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Compound Complementarities in the Study of Motivated Behavior

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In his classic article, Stellar (1954) proposed that diverse motivated behaviors reflected the activity of excitatory and inhibitory centers in the hypothalamus. His specific and testable ideas provided the theoretical focus for a great deal of fruitful research on the biological bases of behavior for 2 decades. Subsequently, new findings and technical developments again changed the perspective and experimental approaches in behavioral neuroscience. The authors suggest that the modern emphasis on the anatomy and chemical function of neuronal systems has come at the expense of understanding the subcomponents of behavior and the hierarchical levels of integration involved in transforming reflexes into operant acts. Increased attention in the future to the infrastructure of the behaviors being elucidated, when combined with reductionistic studies of neurons, will fulfill the potential contribution to behavioral neuroscience that is implicit in Stellar's article.

In 1954, when Eliot Stellar published his seminal article, motivation was not studied in physiological psychology as a separate subject, and the role of the brain in motivated behaviors was only beginning to be investigated. Of course, motivation was not unrecognized; indeed, it was conceptualized as a critical intervening variable in studies of learned behavior (Hull, 1943; Skinner, 1938) and instinctive behavior (Tinbergen, 1951). Such investigations emphasized the nonspecific, energizing aspects of motivation familiar to psychologists but did not explore the physiological bases of motivation. In contrast was the work of Cannon (1932) and Richter (1942–1943) on regulatory ingestive behaviors in relation to the organismal need for water and food, and of Beach (1947) on the role of hormones in reproductive behavior, which emphasized specific biological stimuli that directed animals to discrete goals and thereby allowed one motivational state to be differentiated from another. In addition, there were the studies of Bard (1939, 1940) on the control of emotion and reproductive behavior (see also Wheatley, 1944), of Ranson and his students on the effects of hypothalamic damage on eating (Anand & Brobeck, 1951; Brobeck, Tepperman, & Long, 1943; Hetherington & Ranson, 1942) and sleep (Ranson, 1939; see also Nauta, 1946), and of Hess (1954) on the elicitation of instinctive behaviors by electrical stimulation of the hypothalamus. However, much of this work was not yet known to most psychologists. Instead, behavioral investigations linking motivation to brain function tended to emphasize the importance of the cortex and its role in mediating learning (e.g., Beach, 1944).

Stellar's (1954) article fundamentally changed this approach and perspective. Eleven years earlier, Morgan (1943) had adapted Sherrington's (1906) concept of a "central excitatory state" and proposed a "central motive state" in which peripheral stimuli joined with hormonal and other internal factors to produce motivated action mediated by the brain (see also Lashley, 1938). Stellar extended those ideas and organized existing data into a hypothesis, which stated that diverse motivated behaviors reflected the activity of specific excitatory centers in the hypothalamus. This hypothesis was broad enough to include regulatory behaviors such as eating, drinking, and specific appetites as well as the phenomena of sleep, emotion, instinctive behaviors, and the learning of motivated behaviors. It was captured in a simple diagram (see Figure 1) specifying the way in which environmental stimuli and physiological states could interact in the hypothalamus directly, and indirectly by means of higher (cortical) levels of control. Stellar also emphasized the role of inhibitory hypothalamic centers in the control of every motivated behavior, thus opening the way for the study of release phenomena as a general effect of hypothalamic damage (e.g., Teitelbaum, 1955).

Stellar's article not only provided an up-to-date account of the evidence and issues in the field but also a bold new framework for thought and future experiments. By doing so, it stimulated discussion and drew attention to the subject, attracted a legion of new workers (including the present authors), and provoked numerous research projects that tested new ideas and thereby expanded the field. It accomplished all this in part because the ideas presented by Stellar were specific and testable. They also were readily accessible to the reader; in his lucid presentation, Stellar clearly was an educator stimulating discussion rather than a polemicist, and his article could be characterized as much by the questions he asked as by the new theory he proposed. Indeed, Stellar did not simply present his views and evidence bearing on them, but he also evaluated the theory and noted what experiments must be done to check it and extend it. Thus, Stellar not only provided a model of motivation but also a model of how such models should be presented for consideration.

Not coincidentally, also in 1954, Stellar reported an important development in the methodology associated with the re-

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Sadly, Professor Stellar died of cancer in October 1993. Just a few weeks earlier, we had sent him a copy of this commentary that had been submitted for publication. His pleasure in our comments meant a great deal to us.

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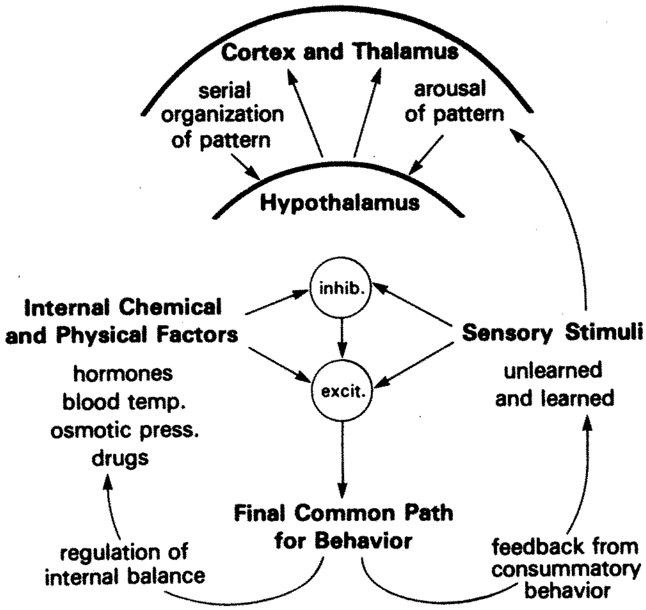

Figure 1. Scheme of the physiological factors contributing to the control of motivated behavior (according to Stellar, 1954). inhib. = inhibition; excit. = excitation; temp. = temperature; press. = pressure.

search that the first article stimulated, which thereby enabled the needed work to get done more easily. This second article (Stellar & Krause, 1954) complemented the first by describing a new design for a stereotaxic instrument for the rat (the animal mainly used in psychology laboratories) and a new principle for moving the tip of an electrode to any place in the depths of the brain, from any angle, without having to compute trigonometrically the distances involved. In using that instrument, Stellar promoted the practice of specifying the stereotaxic coordinates of hypothalamic lesions with reference to directly observable skull coordinates (e.g., bregma and lambda), in contrast with the custom then prevalent of merely showing histological slides of the tissue damage without specifying those coordinates. This procedure had the effect of making it easy for investigators to replicate important behavioral phenomena resulting from hypothalamic damage and thereby facilitated the spread of such studies as well as the likelihood that everyone was working with essentially the same preparation.

In the 2 decades that followed the publication of these articles, there was an explosion of activity in the analysis of the hypothalamic bases of motivated behavior. Theories of hypothalamic centers were supported by studies in which hypothalamic neurons were stimulated (electrically or by chemicals), destroyed, or recorded from electrophysiologically. Such was the emphasis on the hypothalamus that other areas of the brain—indeed, the rest of the body—were virtually neglected (see the "bodiless psychology" decried by Le Magnen, 1971). Such hypothalamocentric thinking continued until the late 1960s and early 1970s, when several new findings and technical developments again changed the perspective and the experimental approaches in the field. Some of the key observations included the following:

1. Most of the essential aspects of the syndrome of marked behavioral deficits (including aphagia and adipsia) seen after large bilateral lesions of the lateral hypothalamus (Teitelbaum & Epstein, 1962) could also be produced by extrahypothalamic damage to dopamine-containing fibers of passage (Ungerstedt, 1971; Zigmond & Stricker, 1972).
2. Such behavioral dysfunctions after lateral hypothalamic lesions apparently did not reflect specific impairments in feeding and drinking but did reflect general impairments in central arousal (Marshall, Levitan, & Stricker, 1976; Marshall, Turner, & Teitelbaum, 1971; Stricker, Cooper, Marshall, & Zigmond, 1979; Wolgin & Teitelbaum, 1978).
3. Recovery of function after large dopamine-depleting brain lesions need not be attributed to increased cortical control of motivated behavior normally mediated by the hypothalamus but appears to result primarily from neurochemical changes at residual dopaminergic synapses at extrahypothalamic sites (Stricker & Zigmond, 1976, 1986).
4. The syndrome of profound hyperphagia and obesity seen after bilateral lesions of the ventromedial hypothalamus apparently did not reflect critical damage to a hypothalamic satiety center but did reflect major disruption in the autonomic neural control of digestion and metabolism, with sympathoadrenal activity severely blunted and parasympathetic reflexes markedly enhanced (Friedman & Stricker, 1976; Powley, 1977).

Supplementing these and other specific findings were a host of new techniques that began to enable scientists to directly study the brain. Physiological psychologists, used to treating the brain like a black box and inferring aspects of brain organization and function by doing behavioral experiments, could now study directly the anatomy of brain circuits, the chemistry of synapses, and the molecular biology of neurotransmitter synthesis. Such studies have become increasingly more common during the past 20 years and have led to a great number of new ideas about brain structure and function.

These developments decreased what seemed to be an overemphasis on the idea that excitatory hypothalamic centers mediated specific motivated behaviors and led workers to take a much broader view of brain function. However, it should be noted that the fundamental questions posed in Stellar's (1954) article remain unanswered: Are motivated behaviors actually organized according to integrative centers in the hypothalamus? Is every behavior actually controlled by dual excitatory and inhibitory centers? Does the function of these putative centers include changes in the periphery of the body that affect behavior through longer loops of control?

The idea of "centers of integration" in the hypothalamus was strongly suggested by the work of Bard (1939, 1940), which was mentioned above. A complete transection below the level of the hypothalamus produced an animal in which only fragmentary reflexes involved in sexual behavior or in emotion, for instance, could be elicited. However, if the transection was made just above the level of the hypothalamus, then a much more coordinated form of sexual or emotional behavior was seen, involving several allied reflexes acting together. Therefore, the tissue located between the two levels of transection must function to integrate the allied reflexes involved.

Because complete transections such as those used by Bard (1939, 1940) and his coworkers could not provide precise localization, they led to a primary emphasis on level of function akin to the thinking of Hughlings Jackson (1884). The work of Grill and his colleagues (Grill & Kaplan, 1990) has continued this approach. When the stereotaxic instrument began to be used, considerations of localized structure became dominant over function. By localizing "centers" in the brain and labeling each with one salient function (i.e., the function missing after damage to that region), many investigators felt that more precision had been achieved than had existed earlier. However, as Sherrington (1906) pointed out, the major job of the nervous system is to integrate its functions, not only quantitatively over time and over spatial areas of the body but also qualitatively, enabling allied reflexes to cooperate while sharpening mutual inhibition between those sensations and actions that compete simultaneously for control of the final common path. Therefore, every "center" must integrate several functions, and it is an extreme oversimplification to attribute to any center the control of only one function. Nevertheless, the illusion of precision that was offered by such localization of function generally took precedence over the analysis of the many functions that remained after the damage (see below for a further discussion of this complementarity).

Like the disintegration of reproductive behavior into uncoordinated reflexes after complete transections (Bard, 1940), isolated fragments of eating and drinking behaviors are all that remain functional after sufficient dopamine-depleting hypothalamic damage. For example, early in recovery, the internal stimuli that normally motivate animals to initiate the act of eating are ineffective, whereas certain externally triggered allied reflexes (e.g., based on the taste and smell of palatable food) remain effective and elicit approach to and contact with food, which in turn recruits ingestion (Teitelbaum & Stellar, 1954). Later in recovery, when caloric regulation of food intake has reappeared, drinking in response to signals arising from body dehydration still does not occur readily. In rats with lateral hypothalamic damage, prandial drinking appears as an allied reflex when the animal eats dry food (Teitelbaum & Epstein, 1962; Teitelbaum, Pellis, & Pellis, 1991). Evidently, hypothalamic damage disrupts parasympathetic reflexive secretion of saliva in these animals and thereby promotes drinking associated with meals. In contrast, such prandial drinking does not occur in rats with extrahypothalamic dopamine-depleting brain lesions, suggesting that their deficits in water intake, associated with activational dysfunctions, cannot be overcome by these particular recruited reflexes (Stricker & Zigmond, 1974). Late in recovery, while drinking during daylight hours is still inhibited (Stricker, 1976), water intake can be facilitated by darkness (Rowland, 1976; Teitelbaum & Epstein, 1962), which is well known to have permissive effects on ingestive behavior.

For a brain-damaged animal, these allied reflexes are vital for indirectly triggering eating and drinking, whereas a neurologically normal animal does not depend on them so strongly. Indeed, each stage of recovery in the lateral hypothalamic syndrome (Teitelbaum & Epstein, 1962) can be understood in terms of the addition of a new allied reflex that indirectly triggers eating and drinking (Teitelbaum et al., 1991). Clearly, the repertoire of behavioral responses to stimulation is still organized at a lower level of integration even after seeming recovery of function when, through such adaptive reflex compensations, the brain-damaged rats again maintain body fluid and caloric homeostasis under basal conditions. Some physiological psychologists are beginning to address anew the role of the allied reflexes that comprise motivated behavior in brain-damaged rats as well as neurologically intact animals (Jacquin & Zeigler, 1983; Stern & Kolunie, 1991; Teitelbaum, Schallert, & Whishaw, 1983). However, a great deal more must be done to determine their interaction and hierarchical organization.

In looking back on the impact of Stellar's (1954) article and its relevance to future work, it is worthwhile to consider in a different way the issue of why its scientific contribution was so great. In a recent review of the history of work in this area, Stellar (1990) used the image of a pendulum swinging from one way of looking at things to another. Using that image, we can see that his article promoted a shift in emphasis from peripheral bodily stimuli to centers of integration in the hypothalamus, from an abstract concept of motivational state to specific and localizable hypothalamic "centers" controlling such states, and from the view that behavior was activated simply by excitatory stimuli to the perspective that it resulted from a complex interaction of excitatory and inhibitory centers in the brain. Each of these swings promoted many new investigations, which used new techniques, uncovered new phenomena, and generated new facts for interpretation. These opportunities were so exciting to students in psychology that work in the field mushroomed.

The metaphor of a pendulum in scientific thought is useful, but there is an alternative image that allows additional issues to be raised: the image of a reversible figure–ground illusion (Hanson, 1969; Kuhn, 1970). An example, shown in Figure 2, illustrates the principle of complementarity, for which Niels Bohr won the Nobel Prize when he applied it to the resolution of the conflict between quantum mechanics and wave mechanics. As Bohr emphasized (H. Bohr, 1967), complementarity applies to all scientific thought, not just to physics (for instance, see Rogers, 1992, for the recent application of complementarity in psychiatry).

The basic point of complementarity is this: When faced with an array of seemingly disparate facts, we seek an organizing principle that links a large fraction of them. In doing so, we use a perceptual process that brings those facts into the foreground while forcing the remainder into the background. Thus, for a meaningful organization to be maintained in thought, facts that do not fit must be suppressed. As Holton (1973) noted, the organizing principles are always based on universal bipolar dimensions in perception and thought (i.e., paired opposites), such as central versus peripheral, abstract versus concrete, and complex versus simple. Each pole represents a consistent way of organizing the facts in a scientific field that is incompatible with the organization provided by the opposite pole. Because each pole encompasses only a fraction of the facts, however, each way of thinking is incomplete without the other. Furthermore, because every scientific approach involves several such complementarities at the same time, each compound complementarity must be unraveled and made explicit for that approach to be fully understood by those using it.

Reexamination of Figure 1 from the perspective of bipolar dimensions of thought reveals it to be a reversible figure in its own right. For instance, as we have pointed out, one of its strengths was that it focused on specific, localized centers in the hypothalamus and de-emphasized the peripheral stimuli that

Figure 2. The old woman–young woman reversible figure–ground illusion. If one stares at the figure, it usually reverses. Some people, however, see only one aspect of the figure, and only with instruction can they see the other. From *Perception and Discovery: An Introduction to Scientific Inquiry* (p. 90) by R. N. Hanson, 1969, San Francisco: Freeman, Cooper, and Company. Copyright 1969 by Jones and Bartlett Publishers. Reprinted by permission.

influence the central states. In fact, such stimuli ultimately received considerable experimental attention, and the important results obtained are critical components of contemporary general schema of motivated ingestive behaviors (Stricker, 1990). However, a compound complementarity is involved here, and other paired opposites need to be unraveled:

1. *Concrete versus abstract.* Embedded in Stellar's theory is the polarity of structure versus function, which was mentioned above. The search for concrete aspects of tissue structure really is the business of experimental medicine (i.e., physiology, biochemistry, pharmacology, etc.), whereas the search for principles of abstract function is that of psychology (Teitelbaum & Pellis, 1992). Physiological psychologists are caught in the middle of this dichotomy. An increasing number have opted to search for subcomponents of tissue (structure), and from their collective activities has emerged the modern subdiscipline of behavioral neuroscience.

This evolutionary development represents wonderful progress. However, it must be realized that in its present form, behavioral neuroscience often is incomplete. By definition, behavioral neuroscience is a "bridge" science that attempts to correlate brain tissue structure with behavioral function. However, the present-day emphasis on brain structure and relative exclusion of analysis of pure function is creating only half a bridge, analogous to the famous half-bridge that can be seen at Avignon, France, which stops halfway across the river. The whole point of behavioral neuroscience is that it attempts to link the hierarchically organized structure of the nervous system to behavior. To create such links requires a parallel, equally detailed analysis of the purely functional reflex infrastructure of behavior, which is hierarchically organized at many, still largely unknown, levels of function from the simplest reflex to the most complex operant act. Some progress is being made: It is now known that allied reflexes can cooperate to act as isolated submodules, after brain damage or in incomplete development (Teitelbaum, Schallert, DeRyck, Whishaw, & Golani, 1980; Teitelbaum et al., 1983), and some rules governing the way allied reflexes promote movement are being formulated (Teitelbaum et al., 1991, in press). Much more work of this sort is urgently needed.

However, the purely functional analysis of the infrastructure of behavior is not likely to proceed well until another complementarity is recognized:

2. *Complex versus simple.* Embedded within the issue of complex versus simple is the difference between reduction and reductionism. Reductionism, the guiding philosophy of much of present-day behavioral neuroscience, is the belief that every scientific field can be explained in terms of the next lower level of complexity. Thus, behavior should be explained by physiology, physiology by biochemistry, and, most recently, biochemistry by molecular biology. Such reductionism can be used fruitfully in the medical sciences, which are concerned with the mechanisms by which biological tissues perform their functions. However, it is not appropriate for psychology, which is a form of systems analysis. It is as inappropriate to apply reductionism to psychology as it would be to apply it to mathematics (Teitelbaum & Pellis, 1992).

Many physiological psychologists have mistaken reductionism for reduction, which definitely is appropriate for psychology (Teitelbaum & Pellis, 1992). The power to simplify (i.e., to reduce) the nervous system physically in order to view more easily the subcomponents of its abstract function is in fact the reason why a psychologist might choose physiological psychology rather than other branches of experimental psychology that do not manipulate brain tissue. In other words, a brain lesion can be used not merely to localize function but to simplify it. Thus, reduction involves the complementarity between the function that is missing (localization) and the functions that remain and recover, which are unlocalized but simpler than normal.

Reduction also involves the study of the abnormal, rather than the normal. All this is embodied in the stages of recovery observed after brain damage. If a sufficiently large lesion is used (which sacrifices the illusion of precision offered by the concept of localization), the simplification of what remains can attain a "zero condition" (Magnus, 1926) in which behavior is completely absent, as in the sensory neglect and catalepsy that is associated with aphagia and adipsia after large dopamine-depleting lateral hypothalamic lesions (Marshall et al., 1971). In a zero condition, the hierarchical organization of a behavior has been decomposed so much that even the simplest reflex elements of its function cannot be activated. Then, each stage of recovery can be seen to add one control system after another, progressively restoring function while revealing hierarchies in its control (Teitelbaum, 1971, 1982, 1986; Teitelbaum & Epstein, 1962).

The fact that the analyses of function and structure are complementary to each other implies that each subfield in behavioral neuroscience must use both approaches and methods to achieve the bridge between brain and behavior. Put another way, even improved studies of brain structure will not be able to elucidate the biological foundations of behavior still mysterious at present without there also being increased scrutiny and articulation of the behaviors being elucidated. Unfortunately, the latter scientific approach has been relatively neglected in the 40 years since the publication of Stellar's (1954) review article. To fulfill the potential that is implicit in Stellar's article, we must look at it also from the less dominant viewpoint of function rather than structure. This major challenge, to determine the hierarchical functional organization of motivated behavior, is another important way in which Stellar's article can serve to build psychology in the future.

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