluate the degree of complexity which must be invoked to account for the behavior of animals and humans? This question was answered long ago by Descartes, when faced with apparently motivated behavior in animals as well as man. In order to avoid having to endow animals with souls, Descartes postulated the reflex, the automatic, built-in nervous connection between stimulus and response, which enabled animals to respond without consciousness, purpose, pleasure, or pain.

Clearly, when an act is a completely automatic consequence of a stimulus, there is no need to speak of motivation. As long as a fixed, built-in relation exists between a stimulus and a response, there is no logical justification for inferring the additional existence of a central motivational state underlying that response to the stimulus. Such a state may exist, but there is no proof of it. Only when one can be sure that a central motivational state exists apart from the stimulus and the response, can one speak of motivated behavior.

To infer motivation then, one needs only to break the fixed connection between stimulus and response. The learning process enables one to do so. Consider a rat pressing a bar for food. How does one train an animal to perform such an operant act? One arbitrarily chooses almost any act from the animal's repertoire and reinforces it (i.e., increase the animal's tendency to perform it) with food, water, or whatever else the animal will work to obtain. One usually trains a rat to press a bar or a pigeon to peck a key, but one could just as readily train either animal to dance around the cage for the food if so desired. Water could be used for thirsty animals, or the termination or avoidance of painful electric shock be employed to reward an animal for performing the appropriate act. Light is usually used to signal the delivery of a pellet of food, but a tone or a buzzer or any other stimulus the animal can detect can be used. Thus, unlike many instinctive responses, the bar-pressing response can be separated from the animal's internal state. In effect, in any operant situation, the stimulus, the response, and the reinforcement are completely arbitrary. Not one of them bears any biologically built-in, fixed connection to the others. One arranges the experimental situations so that the response produces the reward and the animal *learns* the connection between them.

Once having learned this relationship, the animal reveals its motivation by working to obtain the reinforcement. This is what all operant conditioning situations have in common: the animal's motivation to obtain reinforcement. By taking advantage of the animal's capacity to learn, and by training it to respond with an arbitrary act to obtain a given reinforcement, one can be sure the animal is motivated. If an operant occurs, motivation exists (Teitelbaum, 1966).

Consider the behavior of a blowfly which eats and thrives on sugar solutions. The longer it has been without food, the lower the sugar concentration it accepts, and the more of a given concentration it will eat. Thus, food deprivation facilitates its approach to, and ingestion of, food. This has the appearance of motivated behavior; but, if one demands independent proof of motivation as a central state existing independently of built-in nervous reflexes, one finds that no one is yet able to say that the fly is hungry, i.e., that it wants to obtain food. As far as anyone has been able to determine, the act of eating in the blowfly is completely reflexive. (No one has yet been able to train a fly to perform an operant for food.) Such a state can be called a drive state. A hunger drive exists: the fly's approach to, and acceptance of, food are increased *automatically*, in contrast to motivated behavior in which a central state apart from reflexes can be inferred each time the animal uses an operant act to obtain food.

With respect to the regulation of feeding in adult mammals, a great deal of evidence now suggests that such regulations are behavioral and not reflexive. They are accompanied by motivated operant acts and are subject to the same laws of motivation and experience that affect all operant behavior (Teitelbaum, 1961; Teitelbaum and Epstein, 1962; Hoebel and Teitelbaum, 1962).

Models of a Multiple Control System

In addition to the problem of ascertaining the appropriate level of complexity, the analysis of feeding behavior raises the problem of studying a multiple control system. Such a system, designed to be homeostatic (i.e., prevent change), can foil any experimental analysis, since as soon as one aspect of the system is varied the whole system changes and counteracts it; hence, no total change in intake occurs. One then is faced with the problem of distinguishing correlation from causality.

To cope with this problem, Teitelbaum has chosen to study those marked derangements in feeding that are produced by damaging the hypothalamus (Teitelbaum, 1961; Teitelbaum and Epstein, 1962; Hoebel and Teitelbaum, 1962; Teitelbaum and Cytawa, 1965). He assumes that any control system that becomes defective as a result of such damage is likely to be causally related to the regulation of food intake. For example, it is well known that lesion or stimulation in different parts of the hypothalamus affects food intake. Although these hypothalamic areas are parts of much larger feeding systems which involve many parts of the brain, it is assumed by many that integration of food intake is accomplished by the activity of hypothalamic mechanisms whose activity reflects the action of the entire system. Thus, in the lateral hypothalamus, any operation that decreases activity (i.e., destruction, anesthetization) decreases feeding, whereas anything that increases activity increases feeding. By contrast, the medial hypothalamus has a mechanism which acts in an opposite way: any operation that decreases its activity increases eating, whereas anything that increases its activity decreases eating. Presumably, the medial system acts to inhibit the lateral system. Various bodily states like blood sugar and gastric distension are known to affect the activity of these hypothalamic systems and others, as body temperature and body weight are presumed to do so. By using the simple reflex as a model, it is clearly possible to view these hypothalamic systems as control mechanisms similar to the negative feedback loops in a multiple control system. Since mathematical control system theory is now well-developed, we are offered the exciting prospect of a mathematical description of the homeostatic mechanisms involved in the regulation of food intake (Yamamoto and Brobeck, 1965). Such a model, however, is oversimplified because it cannot incorporate an operant into the regulatory process. That is to say, this model does not help us to understand how an arbitrary operant response becomes incorporated into the regulatory process (Teitelbaum, 1967a). For instance, why is taste important in determining *how much* we eat? Our work with hypothalamus-damaged animals shows clearly that, contrary to what would be expected from a homeostatic control system based on reflex mechanisms, taste is literally essential for the adequate regulation of food intake. Taste is a powerful reinforcer—a psychic energizer that maintains the operant behavior involved in the regulation of food intake (Teitelbaum, 1961; Teitelbaum and Epstein; 1962; Teitelbaum, 1966; Teitelbaum, 1967b).

Lateral Hypothalamic Syndrome: Recovery Parallels Development of Feeding

Teitelbaum next discussed his work with Epstein (1962) on feeding, in which they analyzed the recovery process after lateral hypothalamic lesions. Initially, animals with such lesions will neither eat food nor drink water. If tube fed and thus prevented from starving to death, they will first accept palatable foods, then drink water, and finally eat ordinary food. The stages, in greater detail, occur as follows:

1. *Aphagia and adipsia.* The animal eats and drinks nothing and will die unless provided with food and fluids by intragastric feedings.

2. *Anorexia and adipsia.* Later, the animal begins to take palatable foods, but not enough, and does not take water.

3. *Adipsia produces, in turn, dehydration and aphagia.* Still later, postoperatively, there is a sudden increase in the animal's intake of the liquid diet. The animal can regulate its caloric intake, eating more if the caloric content is reduced. It can be weaned to a sweet non-nutritive fluid (saccharin) and will then also eat dry food. It will not, however, drink water. Therefore, if offered only water and dry food, it will die as dehydration leads to lack of feeding. If the sweet fluid is replaced, or water is intubed, the animal will continue to eat. Thus, water is responsible for the animal's lack of feeding.

4. *Eventually, the animal drinks water and eats ordinary food and*

regulates, but a deficiency still exists. Normally an animal can be made to eat either by lowering its blood sugar (i.e., administering insulin) or by putting it in the cold. In recovered, lateral hypothalamus-damaged animals, although their thermostatic control is normal, their glucostatic regulation is not: a cold environment increases their eating, but hypoglycemia fails to elicit eating. Further, these animals have deficits in their drinking: they only drink prandially, i.e., when eating. If deprived of food, they will not drink. They are also very sensitive to the taste of food and will stop eating when the food has been adulterated with quinine long before a normal animal would.

Is there any pattern to these stages that is related to a nervous system function? Teitelbaum, in collaboration with his co-workers, Cheng and Rozin (1968), suggested that there is a parallel between the lateral hypothalamic syndrome just described and the early development of feeding in the rat (Teitelbaum, 1967a,b). The normal infant animal takes liquid food, but does not respond to thirst. This provocative parallel is difficult to study, however, since the earliest age at which a rat can eat voluntarily is about 14 days, and by 21 days it is weaned and regulates perfectly well. Development is so rapid that a deficit may disappear before it can be demonstrated. In order to study the development of feeding behavior in greater detail, Teitelbaum and his co-workers performed thyroidectomies on 1-day-old rats, which slowed down their development considerably. Although the rats were weaned at the normal time, they weighed between 10 and 45 gm instead of the normal 55 gm. They showed all the stages of the lateral hypothalamic syndrome in proportion to their size at weaning. Thus a 15-gm animal is completely aphagic and adipsic (although it sucks reflexively). A 25-gm animal would only lick and nibble at food no matter how wet and palatable; it showed anorexia and adipsia and would typically die. A 35-gm animal would take a liquid diet and regulate its caloric intake. If given merely dry food and water, however, it would not drink water or eat dry food and would die. A 45-gm animal would eat and drink apparently normally, but actually its drinking would be completely prandial. It would not respond to dehydration by osmotic injection and would be very finicky. Like the "recovered" animal with lateral hypothalamic lesions, it would respond to cold but not to insulin.

Teitelbaum noted that the parallel is perfect and concluded that as far as the nervous system is concerned, "recovery recapitulates ontogeny." It was suggested that this may reflect a basic law of recovery of function in general.

C. DRIVE CENTERS AND A DRIVE STATE: S. P. GROSSMAN

Grossman discussed two basic propositions concerning the neural organization of drive:

1. *Basic motivational processes such as hunger or thirst do not seem to be regulated by autonomous hypothalamic "centers" but by complex pathways which include much, if not all, of the limbic system and associated subcortical nuclei.*
2. *All behavior is significantly influenced by a nonspecific motivational state which appears to reflect the response of the reticular formation (RF) to the aggregate input to the brain from external as well as internal receptors.*

Extrahypothalamic Contributions to Regulation of Specific Drive States

It has been traditionally assumed that specific drive states reflect neural activity in specific hypothalamic "centers." The principal evidence for this notion is that: (1) Damage to the lateral hypothalamus produces temporary aphagia and apparently permanent adipsia (Anand and Brobeck, 1951; Teitelbaum, 1961; Teitelbaum and Stellar, 1954); electrical (Greer, 1955; Miller, 1957) or chemical (Andersson, 1953; Grossman, 1960) stimulation of this region elicits feeding or drinking in sated animals. (2) Lesions (Hetherington and Ranson, 1940) or electrical stimulation (Anand and Dua, 1955) of the adjacent ventromedial area produces apparently opposite effects. (3) Sexual motivation also appears to be related to hypothalamic mechanisms. Damage to the anterior hypothalamus of most species produces complete and permanent anestrus without interfering with relevant hormonal functions. A more posterior, medially located hormonal mechanism also influences sexual arousal. (4) Early studies of sleep and wakefulness (Nauta, 1946; Ranson, 1939) suggest a similarly specific hypothalamic representation of drive states related to activity or sleep.

The hypothalamus also contains "centers" which appear to be related to the organism's response to noxious stimulation (Wheatley, 1944), but it has been generally accepted that more complex pathways, involving most of the limbic system and related subcortical pathways, contribute to the regulation of "aversive" drive states (Papez, 1937; MacLean, 1949). Grossman suggested that the neural mechanisms which are related to appetitive drives may be similarly distributed.

The principal reason for the selection of the hypothalamus as *the* anatomical substrate of motivational mechanisms is the fact that the destruction of relatively small amounts of hypothalamic tissue seems to have drastic effects on specific drives whereas lesions in other parts of the brain typically produce only minor changes. However, the research of the past decade has shown that this is not as unique as it once seemed.

Hyperphagia and obesity have been reported following damage to portions of the temporal lobe in monkeys (Fulton, 1951), cats (Green et al., 1957), and rats (Morgane and Kosman, 1959a,b). Hypophagia or aphagia have also been observed following restricted damage to some aspects of the amygdaloid nuclei (Green et al., 1957; Koikegami et al., 1955, 1958). A more detailed analysis of the temporal lobe contribution (Grossman and Grossman, 1963) has shown that even very small lesions in the posterior amygdala increase both food and water intake in rats. Similar lesions in the anterior amygdala also increase food intake but reduce water consumption. Electrical stimulation of these areas produces opposite effects. Microinjection of drugs which elicit feeding or drinking behavior when applied to the lateral hypothalamus (Grossman, 1960, 1962a,b) did not evoke feeding or drinking in sated rats but significantly facilitated food or water intake in deprived animals (Grossman, 1964a). Subsequent research (Booth, 1967; Coury, 1967; Fisher and Coury, 1964; Grossman, 1964b, 1967; Miller, 1965; Miller et al., 1964) has shown that feeding or drinking can be elicited or modified by the injection of adrenergic or cholinergic drugs into a number of "limbic" structures and that much more marked effects can be obtained from some of these sites than from the lateral hypothalamus. (See Stein's discussion, pp. 73-84.)

It is not yet clear how extensive are the feeding and drinking circuits and whether they continue a parallel course through all portions of the central nervous system. It is becoming increasingly obvious, however, that most, if not all, of the components of these complex systems contribute unique influences to the initiation and/or cessation of motivational processes and do not merely represent elements of "series" circuits.

Fisher and Coury (1962) reported some years ago that essentially all aspects of the "limbic" circuit (hippocampus, cingulate gyrus, septal area, diagonal band of Broca, thalamus, hypothalamus, and mammillary region) which Papez (1937) and others (MacLean, 1949) had implicated in the regulation of the organism's response to noxious sitmulation are part of a cholinergic "thirst" circuit. Recent work reported by Coury (1967) suggests that the adrenergic "hunger" circuit may follow a similar trajectory. Reports on the effects of electrical stimulation of various limbic sites on feeding and drinking behavior (Robinson, 1964) confirm this interpretation. Lesions in the limbic system (Ehrlich, 1963; Lubar, 1968; Peretz, 1963) have typically produced only small changes in food or water intake, but this may merely reflect the diffuseness of the neural pathways. Matters are complicated by a recent report by Booth (1967) who failed to observe significant feeding in response to adrenergic stimulation of many aspects of the limbic circuit but did report rather marked effects following similar injections into the distribution field of the stria medullaris (lateral hypothalamus, substantia innominata, nucleus accumbens septi, lateral septum, rostral thalamus, and habenula). No effects on water intake were reported and the possibility must be entertained that the feeding and drinking "circuits" do not run as parallel a course as has been assumed in recent years.

Recent lesion studies have implicated another pathway which may contribute to the regulation of food as well as water intake. Morgane (1961) reported several years ago that lesions in the tip of the globus pallidus produced apparently permanent aphagia and adipsia. Gold (1967) has more recently shown that damage to the internal capsule may itself produce similar results and suggested that the apparent importance of the lateral hypothalamus in the mediation of hunger and thirst might be due to its strategic location in the path of corticifugal fiber systems from the frontal lobe as well as pallidofugal fibers from the globus pallidus. His interpretations appear supported by the demonstration that relatively small lesions in the midbrain tegmentum (where many of these fibers terminate) also produce complete and long-term aphagia and adipsia.

The thirst circuit may also extend into the subcommissural organ of the brainstem. Lesions in this area have been reported to result in hypodipsia or adipsia whereas electrical stimulation increases water intake (Gilbert, 1956). Some evidence has been adduced which suggests that this region may contain volume receptors which may exert a unique influence on water intake (Gilbert and Glaser, 1961).

The results of chemical stimulation studies (Booth, 1967; Coury, 1967; Fisher and Coury, 1964; Grossman, 1960, 1962a,b) have emphasized that the distribution of the neural pathways which regulate food and water intake is, even at the level of the hypothalamus, not nearly as discrete as the "center" notion leads one to expect. A similar conclusion is suggested by studies which have shown that food (Maire, 1956; Morgane, 1961) as well as water intake (Bernardis et al., 1963; Maire, 1956;

Stevenson et al., 1964) is affected by lesions or electrical stimulation in various parts of the hypothalamus.

It is, of course, possible that all of the extrahypothalamic and diffuse hypothalamic portions of the system are afferent to a hypothalamic "center," but the evidence for such an interpretation is not very compelling. It may be more profitable, at this time, to consider the possibility that feeding and drinking behavior may be regulated by a more complex neural circuit.

It may be that the receptor organs which mediate drive stimulation in the case of the appetitive drives may be located in the hypothalamic region and that the rest of the limbic system relates to these receptor organs in much the same way that neocortical "projection areas" relate to other sensory organs. It has, of course, been known for some time that the hypothalamus contains cells which respond apparently specifically to chemical as well as neural signals which are significantly related to the organism's energy and fluid balance.

Andersson and his colleague (Andersson, 1952; Andersson and McCann, 1955) demonstrated that water intake as well as antidiuretic hormone secretion is regulated by osmoreceptors which react to changes in the osmotic pressure of the hypothalamic blood supply. Sawyer and his associate (Sawyer, 1956, 1957; Sawyer and Robinson, 1956) and Fisher (1956) have presented evidence suggesting that the hypothalamus also contains cells which regulate sexual reactivity in accordance with the local level or concentration of sex hormones. Jean Mayer's "glucostatic" hypothesis of hunger is not as directly supported, but evidence for a hypothalamic "glucostat" can be adduced from experiments showing that goldthioglucose concentrates selectively in the ventromedial hypothalamus and thereby induces hyperphagia and obesity (Marshall et al., 1955). The hypothesis also derives a measure of support from experiments showing glucosensitive neurons in the medial and lateral hypothalamus (Anand et al., 1964).

These observations do not, of course, prove that the hypothalamic portion of the feeding and drinking systems must have only sensory functions. It is quite possible that some, or even all, relevant integrative processes take place here as well, but there is no compelling reason to make such assumptions. The paucity of sensory afferents to the hypothalamic "centers" as well as the plentitude of diffuse cortical representations indicates instead that it may be more fruitful to explore alternative possibilities.

Influence of Nonspecific Motivational States of Reticular Origin

The concept of generalized drive is not new to physiology or psychology. Pavlov's (1927) "orienting reflex" and Cannon's (1929) "generalized energy" are some examples of earlier physiological conceptualizations. Duffy (1934) introduced the notion to psychology to account for changes in performance which did not appear to be due to variations in specific drive states. Interest in such a mechanism was revived more recently when the work of Magoun and his associates (Lindsley et al., 1949; Moruzzi and Magoun, 1949) demonstrated an anatomical substrate for physiological processes (EEG, arousal, sensory processing, tonic influences on motor systems) which may be related to the psychological concept of generalized drive.

Largely on the basis of these early observations, Lindsley (1951) proposed that the problem of motivation could be reduced to an innate tendency of the organism to maintain a level of activation or arousal which supports a minimal level of neural firing but is not sufficiently strong to disrupt normal patterns of brain activity. Sensory inputs below or above this range are thought to instigate remedial behavior. More recent versions of the "arousal hypothesis" (Helson, 1964; Hunt, 1965) have suggested that stimuli different in intensity or quality from some "background" level of input (i.e., an adaptation level) may be innately drive-inducing.

Grossman's work on the behavioral effects of experimentally induced changes in reticular function have led to the conclusion that reticular influences may not, by themselves, instigate behavior but, instead, modify the organism's overall threshold of responding. The following briefly summarizes some relevant experimental observations.

Local microinjections of a cholinomimetic substance (carbachol) into the midline nuclei of the thalamus retarded the acquisition of conditioned avoidance responses, depressed performance of food-rewarded instrumental responses, and decreased general exploratory behavior. "Unconditioned" responses such as feeding or drinking in response to 23 hours of deprivation or escaping from painful foot shock did not appear materially affected. Microinjections of carbachol into the reticular nuclei of the thalamus produced similar though more severe effects in all test situations (Grossman et al., 1965).

Atropine injections into the midline nuclei of the thalamus facilitated responding in the avoidance situation as well as in a food-rewarded discrimination test, during acquisition as well as near the asymptote of performance. Atropine injections into the reticular nuclei, on the other hand, produced disruptive effects similar to those seen after cholinergic stimulation of this region (Grossman and Peters, 1966). The latter pattern of effects seems paradoxical unless we accept the notion (Berlyne, 1960; Hebb, 1955; Hunt, 1963) that the efficiency of performance may be nonmonotonically related to reticular activity or arousal and that the shape of this function approximates an inverted *U*. That this interpretation may apply to our observations is supported by the fact that atropine injections into the reticular nuclei increased locomotor activity whereas carbachol decreased it.

The overall pattern of results suggests that an increase in the local concentration of a transmitter substance in the midline and reticular nuclei of the thalamus interferes with performance, presumably because the inhibitory mechanism is activated and the organism's reactivity to the environment thereby decreased. Atropine injections into these sites appear to produce opposite effects. Midline injections of this drug produced effects which were small enough to keep the animals' level of reactivity or arousal on the rising or flat portion of the inverted *U* function. Similar injections into the reticular nuclei may have produced a sufficiently large shift to involve the falling portion of the function and thereby interfere with behavior.

Our investigations of the midbrain reticular formation have suggested a complementary, excitatory mechanism. Small bilateral lesions in the midbrain reticular formation or local injections of cholinolytic substances such as atropine significantly retarded the acquisition and performance of a simple avoidance response without interfering with instrumental escape responses. Microinjections of carbachol into the same region appeared to increase the animals' general level of reactivity or arousal. When the injections were given for the first time, this increase in reactivity interfered with behavior in all test situations. However, the animals seemed to adapt to frequently repeated injections and were eventually capable of using the increased responsiveness (Grossman, 1966).

When we investigated these effects in various appetitive test situations, we found that small lesions (as well as atropine injections) in the midbrain region often facilitated discrimination performance, presumably because these animals were less easily distracted than normal ones. Carbachol injections, on the other hand, tended to disrupt behavior in these test situations (Grossman and Grossman, 1966).

A closer look at the animals' response to drugs in the avoidance situation showed, predictably, that the drug-induced changes in reticular function produced behavioral changes which depended significantly on the intensity of the unconditioned (shock) stimulus. When the animals were trained to escape very painful shock, carbachol injections produced frantic and uncoordinated behavior which interfered with the acquisition and performance of conditioned responses. Atropine injections facilitated responding in these situations. When the animals were tested in very low shock situations, a mirror image of the results appeared. Carbachol-treated animals overreacted to the mild pain and learned to perform appropriate escape and avoidance responses rapidly. Atropine-treated rats appeared less concerned about the threat of painful shock and consequently often failed to avoid the shock at all (Grossman, 1968).

The most interesting aspect of this series of experiments was the animals' response to injections of norepinephrine into the same sites which had produced behavioral reactions to carbachol and atropine. We tested a number of potential transmitters as well as various control substances and found that none would induce overt behavioral changes. However, norepinephrine, even in very small doses, produced a marked inhibitory effect, similar in direction and greater in magnitude than that seen after injection of atropine. Norepinephrine, like carbachol, interfered with the acquisition and performance of conditioned responses in all appetitive situations, but this effect appeared to be related to a general depression rather than the hyperreactivity seen after carbachol. This interpretation is supported by the animals' reaction to norepinephrine in the avoidance situations. The norepinephrine-induced hyporeactivity aided performance in very high-shock test situations (where carbachol produced disruptive effects). However, the norepinephrine-treated animals responded little or not at all in low-shock situations (where carbachol had facilitatory effects).

These experiments suggest that adrenergic and cholinergic substances may selectively act on distinct excitatory and inhibitory components of the midbrain reticular formation, a possibility which may help to explain some of the apparently paradoxical lesion effects which have been reported. More generally, our experiments lead to the following conclusions.

Damage or pharmacological excitation or inhibition of reticular mechanisms produces general changes in behavior which appear most adequately explained in terms of a general change in the organism's reactivity to external as well as internal stimuli. There was no evidence for direct effects on primary sensory or motor functions or modifications of specific drive states. This pattern of behavioral changes provides an operational definition of the nonspecific motivational influences which have been the subject of so much debate at this meeting.

Our observations support the hypothesis that the level of nonspecific drive or activation appears to be nonmonotonically related to performance in all complex test situations. The performance of simple, "unconditioned" responses is apparently little affected by this mechanism. Changes in reticular function produced more marked effects on the behavior in escape-avoidance situations than in appetitive test situations. This may indicate that changes in the organism's level of reactivity may be more "relevant" to situations which involve intense sensory input. We observed, in some situations, that the animals appeared capable of adapting to seemingly marked changes in reticular function and arousal or capable of compensating for them in some as yet unknown fashion. This would seem to provide some support for Helson's (1964) notion of adaptation level and related hypotheses.

V. DRIVE, MOTIVATION, REINFORCEMENT, AND LEARNING

Most theories of drive are concerned with a change in some internal state that influences the effect of a stimulus on behavior. Thus the concept of drive can be considered directly relevant to the physiological basis of learning in so far as drive states may be considered to modify learning through changes in motivation or through changes in the mechanism of reinforcement.

In this section, Miller, who has long been concerned with the relationship between drive and reinforcement, discusses the conditions of the drive state antecedent to learning and the importance of identifying and separating those state conditions from the conditioning stimuli. Pfaffmann, after reviewing different levels of motivation and the limitations of reinforcement as usually tested in arbitrarily contrived test situations for the reinforcing properties of stimuli, discusses taste preference and learning experiments involving the predilections of rats for sweet, salt, and aversive solutions. He concludes that an animal's selection of a particular response to reinforce is governed by its relevance to the animal's total adaptation requirements. Bindra points to evidence showing that motivation, as it affects behavior instigation, is as much a matter of reinforcing stimulus objects (i.e., incentives) as of drive per se. He outlines a view of motivation and reinforcement that incorporates the new findings and suggests certain lines for further research.

A. THE RELATIONSHIP BETWEEN DRIVE AND LEARNING: N. E. MILLER

Antecedent Conditions

Miller stated the empirical fact that some circumstances are obviously much better for producing learning than others. Not having the time to discuss all the parameters that affect learning, he concentrated on the one limited set of parameters that are called motivational, putting emphasis on reinforcement. In the case of instrumental learning (also called operant conditioning), the reinforcement occurs promptly after the response to be learned, i.e., it is a sequel to the response. Some consequences of a response, such as giving food to a hungry animal or turning off a strong electric shock, produce rapid learning, while other consequences do not. But whether a specific consequence will produce rapid learning and maintain effective performance is often dependent on a specific set of antecedent conditions. For a food-deprived animal, food is an important consequence that reinforces learning and performance. For an animal that is completely satiated on food, it is not an important consequence and will not produce a good performance. Antecedent conditions, such as food or water deprivation, that affect the reinforcing value of a consequence are classified as drives.

As Campbell and Kraeling (1953) have shown, if animals are trained to run an alley with shock as motivation and reduction or termination of shock as reward, the effects of aversive or of appetitive motivation appear to be similar. They learn to run faster if the shock is reduced from 200 to 0 volts than if it is reduced from 400 to 200 volts, but they learn to run the fastest if the shock is reduced from 400 to 0 volts. If the shock is maintained at 400 volts, no learning occurs, despite the animal's high drive level. Thus, the learning is a function of the relative amount of drive reduction rather than of the absolute amount or the strength of the drive.

Miller pointed out that, when it is known what drive is being manipulated (hunger, thirst, electric shock, etc.), better learning occurs with drive than without. Also, with a few exceptions, the same unconditional stimuli that are most effective for classical conditioning are effective as either drives or rewards in operant learning.

If the reinforcement is changed, for example, by reducing the amount of food or eliminating it altogether, after an animal has thoroughly learned a response, the effects cannot show up on the first trial, because there is no way for the animal to know that the reinforcement has been changed until after he has performed the response. Thereafter, the animal's performance declines gradually during a series of trials. But, if the drive is changed, for example, by satiating the animal completely on food, an immediate decrement in performance is produced. Furthermore, there is a reduction in the performance of all habits that have been reinforced by the goal objects of that drive. Thus, as Skinner (1938) has pointed out, changes in the antecedent drive conditions affect not only a single performance but a whole family of performances. For example, if one changes an animal's satiety level, performance of any habit reinforced by food is markedly changed, although habits reinforced by water are not so markedly affected. However, performance of a food-satiated but thirsty rat in a food reward situation may be somewhat better than that of one not thirsty. This observation and the evidence cited above suggest to Miller that there may be some general effect of drive on the animal. He speculates that a drive generalization may occur that is analogous to stimulus generalization (Miller, 1948).

In addition to this immediate effect, which presumably works directly on the performance of the habit, it is also possible to get a delayed effect which occurs progressively during a series of trials, and presumably works indirectly by making the goal object a weaker reinforcement. The same sort of observations mentioned above about the effects of reducing the drive also apply conversely to the effects of increasing it.

If drive could be manipulated only by a single operation, for example, food deprivation, and had only a single effect, that on the performance of a learned response, there would be no excuse for introducing it as an intervening variable between the operation of food deprivation and the operation for measuring learning. However, a number of different operations, such as depriving an animal of food, giving him an injection of insulin, stimulating the feeding area in the lateral hypothalamus, have roughly similar effects on a number of consequences, i.e., whether the animal will eat food, whether he will learn or perform habits to get food, and the amount of aversive stimulation it takes to prevent him from getting food. For these reasons, it is convenient to speak of the drive of hunger. (This has been discussed in detail elsewhere (Miller, 1959,1963b).)

Miller next considered curiosity as a drive and agreed that it does seem to fit roughly into the drive paradigm; that is, one can elicit performance with it. For example, animals in a strange goal box will first explore rather than eat. Exploratory behavior will continue to compete and alternate with eating until the animal becomes habituated to the new surroundings. (Berlyne does not consider all exploratory behavior to be motivated by "curiosity"; see Berlyne, 1966.)

Drive and Reinforcement

Miller then discussed why learning is much better with both drive and reinforcement present than with either alone. He mentioned Tolman's (1932) distinction between learning and performance as one possible explanation. Tolman had suggested that animals really learn connections between stimulus and response but do not perform the learned behavior unless motivation and reinforcement are present. Miller believes that the situation is more complicated than Tolman had described. With DeBold and Jensen, Miller (1965) tried to expose rats to learning conditions in the absence of any motivation or reinforcement. They put fistulas in the mouths of rats and, after presenting a conditioned stimulus, injected water so that the animals were forced to swallow. Those animals that had been exposed to the water when they were thirsty learned conditioned licking in tests, whereas the initially satiated rats did not show conditioned licking even when later made thirsty. The simple Tolman idea that the animals learned to expect water and would perform if thirsty was therefore inadequate.

Another possibility was that the animals licked and swallowed vigorously when thirsty but not when satiated. According to Guthrie (1952), the effect of drive on performance in the learning situation was responsible for the different rates of learning. The original experiment countering Guthrie's notion was Loucks's (1935), in which, despite direct stimulation of the motor cortex, animals would not learn a paw-withdrawal response unless given a food reward. Since then, Doty and Giurgea (1961) have shown that about 50% of the animals in that experiment will learn paw withdrawal if the trials are widely distributed. Nonetheless, Miller noted that such learning is still poor compared with the behavior of hungry animals rewarded with food for paw withdrawal. Finally, it is possible that the animals are being rewarded for anticipatory conditioned responses since these make it less likely that the response to the unconditioned stimulus will throw them off balance.

Miller noted that motivation and reinforcement might be involved in screening out the cues and in causing the animal to "pay attention" to the relevant cues, thereby better eliciting the relevant performance. The Doty experiment, however, suggests that elicitation alone may not be enough since, for example, an animal will extinguish if it performs the response without the proper consequences. Learning therefore requires more than repetition; for example, during extinction trials, an animal is learning to "stop" rather than to "continue-to-respond" even though it practices responding during those trials.

General Drive and Arousal

Miller then discussed the notion of general drive as it applies to arousal. He agreed that some degree of arousal is important for learning and noted that learning is poor during sleep (although some learning can occur under appropriate conditions). He reported that one of his students tried to condition insomnia in cats by shocking a cat every time it showed REM sleep (i.e., a deep stage of sleep in which the sleeping subject shows the activated brain waves of an alert subject, accompanied by rapid movements of the eyes under closed lids). The cat awoke when shocked but immediately went back to sleep and the student was unable to make that sleep stage the signal for waking. However, cats given the shock associated with a lighter level of sleep did wake up and did learn not to go to sleep in that situation in which they had been given the shock. Quarton mentioned the study of Williams (1967) which demonstrated some degree of learning in all stages of human sleep. In REM sleep, learning a discrimination response is almost as good as in the waking state. In deep orthodox sleep, learning is very poor, however, showing that level of arousal is indeed very important for learning.

B. REINFORCEMENT AND MOTIVATION: C. PFAFFMANN

When motivation is defined by its role in reinforcement of behavior, the nature of the response being reinforced itself becomes critical. Pfaffmann discussed the relation between motivation and reinforcement, noting first that two levels of motivation may be distinguished by the reinforcement of consummatory or natural behaviors on the one hand or of arbitrary responses on the other.

Concepts of Levels of Motivation

Borrowing a turn of phrase from Miller, Pfaffmann suggested that the first level, "Grade-A certified motivation,"* is that which permits the reinforcement of an arbitrary response, thus breaking the tight link between stimulus and response. "Grade-B uncertified motivation," the second level, refers to changes in the strength of a response, e.g., a consummatory response, due to a change within the organism (hormonal or otherwise) for which the reinforcement of a purely arbitrary response cannot be demonstrated. Pfaffmann suggested further that the reinforcement criterion for motivation may not be applicable to all instances of motivation, since only "stronger" motivations appear to affect reinforcement. It may be possible, for example, to demonstrate a motivational state of such strength that any one of a number of nonconsummatory arbitrary behaviors can be reinforced if it provides the needed or desired object appropriate for motivation. This is, in a sense, the most demanding

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*For a discussion of Miller's "Grade-A certified learning" see R. B. Livingston (1967).

definition for a motivational concept. But there may be other responses that are not arbitrary and more closely tied to the behavior patterns relevant to or part of the drive sequences seen in the natural situation. To illustrate this latter point, Pfaffmann discussed some of his studies and those by others on the salt-preference behavior of rats.

Responses Associated with Behavioral Patterns Related to Drive

Pfaffmann began by describing Richter's (1942) two-bottle preference situation in which rats have access to two bottles, one of which contains pure water and the other, water of variable salinity. Normal rats show a strong preference for saline solutions at low concentrations, but they reject these solutions at higher concentrations. Salt deprivation (by salt-free diet or adrenalectomy) results in increased intake. According to Pfaffmann, these experiments illustrate that a change in the response to any one stimulus is dependent upon a change of state in the organism. Expressed in Hinde's terms, there is a variation in response to a constant stimulus. Richter had viewed his experiments in terms of the maintenance of physiological homeostasis. To him there existed a tightly bound system in which changes in the internal state of the organism resulted in rather precisely regulated behavioral changes. However, it has subsequently been shown that the system consists of a rather loosely coupled series of mechanisms which, with some experimental manipulation, may be decoupled to induce behavior counter to homeostasis. For example, a salt-deprived rat will take in more salt than needed, once allowed access to it, and its intake will continue well beyond the repletion period. Denton (1965), on the other hand, has shown that in sodium-deprived sheep there is a sharp decline in motivation long before the sodium drunk could be absorbed from the intestine and could correct the internal changes supposedly provoking the sodium appetite. In effect, the consummatory act causes a discharge of what ethologists call "action-specific energy" for sodium ingestion, although the sheep does ingest more than sufficient quantities of salt to alleviate the deficiency.

Since normal rats preferentially ingest saline solution in the absence of physiological need for sodium, one might suppose that the sodium stimulus has reinforcing efficacy. However, the inference of motivational value from intake curves of the Richter sort appears to be unwise in view of the following experiments: If salt is indeed reinforcing, the salt preference of non-deprived animals should be demonstrable in a T-maze. However, Deutsch and Jones (1960), Chiang and Wilson (1963), and, more recently, Brookshire (1967) found that mildly thirsty animals learned to run to the water cup and not to the saline in a T-maze. Deutsch and Jones concluded, therefore, that the drinking of the salt solution in the two-bottle situation is an artifact of a "dilute water" mechanism. Water tends to suppress spontaneous neural activity, i.e., the signal for water is a reduction in the spontaneous discharge of taste afferent impulses. Weak saline solutions depress this activity also, but not to the same degree as water. Thus, the "dilute salt" is not as good as a "water signal" and the animal must ingest more solution to give an equivalent amount of gustatory inhibition. Thus, the animal has been fooled by the saline and treats it as dilute water. Yet, when given the choice of water over salt in a T-maze, it will run for the water. The effect of the mild thirst in the T-maze test makes the simple interpretation of this experiment difficult. At least one investigator has reported that, when the animal is given one trial a day with ample opportunity to ingest the solution of either salt or water that it needs, the animal will show a preference for the salt side of the T-maze. That is, the T-maze experiment may be confounded by thirst. Brookshire has also shown that animals reared on water learn to go to the water side; those reared on salt learn to go to the salt side. Therefore, learning factors also interact significantly in the T-maze test.

According to Pfaffmann, if the dilute water hypothesis were true for the two-bottle test, animals would simply drink more water when they randomly happen to hit the saline-containing bottle as compared with the water bottle. Yet by measuring the number of approaches to the drinking spout, Chiang and Wilson (1963) have shown that, in fact, the rats make more approaches to the saline solution in a two-bottle preference test. A similar observation has been made by Fisher (1965) with a two-bottle-contingent drinking apparatus. In this apparatus, one bottle was presented containing a stimulus solution, either water or salt. Ten licks at this first bottle would activate a device that introduced a second bottle containing either water or salt. It was therefore possible to present either salt solution first, which would deliver the water, or water first, which would deliver the saline. If the animal had been really motivated for water, one would expect that in this situation the animal would drink just enough saline to produce the water bottle, or if water were first, he would stay at the water bottle and not shift over to the salt. Actually, the results were clear and showed that the animal had a strong preference for saline; it would lick instrumentally at the water bottle just enough times to get the second bottle containing saline. When the saline was first, the rat drank actively at the saline and showed very little tendency to shift to the water. In other words, when licking rather than running down a T-maze was the instrumental response, the animal clearly showed indications of the reinforcing effect of the saline. Pfaffmann also pointed out that the animal's behavior for sucrose resembled that for salt.

Thus Pfaffmann concluded that: (1) The normal nonneedy preference for saline will not motivate a purely arbitrary response like bar pressing even if it leads to saline. (This work was done by Lewis (1960) in Miller's laboratory.) (2) On the other hand, instrumental licking is readily reinforced by saline. (3) The T-maze test for preference is, like the bar-pressing task, less sensitive to salt preference, but, in addition, is compounded by other variables like thirst and prior experience, which obscure the mild motivational effects of saline.

Hierarchy of Behaviors

Pfaffmann stressed that response to drive may be an important factor in determining the applicability of Teitelbaum's treatment of motivation (cf. page 45). Experiments from the ethological literature show evidences that the reinforcement value of a stimulus is strongly determined by the natural hierarchy of behaviors related to the drive being activated. Lehrman described the wasp, which returns to the hole where its nest is located, orients to the hole leading to the nest by visual landmarks, and makes an orientation flight when it leaves. If the landmarks are altered while the wasp is gone, as for example, if there had been a circle of pine cones around the nest at the time of the animal's leaving, but the circle is moved, or its form is changed to that of a square, or it is moved to a neighboring area, the wasp will return to the wrong place, i.e., it will go to the displaced circle. This appears to be an example of one-trial learning and takes place each time the wasp visits its nest. Pfaffmann maintained that, if the same animal were placed in a normal laboratory-type training circumstance or situation, it would be very difficult to demonstrate by some standard discrimination test the learning of visual figures of the degree of complexity of circles and squares. However, if these circles or squares are relevant or placed in the context of the animal's normal behavior patterns, it learns them readily.

Pfaffmann extended this line of argument by citing recent experiments by Garcia (Garcia and Koelling, 1966; Garcia et al., 1966) and by Nachman (1963) in which the association of a taste with poisoning was examined. In the Nachman experiments, rats were given a poisonous lithium chloride solution that is very similar in taste to that of a sodium chloride solution. The rat ingested the LiCl and, in about 3 minutes, its intake slowed down and it began showing toxic symptoms. After recovery in a day or two–an inordinately long delay for reinforcement–it was found that the acquired aversion to LiCl had generalized to NaCl.

Looking further at this delayed aversive effect from poisoning led Garcia to determine whether taste cues were more readily associated with nausea or internal states than audiovisual cues. An audiovisual stimulus contingent upon the rat's licking at a water spout produced "bright-noisy water" as an analogue to "tasty water" due to the flavor of saccharin in the water. The "bright-noisy water" in one case and "tasty water" in the other were conditionally paired with radiation, toxin, immediate electric shock to the four paws, and delayed shock. The avoidance response, when audiovisual and gustatory stimuli were paired with electric shock, was found to transfer to the audiovisual stimulus but not to the gustatory stimulus. Conversely, avoidance reaction due to toxin or radiation was transferred to the gustatory stimulus but not to the audiovisual one. In other words, the "bait shyness" of once-poisoned wild rats is relevant to the taste and not to the place of the poisoned bait. Of particular interest are more recent experiments of Garcia and his co-workers (1967) showing that the beneficial effects associated with the injection of vitamin B into a vitamin-deprived animal can also be conditioned to the taste of a solution and so increase intake. Thus, the objection that the persistent taste or regurgitation of the solution from the stomach could mediate the long-delayed reinforcement in the case of poisoning *does not* seem applicable to the case of the positively reinforcing effect of vitamin injections. Pfaffmann pointed out that associating a sound or other exteroceptive stimulus with vitamin injections did not work.

Pfaffmann concluded that relevance to the animal's total adaptive behavioral repertoire governs the character of the response that can be reinforcing. When motives are strong ("Grade-A motivation"), it may be possible to use any arbitrary response that the animal is capable of making as a reinforcement. As the strength of the motivation drops, the arbitrarily reinforced behavior will drop out first, whereas responses related to the drive and its consummatory response may still show evidence of reinforcement. Finally, when motivation drops still further, changes in response strength of consummatory behavior may be the only sign of motivation or drive.

C. DRIVE, INCENTIVE-MOTIVATION, AND REINFORCEMENT: D. BINDRA

The concept of drive has served two theoretical functions in psychology: It has been considered as (*a*) a motivational factor that energizes or instigates behavior and as (*b*) a source of reinforcement. Bindra examined the adequacy of the concept and outlined additional theoretical concepts that may be required to provide a better explanation of the phenomena of motivation and reinforcement.

Drive as a Motivational Factor

Bindra noted that when the concept of drive was first introduced into psychology, around 1920 (Woodworth, 1918; Richter, 1922), specific "drive manipulations" (e.g., food deprivation, induction of estrus) were thought to create distinctive physiological processes that directly increased the level of general activity and facilitated the occurrence of particular learned and unlearned responses (see Figure 5). This view prevailed until recently, and drive has been considered the main, if not the only, motivational factor. In Bindra's opinion, recent findings show that the motivational factor is broader than drive; the concept of drive needs to be supplemented by that of incentive-motivation. The relevant evidence comes from studies of both general activity and specific instrumental responses.

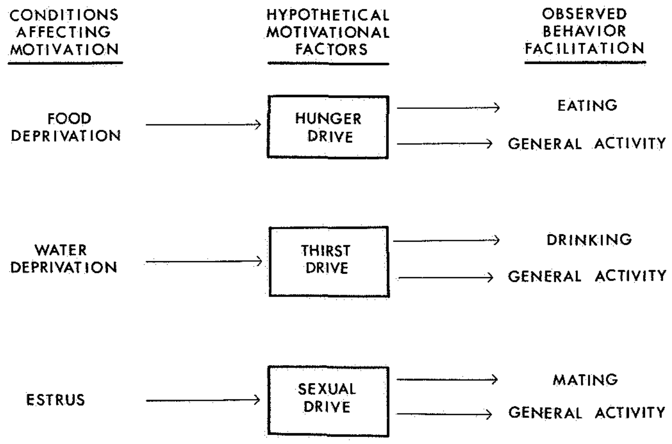

Figure 5. A schematic representation of the traditional drive theory of motivation [Bindra]

Studies of general activity. A number of investigations have shown that situational cues that have been repeatedly associated with a positive reinforcer may themselves evoke a marked increase in general activity. Such reinforcement-linked or "incentive-motivational" increases in activity are commonly seen around the normal time of feeding in animals maintained on fixed schedules of food or water deprivation. Several experiments (e.g., Bolles, 1963; Finger et al., 1957, 1960; Sheffield and Campbell, 1954) have shown that these activity increases are a function of conditioning, with situational cues serving as CS (conditioned stimulus) and the reinforcer as US (unconditioned stimulus). At the same time, other investigations have shown that drive in itself, in the absence of confounding incentive-motivational effects, can be sufficient for increasing the level of general activity (Bolles, 1965; Campbell et al., 1961; Duda and Bolles, 1963). Thus general activity can be increased by two separable factors: drive and incentive-motivation. At a given level of drive-induced activity, the introduction of an incentive-motivational stimulus (a CS that has been previously paired with a reinforcer) produces an additional increase in activity.

There is some evidence (Bindra and Palfai, 1967; Bolles, 1963) that the pattern of incentive-motivational increases in general activity is different from the drive-induced pattern. Incentive-motivational stimuli seem to elicit exploratory behavior (e.g., the rat systematically sniffs around as if searching for something). Drive-induced activity increases, on the other hand, seem to arise mainly from the animal's remaining awake or randomly active a greater proportion of the time. Thus, incentive-motivational increases in general activity may be more directly relevant to the problems of learning and organized behavior than are drive-induced ones.

To be exact, the distinction drawn here is not between drive and incentive-motivation, but between drive and incentive-motivation *plus* drive, for a minimum level of drive seems to be necessary for obtaining any incentive-motivational effect. For example, an incentive-motivational stimulus does not increase the level of general activity when the animal is satiated (Bindra and Palfai, 1967; Black, 1965). But the point is that an incentive-motivational stimulus (in the presence of drive) is capable of producing a level and type of general activity that is different from that produced by drive alone (see Figure 6).

By what processes do drive and incentive-motivational stimuli raise the level of general activity? Bindra first considered the source of drive's energizing effects on behavior. He believes that drive in itself, when

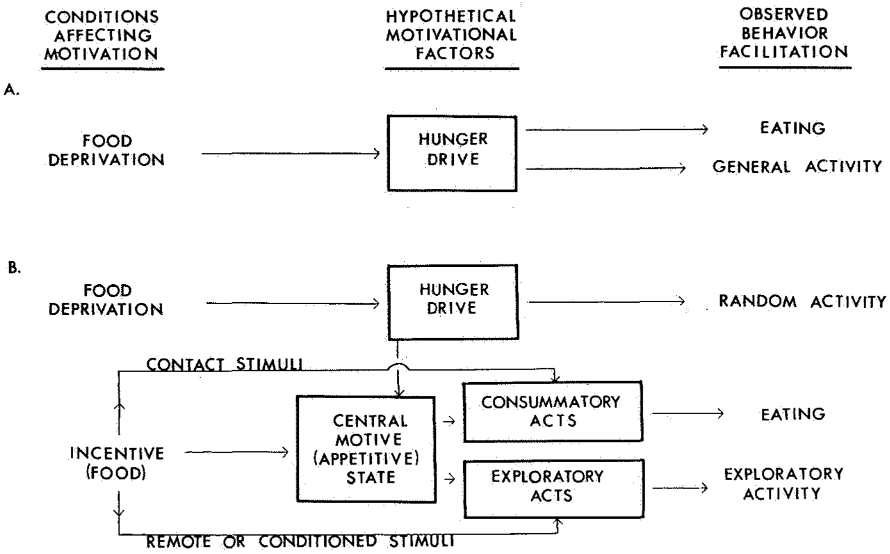

Figure 6. A schematic comparison of the drive (A) and incentive (B) views of (hunger) motivation. [Bindra]

unaccompanied by confounding reinforcement or incentive-motivational factors, energizes behavior by enhancing what he calls the "general motor readiness" of the animal. The idea of a general motor readiness factor arises from the observations that there are two opposing types of disturbances of movement initiation or response instigation. Under certain conditions (i.e., lesions in frontal lobes and large doses of amphetamine and other stimulant drugs), the tendency to initiate movement is grossly exaggerated; thus the animal is unable to withhold a response even when it is incorrect or unadaptive. Conversely, lesions in the medial thalamus and the administration of chlorpromazine or other depressant drugs interfere with the animal's ability to initiate movement. These extreme end-points of inability to withhold response and inability to initiate movements define, then, the variable of general motor readiness. Bindra's view was presented as an alternative to that held by some investigators (e.g., Campbell and Sheffield, 1953) who have suggested that an increase in drive reduces the perceptual thresholds of the animal and thereby make it more reactive to the environmental stimulation.

The most commonly encountered explanation of the observed incentive-motivational increase in general activity is in terms of instrumental conditioning; it is said to result from the strengthening by reinforcement of locomotory and other acts that spontaneously occur in the experimental situation (Amsel and Work, 1961; Bolles, 1963; Baumeister et al., 1964; Finger et al., 1957, 1960). Specific situational cues are thought to become conditioned to certain specific "activity responses" by virtue of the reinforcement provided by, say, food in the case of a hungry animal. The other, less common, view regards the conditioning as consisting not in the association of specific responses with the stimulus situation, but in the association of some sort of a central state with the situational cues (Campbell, 1960). Through a process of classical conditioning, the central state, originally created only by the reinforcer (US) comes to be evoked in advance of the US by the stimulus situation (CS); this central incentive-motivational state then facilitates the responses that make up "general activity."

Bindra and Palfai (1967) have experimentally examined the above explanations. They exposed thirsty rats to paired presentations (classical conditioning) of a CS (metronome) and US (water) while the animals were immobilized in restraining cages. Then they measured their activity in another situation both in the presence and absence of the CS. This arrangement insured that the stimulus characteristics of the conditioning situation were different from those of the situation in which activity was to be measured. Also, as the animals were tightly restrained during conditioning, they were prevented from displaying the type of acts (e.g., rearing, walking) that could contribute to the activity scores in the test situation. Nevertheless, the level of rat activity during CS presentation in the test situation was higher than the level in the absence of CS. Further, the acts displayed in the test situation were quite different from those that occurred in the conditioning situation. Bindra and Palfai interpret these data by assuming that, during conditioning, a central state that facilitates the organization of environmentally oriented acts becomes associated with the CS.

Studies of specific responses. Regarding the instigation of particular instrumental responses, there is ample evidence that drive manipulations (e.g., food deprivation) facilitate performance (e.g., lever pressing for food), but it is not clear that the observed facilitation is attributable to drive per se. The possibility has not been excluded that the facilitating effects attending drive manipulations may result from some confounding incentive-motivational factors. Thus clear proof has not yet been given that drive in itself can directly facilitate specific instrumental responses. Bindra cited an experiment by Mendelson (1966) as a case in point. By intracranial electrical stimulation of lateral hypothalamic feeding areas in satiated rats, Mendelson separated the effects of drive and drive-plus-reinforcement. He found that the only necessary condition for prompt and correct performance in a T-maze was that the animal be given intracranial stimulation in the correct goal box, with food available, so that the animal would eat in the goal box. If the stimulation was not given in the correct goal box (even if present while the rat was in the start box and while the rat ran the rest of the maze), the rat's choice-point behavior was quickly reduced to a random level and running time was greatly increased. Thus, hunger drive (produced by intracranial stimulation) facilitated instrumental responding only when food was also present; the presence or absence of the drive in other parts of the maze made no difference in the choice or vigor of response. This suggests that, even in cases in which hunger appears to facilitate a response, the facilitation may, in fact, arise from incentive-motivational stimuli, that is, stimuli that have become associated with food. Thus, hunger may merely serve as a condition that enhances the reinforcement value of the food and, hence, the incentive-motivational value of the associated stimuli.

Several of the participants pointed out that there are difficulties in interpreting the Mendelson experiment because of the possibility that brain stimulation by itself may have had some reinforcing characteristics. If this were so, then it would not be surprising that the rat stimulated in the start box did not perform at better than a random level. However, it still remains true that intracranial stimulation given only in the goal box was sufficient to instigate running from the start box and to make the animal choose the correct turn at the choice point.

The facilitation of instrumental response by incentive-motivational stimuli was also attributed by Bindra to the creation of a central motivational state by the stimuli. He has elaborated this view in a subsequent paper (Bindra, 1968).

Relation of Drive to Reinforcement

Bindra then turned to the problem of the relation of drive to reinforcement. Hull's (1943) idea that drive reduction is a necessary condition for reinforcement, though no longer tenable, was, in Bindra's opinion, an excellent first approximation of the relation between drive and reinforcement. While the close relation between the two cannot be denied, its exact nature remains a matter for speculation. Bindra cited the following points as being relevant to the formulations of any new theory of reinforcement:

1. The current conception of drive must be revised radically. The new conception of drive that seems to be emerging is that drive is not equivalent to *any* strong stimulation or to the arousal of the reticular formation or to the sensory discharge associated with certain homeostatic disequilibria. Rather, drives appear to be a function of a change in the pattern of neural firing in certain specific neural sites in the "motivational brain." By and large, these are neural sites whose electrical stimulation produces some form of consummatory responses in the presence of appropriate stimulus objects (Mendelson, 1966; Roberts and Kiess, 1964; Tenen and Miller, 1964; Vaughan and Fisher, 1962).

2. Reinforcing effects arise not from drive reduction or drive induction, but from an interaction of the sensory input arising from reinforcing (incentive) stimulus objects (e.g., food, water, sexual partner) and the corresponding drive state. In terms of neural mechanisms, this means that the sensory input arising from incentive objects and the neural changes arising from drive manipulation (e.g., food deprivation) must reach a common neural locus in order to produce reinforcing effects. Indirect support for this point of view comes from recent investigations showing that the firing of neural units in the hypothalamic area can be affected by certain classes of incentive stimuli (Scott and Pfaffmann, 1967; Campbell and associates*).

3. The interaction of incentive stimuli and physiological drive states, quite apart from strengthening *prior* responses, also seems to create a central motive state that affects the *subsequent* actions of the animal (as noted in the above sections on general activity and instrumental responses). In other words, what we call reinforcing conditions (drive-incentive interaction) are not only reinforcing (response-strengthening) but are also motivating. The question then arises whether response-strengthening effects seen in learning may not themselves be a function of motivational arousal caused by incentive stimuli. In other words, the response-strengthening effects of reinforcers (incentives) may arise not from their retroactive strengthening influence on the prior responses but from their motivating influence on subsequent responses. The response-strengthening view of learning has been the dominant one so far, but we must recognize that the motivational view also remains a possible alternative. An experimental examination of these alternative views is now being undertaken by some investigators (e.g., Bindra and Campbell, 1967).

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*Campbell, Krebs, and Bindra, manuscript in preparation.

VI. BIOLOGICAL MECHANISMS OF REINFORCEMENT

An understanding of the biological basis of reinforcement is perhaps as important to a general understanding of behavior as is an understanding of the biological basis of drive. Stein was the only representative of this area of interest at our Work Session, and his discussion helps clarify some of the issues that must be further studied. In his paper he takes what is known about brain mechanisms involved in drive and explores the role of these same mechanisms in positive and negative reinforcement. He makes use of data from neurophysiology and brain stimulation studies, but in his effort to separate out two systems of reinforcement within the limbic system, one adrenergic and the other cholinergic, he emphasizes the pharmacological aspects of these systems.

A. NEUROCHEMICAL SUBSTRATES OF REINFORCEMENT: L. STEIN

Following the pioneering studies of Olds and Milner (1954), on the one hand, and Delgado and co-workers (1954), on the other, a considerable amount has been learned recently about the so-called "reward" and "punishment" systems of the brain (see Figure 7). Stein addressed himself to describing some of the anatomical and biochemical features of these reinforcement systems, beginning with the reward system. He pointed out that evidence from the self-stimulation experiments of Olds (1962) indicates that the system for positive reinforcement or reward occurs mainly along the medial forebrain bundle, which connects olfactory and limbic system structures in the forebrain with midbrain structures. The medial forebrain bundle is a two-way system according to Nauta (1960): messages are sent rostrally into the limbic system and cortex and caudally to midbrain structures with a way station in the lateral hypothalamus. Electrodes placed anywhere along the medial forebrain bundle produce an effect of positive reinforcement as reflected by self-stimulation behavior.

Effect of Drugs on Reward System

Stein next described the pharmacology of the reward system and its response to various drugs. He compared the effects of four psychoactive drugs on self-stimulation of animals on a variable-interval schedule.

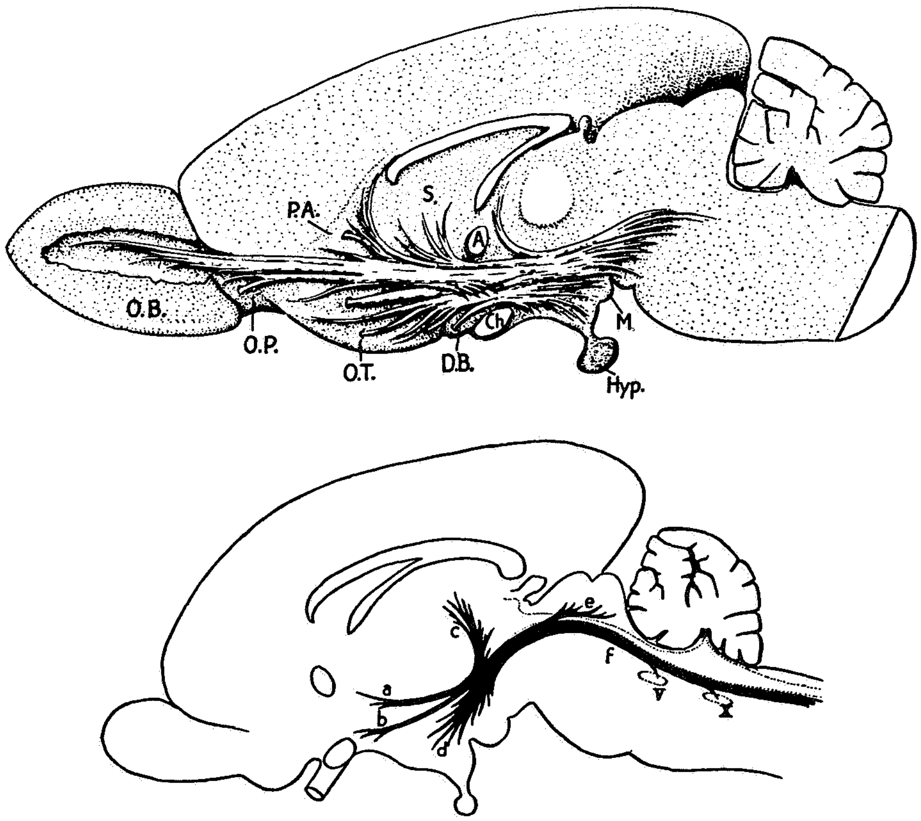

Figure 7. *Upper figure:* diagram representing medial forebrain bundle (the presumed substrate of reward mechanism) in a generalized and primitive mammalian brain. The abbreviations are as follows: A., anterior commisure; Ch., optic chiasma; D.B., nucleus of the diagonal band; Hyp., hypophysis; M., mammillary body; O.B., olfactory bulb; O.P., olfactory peduncle; O.T., olfactory tubercle; P.A., parolfactory area; S., septum. *Lower figure:* similar diagram representing the periventricular system of fibers (presumed substrate of punishment mechanism). The abbreviations are as follows: a, periventricular neclei; b, supra-optic nuclei; c, thalamic nuclei; d, posterior hypothalamic region; e, tectum; f, motor nuclei of cranial nerves. [W.E.L. Clark et al., 1938]

(Such a "reinforcement schedule" generates a moderate rate of response that can be augmented or depressed by facilitatory or inhibitory drugs. Further, since the rate of reinforcement is largely "clock-controlled" and not dependent on the rate of the animal's response, drug-induced changes in response rate may occur unconfounded, within broad limits, by changes in the reinforcement rate.) Amphetamine, an arousal-producing drug, produces a fourfold augmentation in response rate. Chlorpromazine, by contrast, produces selective depression. Neither sodium pentobarbital (in a dose having a strong antipunishment effect) nor scopolamine has a strong effect on self-stimulation (Stein, 1964a).

In general, Stein pointed out that adrenergic drugs appear to have important effects on the self-stimulation system (Stein, 1966,1967). Drugs that release norepinephrine rapidly from stores in the brain (amphetamine, α-methylmetatyrosine, tetrabenazine in combination with a monoamine oxidase inhibitor) facilitate self-stimulation. Conversely, self-stimulation is inhibited by drugs that deplete the brain of norepinephrine (reserpine, α-methylparatyrosine) or drugs that block adrenergic transmission (chlorpromazine). These results suggest that (*a*) the reward mechanism contains adrenergic synapses and that (*b*) these synapses are sensitive to pharmacological manipulation (see Kety and Samson, 1967).

Stein went on to point out that amphetamine, an artificial compound not found in the brain, is structurally similar to norepinephrine (a natural compound presumed to be a transmitter and found particularly in brain reward regions) in having a phenethylamine nucleus. If amphetamine works through norepinephrine, phenethylamine should also facilitate self-stimulation. Stein (1964c) found that it does, indeed, so long as it is protected from the degrading effects of a monoamine oxidase (MAO) to which it is susceptible (amphetamine is not). After pretreatment with the MAO inhibitor, iproniazid, phenethylamine produces an effect behaviorally indistinguishable from amphetamine. Thus, a very close structural link is provided between the actions of amphetamine, which facilitates behavior, and norepinephrine, which is known to be present in the reward system. How, then, does amphetamine act upon the norepinephrine system?

If animals are pretreated with reserpine, their brains can be depleted of norepinephrine, and the action of artificially administered amphetamine studied in its absence. Stein (1964c) found that, after reserpine pretreatment, the stimulant effect of amphetamine was definitely diminished, suggesting that amphetamine requires norepinephrine to be present. Further, he found that the time-course of norepinephrine depletion after administration of reserpine corresponds to the pattern of diminished amphetamine efficacy after reserpine. Conversely, drugs that enrich catecholamine levels, such as MAO inhibitors (iproniazid), have an enhancing effect on amphetamine action.

If stimulation by amphetamine is noradrenergic, then other agents that release norepinephrine should also be stimulants. α-Methylmetatyrosine, for example, which has an effect on norepinephrine similar to that of amphetamine, does have such a stimulating effect. Some catecholamine-depleting drugs, however, such as reserpine and tetrabenazine are tranquilizers rather than stimulants. According to Glowinski and Axelrod (1965), most of the catecholamines released by these drugs are deaminated by monoamine oxidase and are thus largely deactivated. If the effects of monoamine oxidase are prevented, however, by pretreatment with an MAO inhibitor, tetrabenazine then has a stimulant effect. Stein thus feels reasonably certain that the release of norepinephrine, or at least some catecholamine, is involved in stimulation.

Adrenergic Synapses and Self-Stimulation

Stein next turned to the anatomical question of the location of the adrenergic synapses in the self-stimulation system that might mediate the stimulant effects of amphetamine and other norepinephrine-releasers, and the reciprocal depressant action of the adrenergic blockers or depleters, chlorpromazine and reserpine. Hillarp and his co-workers (1966) have developed a histochemical technique for visualizing catecholamines at the cellular level. They report a system of catecholamine-containing neurons whose cell bodies have their sites of origin in the ventromedial part of the mesencephalon (the limbic midbrain area of Nauta). Fibers ascend from this region and terminate at adrenergic synapses in the lateral hypothalamus, limbic lobe, and neocortex. Using a completely different technique, Heller and his co-workers (1966) have reached a similar conclusion. By placing lesions in the medial forebrain bundle and then assaying various parts of the system for norepinephrine, these workers confirm the conclusion that the adrenergic fibers comprise an ascending system, since decreases in norepinephrine were observed only in structures rostral to the lesion. Stein suggested that it may be possible to identify this adrenergic ascending system with at least part of his positive-reinforcement brain system (Stein, 1966,1967).

However, in apparent conflict with these neuroanatomical studies are the behavioral studies which suggest that the self-stimulation system is largely a descending one. For example, the reward effect of an implanted electrode is increasingly strong and requires decreasing amounts of current the more posteriorly it is placed along the medial forebrain bundle. More direct evidence has been provided by the lesion studies of Olds and Olds (1964) and by Fonberg (in work described by Miller (1963a)), which indicates that lesions posterior to the electrode site abolish or diminish self-stimulation. (Valenstein (1966) has summarized data in conflict with these reports.)

According to Stein, there may be an error in the logic of the electrolytic lesion experiments. Time is allowed for recovery between the lesion and the test, during which degeneration could occur. If one assumes that degeneration in fact does occur, one could then explain the results in another way. As a result of the degeneration, nerve fibers directly under the stimulating electrodes could be destroyed, and this destruction could explain the abolition of self-stimulation. Stein explained that, since the medial forebrain bundle is more compact posteriorly and fans out anteriorly, posterior lesions would result in greater total destruction of the system simply as a result of the geometry of the fiber distribution. The lesion experiments may thus only confirm the anatomical fact, while indicating nothing about the traffic direction in the medial forebrain bundle. Furthermore, other changes that may occur during the course of recovery, such as denervation supersensitivity, would tend to confound the picture.

To Stein, studies which involve no opportunity for degeneration and other complications are more informative about the traffic pattern. If, as Stein has done, one implants a cannula instead of a lesioning electrode and provides a xylocaine block anteriorly with posterior self-stimulation, the animal stops responding (Figures 8 and 9). This indicates that the medial forebrain bundle does conduct rewarding impulses anteriorly. By reversing the arrangement, Stein has shown that rewarding impulses may also descend, but the critical point is that they do ascend. This is further evidence that the Fuxe-Hillarp adrenergic ascending system can be identified with the system in the medial forebrain bundle responsible at least in part for reward.

Perfusion Studies

The next series of experiments, performed in collaboration with Wise, were designed as a direct test of the idea that norepinephrine is released when the medial forebrain bundle reward system is activated. Using a permanently indwelling, Gaddum push-pull cannula, Stein and Wise (1967) continuously perfused specific areas in the brains of unanesthetized rats with Ringer-Locke's solution for periods up to 6 hours. Among the areas perfused were the terminal sites of the medial forebrain bundle in the rostral hypothalamus and amygdala. At intermittent periods, rewarding points in the medial forebrain bundle (as well as nonrewarding control points) were electrically stimulated in an attempt to release norepinephrine or its metabolites into the perfusate. In order to measure the small quantities of norepinephrine that might be released by rewarding stimulation, a sensitive radiotracer method was used (Glowinski

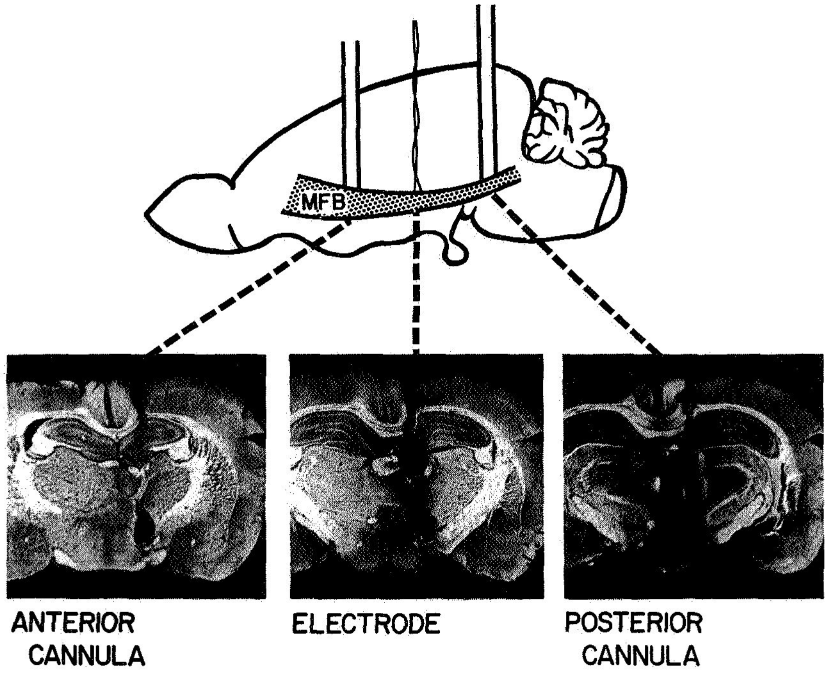

Figure 8. Diagram of experiment testing direction of flow of rewarding impulses in the medial forebrain bundle (MFB). A self-stimulation electrode is implanted in the MFB at the level of the ventromedial nucleus, and cannulas for injection of xylocaine are implanted in the MFB 1-2 mm anterior and posterior to the electrode. A xylocaine-induced block of self-stimulation at the anterior cannula would suggest that the reward message must ascend in the MFB toward the forebrain; a posterior block would suggest that rewarding impulses are conducted caudally in the MFB toward the midbrain. [Stein]

et al., 1965). Forty-five minutes before the start of the perfusion experiment, ^{14}C-labeled (41-250μg) or tritiated norepinephrine (0.3μg) was injected into the lateral ventricle. Regional and subcellular distribution studies suggest that the labeled norepinephrine introduced into the brain in this way mixes with the endogenous store and can be used as a tracer.

After a control period of 1 to 3 hours to allow the washout of radioactivity to stabilize, application of rewarding electrical stimulation caused substantial increases in the release of radioactivity in a large number of experiments (Figure 10). Often there was a lag of about 15 minutes before the peak release occurred. Radioactivity levels declined after prolonged stimulation, owing, presumably, to exhaustion of the

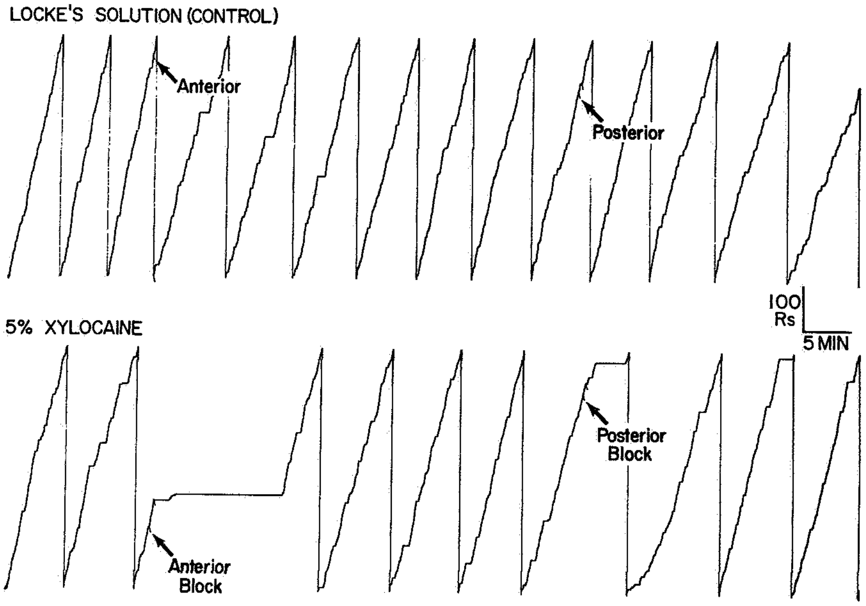

Figure 9. Effects of anterior and posterior injections of xylocaine in the medial forebrain bundle. *Lower record:* anterior injection blocks self-stimulation for more than 10 minutes; posterior injection also blocks self-stimulation but less effectively (despite the fact that the posterior cannula was closer to the electrode than the anterior cannula). *Upper record:* control injections of Locke's solution have negligible effects. See Figure 8 for design of experiment and histclogy. [Stein]

reserve of radioactive material. When the current was turned off, the control baseline was rapidly recovered.

Releases of radioactivity have been obtained only with highly rewarding electrodes which supported a self-stimulation rate of 1000 responses per hour or more (assessed in a self-stimulation test conducted before the perfusion experiment). Nonrewarding electrodes did not release radioactivity and, in some cases, if the stimulation was punishing or aversive, even inhibited its spontaneous release (Figure 10,E). In other control experiments, the radioactivity of cortical and thalamic perfusates did not increase during rewarding stimulation.

Chemical analyses of the perfusates revealed that O-methylated, deaminated metabolites of norepinephrine accounted for most of the radioactivity. Interestingly, samples of perfusate collected during rewarding stimulation contained a higher proportion of metabolites than did the control samples. If it is correct to assume that metabolism of norepinephrine is maximally efficient at synapses, this shift toward metabolites perhaps indicates that, during stimulation, the amount of norepinephrine released at synapses is increased relative to that which is washed out nonspecifically.

These results and those of the foregoing experiments, taken together, provide evidence that norepinephrine is released into the hypothalamus and forebrain from terminals of the medial forebrain bundle during rewarding stimulation. What is the physiological significance of this release? Is the rewarding effect of activation of the medial forebrain bundle wholly or partially dependent on the release of norepinephrine into the forebrain? If so, does the rewarding effect depend on the excitation of cells in the forebrain that facilitate behavior, or on the inhibition of cells that suppress behavior? Further research is needed to settle these questions, but a vast literature may be cited which demonstrates suppressor influences of the forebrain on behavior. Hence, it is

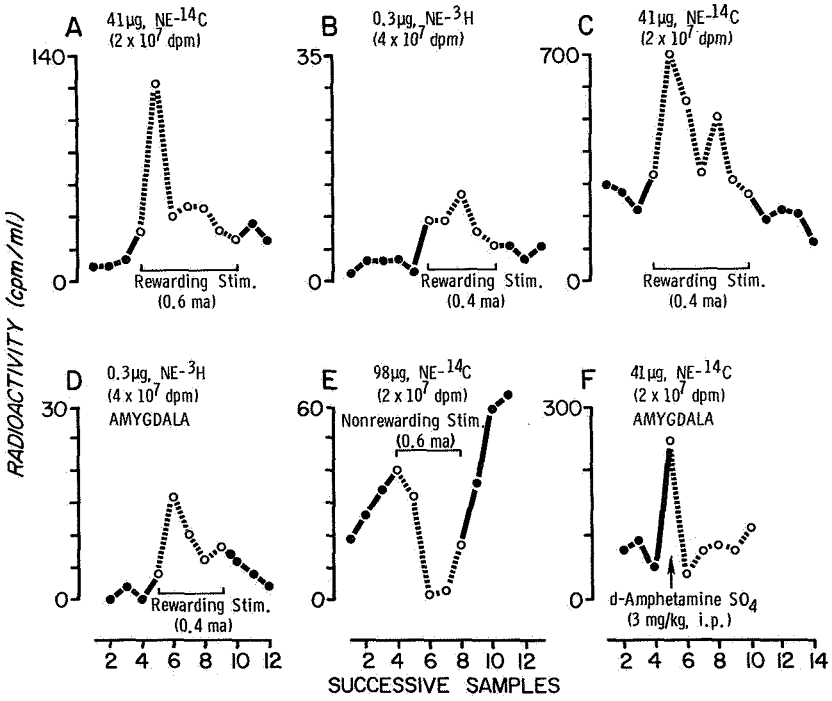

Figure 10. Sample experiments illustrating effects of rewarding brain stimulation, nonrewarding stimulation, and amphetamine on the release of radioactivity in hypothalamic (A-C, E) and amygdaloid (D,F) perfusates. In (C), the monoamine oxidase inhibitor, pargyline (50 mg/kg), was injected intraperitoneally 16 hours before the start of perfusion. The radioisotope tracer and dose used in each experiment are indicated. [Stein and Wise, 1967]

entirely likely that norepinephrine released by rewarding stimulation acts mainly as an inhibitory transmitter which depresses the activity of behaviorally suppressant cell groups in the forebrain. In other words, rewarding stimulation may facilitate behavior by a disinhibitory action.

Effect of Drugs on Punishment

Stein then turned to the discussion of experiments, performed in collaboration with D. L. Margules, on the chemistry of the punishment system. There is a class of drugs, i.e., the minor tranquilizers, that appears to have selective attenuating effects on the response suppression produced by punishment. These drugs include barbiturates, meprobamate, and the newer "antianxiety" agents like chlordiazepoxide (Librium*) and oxazepam (Serax*) (Geller, 1962; Margules and Stein, 1967, 1968). In the punishment test, animals work on a schedule with both a punished and a nonpunished component. In the nonpunished component, a drink of milk is obtained on a variable-interval schedule. Periodically a tone comes on, indicating that the schedule is being changed in two ways. On the one hand, the frequency of "pay-off" (milk reinforcement) is increased; but, on the other hand, a shock to the feet will accompany each response during this tone period. (This schedule was developed by Geller and Seifter (1960).) By careful adjustment of the level of shock, any desired level of response suppression can be obtained. In these tests, the shock level is adjusted so that animals will accept only about one or two shocks during each 3-minute tone period. Increases in food- or water-deprivation beyond the usual 24-hour deprivation period do not affect this behavior; nor does chlorpromazine, a major tranquilizer. Oxazepam, however, has a pronounced antianxiety effect; under its influence the animals immediately respond as if fear of the shock loses its capacity to suppress behavior. Stein noted that the immediacy of the effect suggests that oxazepam's action is not analgesic, since perfect analgesia, i.e., no shock, does require a period in which lever pressing gradually returns during the presentation of the tone. Furthermore, the powerful analgesic, morphine, fails to release punished behavior in this test (Geller, 1962).

In order to study the generality of the antipunishment effect, Margules and Stein (1967) studied oxazepam's effect in several different situations using different response measures and means of producing response suppression. In one study, involving nonreward rather than punishment, animals were placed on a regular reinforcement schedule in

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*Registered trade names.

which for 10 seconds out of every 2 minutes a light was turned on and food rewards were given. During the remaining time the animals were unrewarded and kept in darkness. At the time when the animals are learning to suppress responding during the unrewarded period, oxazepam has a strong effect in restoring responding; chlorpromazine, on the contrary, increases the suppression produced by nonreinforcement.

In another experiment, milk drinking was suppressed by putting quinine in it. With oxazepam, however, the animals drank twice as much quinine milk as the normal ones; in contrast, they drank less than a normal amount with chlorpromazine. A similar pattern results if response suppression is produced by satiety rather than by quinine. Despite a full stomach, animals given oxazepam will drink twice as much as normal, sated controls; that is, they do not "shut off" when full. Chlorpromazine has no such effect. Teitelbaum (1961, 1967a) and others have demonstrated that animals with ventromedial hypothalamic lesions do not "shut off" when full; they do not stop eating as soon as normal animals.

Basing his argument on this similarity between the effects of ventromedial lesions and oxazepam, Stein surmised that the ventromedial nucleus and its connections may be involved in the disinhibitory effects of oxazepam. He and his colleague (Margules and Stein, 1967) therefore implanted cannulas into the ventromedial nucleus to test the effect of direct administration of drugs on punishment-trained animals. They found that the bilateral lesions produced by introducing the cannulas were sufficient to reduce the effectiveness of punishment. The effect could be reversed, however, by injection of the cholinergic agents, carbachol and physostigmine, through the same cannulas. Carbachol restored the punishment effect sufficiently to abolish initially all lever pressing, and to suppress it considerably during the punishment component of the test 1 day after injection (Figure 11). The cholinergic blocking agent, atropine methyl nitrate, had the expected opposite effect and caused a further disinhibition of punished behavior (Figure 12). The effects of carbachol stimulation of the lateral hypothalamus were opposite to the ventromedial effects described above. Finally, the suppressant effects of applying carbachol or physostigmine to the ventromedial nucleus could be antagonized by systemic injection of oxazepam; this finding suggests that oxazepam and related drugs exert at least part of their disinhibitory action by blocking the inhibitory outflow of the ventromedial hypothalamus or its efferent connections (Figure 13).

Stein interprets these findings to indicate that, like the system established for feeding behavior, the reinforcement system for operant

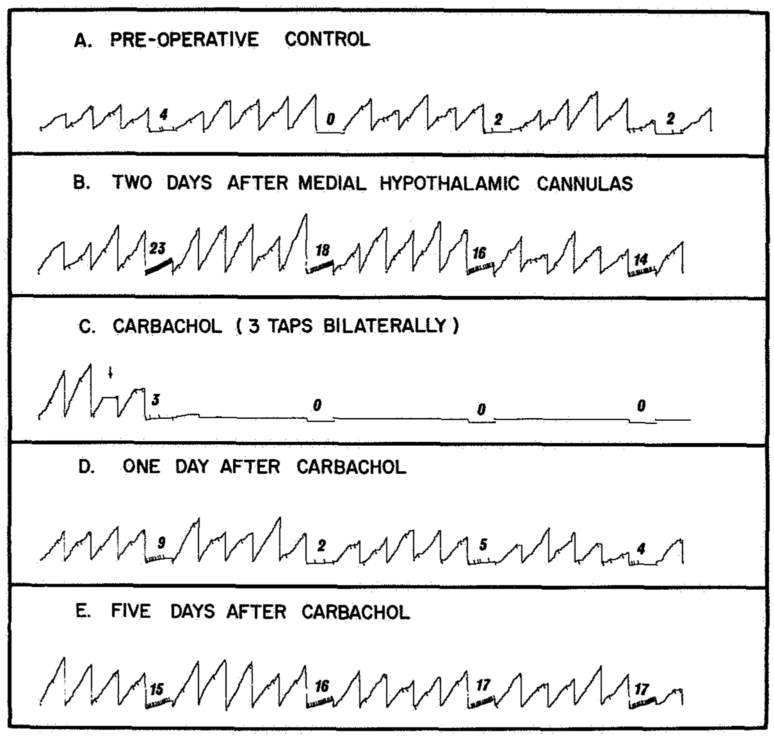

Figure 11. Cumulative curves of response in the reward-punishment test showing increase in punished responses (a decrease in the effectiveness of punishment) caused by hypothalamic implantation of cannulas (ventromedial lesions) and restoration of punishment effects by hypothalamic application of carbachol (10 μg). Pen resets every three minutes; responses in punishment periods are numbered and indicated by upward strokes of the pen. [Margules and Stein, 1967]

behavior appears to depend on reciprocally inhibitory subsystems (Stein, 1964b): a medial hypothalamic punishment system is response-inhibitory, while a lateral hypothalamic reward system is response-excitatory. The medial system contains a cholinergic synapse in the region of the ventromedial nucleus; this synapse is thought to be excitatory at the cellular level since lesions of this region produce an effect opposite to cholinergic stimulation. The lateral system synapses extensively in rostral hypothalamus, amygdala, and other limbic and neocortical structures; these synapses are noradrenergic and mainly inhibitory in sign at the cellular level, since the limbic system and frontal cortical lesions often produce effects similar to noradrenergic stimulation.

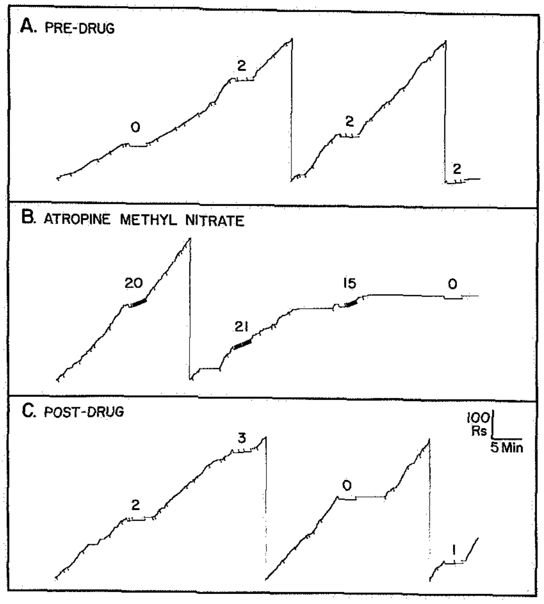

Figure 12. Disinhibition of punished behavior by medial hypothalamic application of atropine methyl nitrate. A first dose of approximately 10 μg was administered bilaterally 15 minutes before the test and a second dose immediately before the test. Responses are numbered and indicated by upward strokes of the pen. [Margules and Stein, 1967]

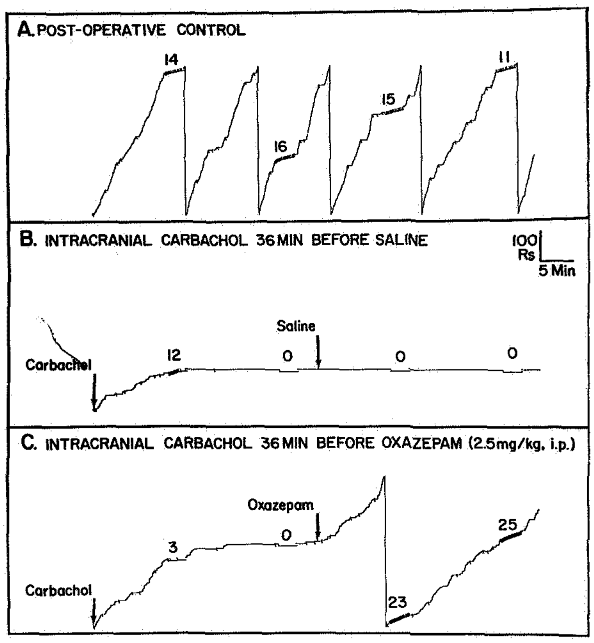

Figure 13. Antagonism of response suppression induced by medial hypothalamic application of carbachol by systemic injection of oxazepam. Since oxazepam releases punished behavior despite intense cholinergic activation of the ventromedial nucleus, the drug must act at some point efferent to this structure. Responses are numbered and indicated by upward strokes of the pen. [Margules and Stein, 1967]

VII. EPILOGUE: E. S. VALENSTEIN

It was, of course, not realistic to expect that the Work Session would resolve the complex problems under discussion. New and interesting data were presented and the discussions of theoretical issues and the relative values of different experimental approaches were much livelier than a summary report can convey. Initially, a fair amount of time was devoted to the problem of defining drive and motivation, but it soon became clear that no precise definition could be offered at this time. It is typical of psychology that it has had to face the problem that topics considered to be of major interest cannot be precisely defined. Few would deny the centrality of "learning," for example, to most psychological problems; but even those monographs which deal exclusively with the subject fail to provide an adequate definition of the term. A similar situation exists with the terms drive and motivation. It would appear that each person must establish for himself the extent to which it is helpful to wrestle with definitional problems, since we seem to be dealing with individual differences in temperament and styles of investigation. Undeniably, as we learn more about underlying mechanisms, definitions will become more meaningful. The present does not seem to be the time for a new synthesis; rather it is one of rapid accumulation of data on the physiological bases of the categories of behavior which traditionally have been considered to be basic to the problem of drive and motivation.

One recurrent theme throughout the Work Session involved the value of a general or nonspecific drive construct in addition to specific drives. Hinde's presentation included a discussion of some of the difficulties with a general drive construct, whereas Berlyne explored the relationships between a general drive and the more recent and more physiologically based constructs of arousal and activation. Experimentation in my laboratory, performed in collaboration with Verne Cox and Jan Kakolewski, bears on the question of the specificity of the motivated behavior activated by stimulation of discrete hypothalamic centers. A brief description of this work may be appropriate as the results suggest that there may exist an overestimation of the degree of specificity existing within the hypothalamus.

Behavior Elicited by Hypothalamic Stimulation

There have been a great number of reports of motivated behavior elicited by electrical stimulation of the hypothalamus. The behavior described has included eating, drinking, gnawing, hoarding, stalking-attack, coprophagia, and male copulatory behavior. The neural structures from which these behaviors could be elicited have been considered to be critical portions of the anatomical substrate of specific biological drives. The elicited behavior is thought to be a motivated rather than a stereotyped motor act because it is not exhibited unless appropriate goal objects are present and because stimulated animals will perform some learned task in order to obtain access to the relevant goal object. The behavior is normally not exhibited by the satiated animal except when being stimulated; therefore, the term "stimulus-bound behavior" has been applied. Even a casual review of the relevant literature reveals that there exists a widespread acceptance of the idea that stimulus-bound eating is elicited by activation of specific neural circuits underlying hunger, and that drinking is elicited from activation of specific thirst circuits; similar conclusions have been drawn with regard to the other elicited behaviors that have been studied.

At the Fels Research Institute we have been investigating the possibility of modifying the behavior elicited from hypothalamic stimulation (Valenstein et al., 1968a). Our work with three of the behaviors, eating, drinking, and gnawing, has progressed the furthest. It is now clear that, in every case that hypothalamic stimulation elicited any one of these three behaviors, it has been possible to change the elicited behavior to one of the other two. This was accomplished by stimulating the animal in the absence of the goal object first selected. If, for example, the rat just exhibited drinking during stimulation, and the water bottle was removed and the animal was stimulated with only food pellets and wooden wedges (for gnawing) present, the second elicited behavior was exhibited with as much reliability and vigor as the first.

Table II presents the results with the 11 animals studied in our first experiment. Seven of the 11 animals exhibited only one stimulus-bound behavior during the first three standard tests. During this first series of tests, the elicited behavior was exhibited with almost every stimulus presentation. The second series of tests was administered after a variable amount of experience in receiving stimulation in the absence of the goal object to which the animal was first oriented. It can be seen that, in general, the second elicited behavior was exhibited as consistently as the first. During the "competition test," when all three goal objects were present, approximately equal amounts of the two elicited behaviors were displayed in most instances.

As the stimulus parameters were not changed in any way, it may

TABLE II

EATING (E), DRINKING (D), AND GNAWING (G) BEHAVIOR ELICITED DURING HYPOTHALAMIC STIMULATION*
[Valenstein et al., 1968a]

		TEST SERIES						Stimulus Parameters
Animal	Behavior	First Series			Second Series		Competition	S – Sine Wave R – Rectangular Pulses
		1	2	3	1	2		
60S	E	0	0	0	15	17	11	R, 80μA
	D	20	20	20	–	–	14	
	G	0	0	0	0	0	0	
61S	E	0	0	0	20	20	15	R, 120μA
	D	20	20	20	–	–	12	
	G	0	0	0	0	0	0	
63S	E	0	0	0	0	0	0	R, 500μA
	D	0	0	0	20	20	12	
	G	20	20	20	–	–	8	
74S	E	0	0	0	20	20	12	S, 20μA
	D	20	20	20	–	–	13	
	G	0	0	0	0	0	0	
80SR	E	19	16	12	–	–	10	R, 120μA
	D	1	5	8	19	16	10	
	G	0	0	0	2	2	6	
91S	E	0	0	0	20	20	11	R, 120μA
	D	20	20	20	–	–	9	
	G	0	0	0	0	0	0	
93SR	E	0	0	0	15	16	10	R, 100μA
	D	17	17	19	–	–	9	
	G	3	2	2	0	0	0	
89S	E	0	0	0	18	20	16	S, 24μA
	D	19	19	20	–	–	4	
	G	0	0	0	0	0	0	
5T	E	0	0	0	20	14	13	R, 80μA
	D	15	18	19	–	–	9	
	G	0	0	0	0	0	0	
84SL	E	14	10	10	–	–	5	R, 80μA
	D	14	12	11	–	–	10	
	G	0	0	0	10	5	1	
33TL	E	20	20	17	–	–	16	R, 120μA
	D	2	2	0	20	20	10	
	G	0	0	0	0	0	0	

*Each test had 20 stimulation periods. Maximum score for any one behavior is 20 but the animal could exhibit different behaviors during each period.

be assumed that the activation of the same neural substrate could elicit a variety of behaviors. As we have had no failures in our attempt to switch the stimulus-bound behavior, it has been necessary to conclude that no assumption can be made from electrical stimulation studies that eating, drinking, and gnawing have independent neural circuitry, and we feel that it may be appropriate to reexamine the question of whether hypothalamic stimulation produces an excitation of specific motivational states.

One of the principal reasons why many have concluded that hypothalamic stimulation was activating specific motivation centers is that most previous investigators of stimulus-bound behavior have focussed on a specific behavior. As a result, the animals received either, or both, special training or limited opportunity to display different patterns. Those few instances in which an animal was given a brief "competition test" with another goal object present usually followed an extensive amount of opportunity to display the initial behavior pattern and very limited experience with stimulation in the absence of the initial goal object. Evidence for specificity has come from such demonstrations as hungry animals leaving a food dish and gnawing when stimulated and thirsty animals leaving water and exhibiting stimulus-bound eating (Coons, 1963; Roberts and Carey, 1965). We now know that this is not sufficient evidence that these behaviors are subserved by separate neural systems since such animals could be switched to exhibiting a new stimulus-bound behavior if they had received sufficient stimulation with the first goal object removed.

Need to Reexamine Basis of Motivation of Stimulated Animals

In addition to raising questions about the presumed fixed relationship between specific motivational states and discrete hypothalamic areas, the present series of experiments also call for a reexamination of the basis of the motivated behavior displayed by the animals. It is true that a number of experiments have demonstrated that animals exhibiting stimulus-bound eating, drinking, or gnawing have much in common with animals under the influence of natural drives such as those induced by deprivation. Animals will work to obtain appropriate goal objects and appear willing to tolerate aversive stimulation, such as shock or quinine additives, in order to obtain the desired objects (Morgane, 1961; Tenen and Miller, 1964). However, animals that were stimulus-bound drinkers appear just as motivated to obtain food after switching; this observation forces us to ask whether thirst and hunger motives are involved at all.

There is no questioning the conclusion that the animals are motivated, but we do feel that the question of the nature of the motivation, particularly its specificity, may have to be reexamined. We have been able to demonstrate that thirsty animals prefer water to a 30% glucose solution, although the same animals prefer glucose when satiated. Animals displaying stimulus-bound drinking do not exhibit the preferences of thirsty animals as they clearly prefer the glucose solution. Furthermore, animals displaying stimulus-bound eating of a canned cat food are just as likely to switch to stimulus-bound drinking of water when deprived of the cat food rather than to eating food pellets when both alternatives are available. In other words, the animals do not generalize along a dimension of appropriateness for satisfying a hunger need.

Our experimentation points to a lack of specificity between a given behavior pattern and stimulation of discrete hypothalamic areas and suggests that it may be necessary to reexamine the basis of the motivation exhibited by the stimulated animals. These conclusions should not be confused with a position of neural equipotentiality for the hypothalamus. First, we were not able to evoke either eating, drinking, or gnawing from a number of lateral hypothalamic sites. Furthermore, in several animals in which electrodes were placed in somewhat different lateral hypothalamic sites on both sides of the midline, the animal exhibited stimulus-bound behavior only when stimulated on one of the sides. We seem to be dealing *with the activation of a physiological state which permits a strong* association to be created with well-established behavior patterns. Such a hypothesized state would have much in common with a general drive construct and might be somewhat less complex to characterize physiologically than arousal and activation.

Although we have demonstrated the existence of considerably more plasticity in establishing connections between hypothalamic circuits and motivated behavior than previously suspected, we do not know the mechanism for establishing the connections nor do we understand the conditions which determine which behavior will become associated with the stimulation. Employing the distinction made by Bindra, we have taken the obvious first steps in analyzing the latter problem by manipulating both the specific drive states of animals through deprivation as well as the factor of incentive motivation by attempting to create within the animal a specific expectancy from the experimental test chamber. There is no doubt that in the future we will ask different questions and thereby generate different "facts." However, the persistence of the germinal idea contained in the terms drive and motivation testifies to the importance of the issue. As Berlyne indicated, different words have been used in the past and no doubt others will be used in the future, but there seems to be a clear need to include some such concept in our theories. The trend at present is to explore the possibilities of anchoring the terms to physiological mechanisms.

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