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Ethological Concepts

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Two publications dealing with theoretical aspects of animal behavior which are of considerable importance have appeared recently—the proceedings of the Josiah Macy Conference No. 1 on *Group Processes* and a paper by Prechtl (*1*) entitled "Neurophysiologische Mechanismen des formstarren Verhaltens." The Josiah Macy Conference served to bring together, in discussions, leaders of the European school of comparative ethology and American workers, who have in general been either very little influenced by, or highly critical of, the approach and ideas of ethologists. In this connection the papers given by Tinbergen (*2*) and Lorenz (*3*) are of most relevance. The discussions could hardly be expected to settle all outstanding problems, but they went far to make clear exactly where the divergences of opinion lie. Prechtl's paper, written independently of the conference, treats of a number of the same problems from a neurophysiological viewpoint. It is therefore convenient first to outline some of the problems that were raised at the conference and then to consider the bearing on certain of them of Prechtl's ideas.

There appear to be two main foci at which objections to the concepts of the ethologists converge: first, are the behavior patterns which they study really innate? and second, are they based on the accumulation of "action specific energy"?

Innate Behavior Patterns

The protagonists in the discussion of innate behavior patterns are Tinbergen and Lehrman. In the past, Tinbergen has tended to refer to an activity as an innate behavior pattern, without further ado, if it is characteristic of the species and does not require, for its manifestation, previous conditioning in the stimulus situation in which it does occur. At the other extreme, Lehrman (*4*) has emphasized that all behavior has an ontogeny and that, in this ontogeny, processes akin to learning may occur. This makes it difficult to decide on criteria of innateness, and ultimately Lehrman reaches the position of almost implying that there is no such thing as innate behavior. At the conference, Tinbergen was more guarded in his formulation and, acknowledging the justness of much of Lehrman's criticism, tended to avoid using the word *innate*.

It is true that the ontogeny of behavior is not only a legitimate but a very important study; it is true that *innate* may be the wrong word; but it is also true that anyone who has ever watched animals can hardly fail to be struck by the difference in the way in which, for example, a newborn kitten finds the maternal teat, and sucks, and the way the same kitten presently learns to come running to the kitchen the instant it hears the refrigerator door being opened. To say that "all behavior is to some extent learned" or that "no behavior is fully innate" does not advance us. The difference is real, and the point is to try to find out what is the essential nature of the difference. It seems best, even at the risk of appearing platitudinous, to try to look at the issue again from the very beginning, paying particular attention to Lehrman's insistence on the importance of ontogeny—an aspect that is stressed also by Beach (*5*) in his contribution to the Josiah Macy Conference.

Since an animal is an active metabolizing system, it must include, in its developmental make-up, regulatory mechanisms, many of them worked by the nervous system (such as regulation of respiration and of heartbeat) that keep it a metabolic going concern. These mechanisms are usually regarded as belonging to the domain of physiology, rather than behavior; physiology deals with internal regulation, behavior with relations with the environment, but the distinction, although it is often convenient, is largely artificial. Most animals do not live in a nutrient soup that is absorbed without the necessity of behavior. They must therefore include, in their developmental make-up, responses which insure that, shortly after birth or hatching, they do get food. These responses will count as behavior, but the responses of the gut muscles and glands to the food, once it is inside the animal, count as physiology.

As Pavlov pointed out long ago, unless an animal "has" a certain amount of behavior, there is and can be no basis on which learning can build. For a newborn mammal that has extensive parental care, the necessary behavioral equipment for beginning to live in the outside world is small. Apart from a response to the maternal teat, such behavioral equipment includes very little: possibly some form of vocalization in response to nocuous stimuli, such as being sat on by the mother, and some form of response to "danger" signals. In kittens it also includes a tendency to be at rest only when receiving stimuli provided by contact with litter-mates and, in ungulates, a following response.

These responses of the newborn are innate, in the strict sense of the word, but the point which is more important in the present context is that they are self-differentiating—that is, they come into being as part of the normal development of every individual; provided that the environment is not so inimical as grossly to interfere with development, they will be there. Haggling about the environment will not help us here; we cannot avoid it or remove it or see how an animal would develop without an environment, although the investigation of what constitutes a "normal" environment is as legitimate a study, in behavioral terms, as is a study of dietetic requirements in physiological terms. We might well remember Carlyle's comment on Margaret Fuller's declaration that she accepted the universe: "By gad! She'd better!" In this use of the term *self-dif-*

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ferentiating, we assume that the environment permits of normal development.

As the animal grows, further self-differentiating responses become necessary; behavior which will permit it to become self-supporting must start to mature. (In an animal that is without parental care, such behavior will be present from the start, or at any rate from the time when egg food-reserves are used up.) This process will involve the development of locomotory behavior in a previous nest-dweller, and of responses to potential food or to "instructions" from the parent. It will probably also include some form of toilet behavior; in a nest-dweller that previously excreted in response to maternal stimulation, it will include behavior concerned with micturition and defecation, and it may include responses to "danger" signals. Once this basis has been laid, the animal can learn to the limit of its capacity, but unless there is self-differentiation of the basis on which to learn, the animal will die, or remain in permanent infantile dependency.

At the end of this stage, the animal will be self-supporting and may be capable of learning to support itself more and more effectively. All necessity for self-differentiating behavior is, however, not yet at an end. Reproduction as well as individual survival is necessary. Therefore, at some stage, which may be later, there must be self-differentiation of behavior concerned with reproduction (*6*). This may consist of highly specific responses to highly specific releasers and is likely to be of this type in a species where individuals live in isolation. In a communal species, less specificity is permissible; the essential minimum could theoretically be reduced to a mere shifting of "interest" (that is, a change in the times allotted to various activities) and readiness to learn the appropriate behavior patterns by imitation or instruction. Parental behavior is part of reproductive behavior, but it may develop a little later and may be conditional on the physiological changes which occur during the process of reproduction. Nevertheless, the conditions with respect to the degree of specificity of response necessary are the same as for sexual behavior.

All this may be summarized by saying that to think about innate or learned behavior in an abstract manner is unbiological and unprofitable. Behavior must be considered in terms of real, live animals, each with its own particular mode of life. It then becomes obvious that, while it would be theoretically possible to have an animal all of whose behavior was self-differentiating, it would be quite impossible to have one without a basis of such behavior. The nature and extent of the self-differentiating basis, however, vary from group to group, always in a manner that is correlated with mode of life. Factors which make for the presence of highly complex and highly specific self-differentiating patterns will be lack of parental care, short duration of life, and solitariness of the individual, and, conversely, self-differentiating patterns may be reduced where there is parental care, longevity, and communal life.

Advantages of Present Approach

This approach has certain advantages:

1) It avoids all the confusion caused by the word *innate,* with its connotation of "present at birth." Birth is not the only nodal point in development, and it is therefore undesirable to use a term that focuses attention on this particular developmental step. A life-history may, but does not have to, include the following three stages: infancy under parental care, individual independence, and the adult reproductive phase; further nodal points may be present in cases where larvae have a mode of life different from that of adults.

2) It clarifies the distinction between a rigidly stereotyped "species specific pattern" (which may be essential in a short-lived, solitary creature without parental care) and, at the other extreme, a mere redirection of interest, which could be all that is required to insure successful reproduction in a highly social species.

3) It emphasizes the fact that a self-differentiating piece of behavior includes the phase during which it is in the process of differentiating; this makes it easier to understand that processes akin to learning can be an integral part of the differentiating process. On the sensory side we have imprinting, and, on the motor side, there is frequently a phase in which coordination improves with practice and the component parts of a total pattern become more effectively integrated. As examples, one may cite (i) "learning to walk," in kittens or babies; here the locomotory pattern is self-differentiating but involves increasingly improved coordination; (ii) micturitional behavior in kittens; here the scratching pattern is at first very imperfectly coordinated with the place at which urine is voided, but coordination develops gradually. Although maturation is undoubtedly important in such cases, it appears rarely to account for the whole of the improvement; for example, puppies which have been prevented from walking, although they catch up with their normal litter-mates quite soon after the removal of restraint, are at first inferior in coordination.

4) It adds to an understanding of the interaction of various factors in selection. Two examples will illustrate this: (i) We know that, in mammals, complex species-specific patterns are less important than in lower invertebrates. This is clearly secondary; the development of parental care permits the loss of the specificity of pattern and the build-up of learning ability. That learning "goes with" parental care is obvious; the point is that parental care not only provides opportunities for learning but also makes possible the remodeling of the whole basis on which the learning is built. (ii) In social insects, learning by experience and by tuition is poorly developed, despite the presence of two of the factors which are conducive to reduction in stereotyped, specific patterns. This appears to be the result of central nervous conservatism. Before these animals became social they were already insects—a complex and highly evolved group in which the trend has been toward perfection and elaboration of the specific patterns. The adoption of social habits did not result in a reversal of this trend, already well advanced, but in an elaboration of patterns and development of releasers concerned with social activities other than reproductive ones (for example, dancing, in bees).

Thus it seems that a strong case can be made for abandoning the term *innate* and replacing it with *self-differentiating* or with something similar (and preferably shorter). *Autonomous, autogenous,* and *endogenous* are all possibilities. Of these, my preference is for endogenous, and the phrase *endogenous behavior patterns* could be substituted for *innate behavior patterns* without great increase in cumbersomeness. A piece of behavior will be judged to be endogenous if it (i) is shown at the appropriate stage, in the appropriate situation, by all members (or all members of one sex) of a species and if it (ii) has not required either "instruction" from another member of the species or previous conditioning by means of an externally provided reward or punishment which does not form an essential component of an environment that permits of normal physical development.

This last formulation is intended to allow for the fact that the process of differentiation of an endogenous pattern may include the type of learning that was referred to in paragraph 3 of this section. Here, the reward, if any, is internal to the animal and consists of attaining the consummatory state of having performed the pattern adequately. If such performance does act as a reward, this itself is part of the animal's make-up; the situation is not identical with an externally imposed reward or punishment. In the latter case, the stimulus results from the operation of factors outside and independent of the animal, and its presence or absence is controlled by these external factors; in the former, the reward is included in, and inseparable from, the healthy animal itself. Precisely because it is internal, this sort of reward can become an integral part of the way in which an endogenous mechanism does differentiate. One will, of course, expect to find differentiation involving this type of learning only in cases where it does not matter if first attempts are imperfect. A kitten or a baby, protected by its mother, can afford to "learn to walk," but a baby whale must be able to swim very soon after birth. A tomcat can learn to copulate, but a male spider has to get his mating pattern right the first time or his mate may eat him.

We are now in a position to consider a problem that was posed by Beach (*5*) at the Josiah Macy Conference. Grooming is an activity that is normally performed by all chimpanzees and appears to be an innate pattern. However, if a young chimpanzee has its hands and feet enclosed in boxes which prevent it from touching its own body, it will not groom when the restraint is later removed. Grooming, therefore, appears to be learned—but, as Lorenz pertinently remarked, "has it not learnt to groom, or has it learnt not to groom?" If we abandon the false antinomy of *innate* versus *learned,* it is clear that grooming is, by the criteria that I have given, an endogenous pattern. The fact that some form of learning may be involved does not affect the issue; that particular learning has involved only other parts of the single differentiating system that constitutes the organism and is independent of instruction or of external reward or punishment. The experiment is not meaningless, although the question it set out to answer may be; the question it does answer is not about how to classify the behavior but about the factors that are involved in the differentiation of this particular pattern.

It is clear that the criteria that I have given for endogenous patterns are virtually the same as those that Tinbergen uses for innate behavior patterns. It therefore looks rather as though we had just come 'round in a big circle and got back to our starting point. This is true, insofar as we end by agreeing that the category of behavior studied by ethologists is a real category. But it is also true that, by turning from *innate* to *endogenous,* we have shifted our emphasis from the time at which a piece of behavior occurs (which may not be very meaningful) and have focused it instead on how that behavior comes into being. I believe that this shifting of viewpoint, while it results in agreement with the ethologists that we were really looking at something all the time, allows us to see a little more clearly what it was we were looking at and a little more of its relationship to other phenomena. If this is so, then the change is worth making.

Accumulation of Action-Specific Energy

In the case of "innate behavior" the problems are largely those of definition, and, although we remain largely ignorant of the neural basis of patterned behavior, considerable clarification of our ideas appears possible, along the lines that have been indicated. With "action-specific energy," however, we are dealing directly with the question of the neural basis of the type of behavior that is studied by the ethologists. Our ignorance of central nervous function seems to preclude any immediate solution, but consideration of what the difficulties are does permit some tentative ideas about where their solutions may lie and what sort of experiments might be expected to be of value.

Lorenz has been mainly responsible for emphasizing the differences between reflexes and endogenous behavior patterns. The basic difference is that a reflex is a response to a detectable stimulus whereas, with endogenous patterns, there appears to be a spontaneous accumulation of something which facilitates the response and which is dissipated by the performance of the appropriate behavior pattern. Normally, the response will be made in the presence of a releasing stimulus, but even in the absence of any such stimuli, a vacuum response may be made. A second difference between reflexes and endogenous patterns is the fact that appetitive behavior is characteristically associated with the latter but not with the former. Lorenz was himself originally a reflexologist, but his own observations forced on him the recognition of these differences; to describe them, the expression *accumulation of action-specific energy* was devised. Concentration on the differences, which was very necessary at first, gradually resulted in a viewpoint that implies an essentially dualistic mode of action of the central nervous system. On the one hand were reflexes, explicable in terms of the known physiological properties of nerve axons, cells, and junctions; on the other was something different, involving the phenomena of accumulation and dissipation of action-specific energy and not explicable in the same terms. Needless to say, this attitude was repugnant to physiologists, who, although they would readily agree that the brain is more complex than the spinal cord, are not willing to believe that its functions are not based on physiologically similar processes. The objections to such physiological dualism are well summarized by Kennedy (*7*).

Such dualism becomes unnecessary if it can be shown that the phenomena studied by the ethologists can be accommodated within the framework of known neurophysiological processes. Prechtl's paper (*1*) is an attempt to show how modern developments in neurophysiology offer the possibility of such a reconciliation and unification.

It will be convenient to deal first with the minor point—the linkage of appetitive behavior with endogenous patterns but not with reflexes. Since this difference concerns only the connections to other neural mechanisms of the centers that are responsible for the two types of behavior, it does not necessarily imply any fundamental difference in the physiology of the centers themselves. Prechtl points out that the functional significance of the difference is clear enough. Reflexes deal, on the one hand, with internal regulation of function and, on the other, with protective responses to potentially nocuous stimuli. In the first case, appetitive behavior is unnecessary, since the stimulus is generated inside the animal; in the second, it is undesirable. In endogenous patterns, appetitive behavior is essential; food, a mate, a suitable nesting site or the like may not be met with in its absence. The case of breathing, discussed by Spurway and Haldane (*8*), is an example of a reflex center which does have an appetitive component (albeit a vestigial one, in land mammals), showing clearly that it is functional, not physiological, criteria which determine the presence or absence of an appetitive component.

Some Possible Mechanisms

The more fundamental difference—the spontaneity of the endogenous pattern in contrast with the stimulated reflex response—must now be considered. In the Josiah Macy Conference, Lorenz quotes observations which make it clear that it would be impossible to explain the type of behavior which he is studying in terms which do not involve the accumulation of something, somewhere inside the animal. His examples of vacuum activities are particularly cogent. Since this is the case, the first point to be considered is, "What is accumulating, and where?" Differential effects are involved, since an animal may be in a state of readiness to perform one particular pattern but not another.

There are two ways in which this might be achieved (one has a chemical, the other a topographical, basis): (i) Production of diverse excitatory substances anywhere in the body and their accumulation in the blood. Each center must be assumed to be specifically sensitive to its own particular excitant; the nature of the excitant produced therefore determines what center is activated and, consequently, what behavior results; (ii) production and accumulation of an excitatory substance within the centers themselves. Only a single substance has to be invoked, since the activation of one center rather than another depends on the locus in which the excitant is being accumulated.

The ethologists have favored the second view: the hydraulic analogy of Lorenz (*9*) implies that the "excitatory fluid" accumulates within a particular instinctive center and is drained from it in the discharge of the activity that is characteristic of the center. The latter is thus seen as being largely autonomous and as spontaneously generating its own excitation. No neurophysiological analysis of an instinctive center has, as yet, been made, but such studies have been carried out on a number of centrally initiated internal regulatory mechanisms. In each case, the regulation has been found to be of reflex type and to depend on the presence of intracentral receptors. For example, the automatism of the medullary respiratory center depends on the presence of cells that show the normal properties of receptor cells, which are specifically sensitive to carbon dioxide (*10*). In the absence of carbon dioxide, the receptors are unstimulated, and the apparent spontaneity of the center disappears. Similarly, there are osmosensitive structures in the anterior hypothalamus (*11*) and heat-sensitive cells, also in the hypothalamus (*12*), that are responsible, respectively, for the initiation of responses dealing with the regulation of blood concentration and body temperature. These particular automatisms thus work on the basis of alternative i in the preceding paragraph—differential sensitivity of the centers (based on specific receptor-type cells) to differences in blood characteristics.

The suggestion that the instinctive centers of the ethologists are also activated, by way of specific intracentral receptors, by substances that are circulating in the blood is an obvious one. Certainly, substances that are circulating in the blood do affect them, as is evidenced by the onset of sexual behavior after hormone injection or by the effects of fluid depletion on drinking, and so forth. The postulation of other types of intracentral receptors might suffice to account for the initiation of endogenous behavior patterns; the difficulty arises when we consider what turns them off. In the case of the afore-mentioned physiological regulations, the answer is simple. The act itself sets in train a series of events which results in abolishing or reducing the intensity of the stimulus to the intracentral receptors. In breathing, the muscle contractions initiated by the respiratory center start a series of events, each one of which is well understood, which finally results in reduction of the carbon dioxide concentration of the blood.

For endogenous patterns, however, an answer in these terms alone cannot be the correct one, since an activity may cease regardless of whether or not it has attained its biological end, as in the gaping of nestling birds. Inhibitory feedback is the obvious candidate for the role of "turner-off"; but it is clear that the feedback that is responsible for the cessation of a behavior pattern cannot originate in the muscles involved. The same muscles are used in one pattern after another and cannot, therefore, provide the necessary specificity. Muscular feedback is concerned with the regulation of movement, as such—with insuring that the correct movement is made, regardless of whether the animal is heavy or light, the ground rough or smooth, the starting point with the weight on this foot or that, and so forth—and not with the major patterns into which the movements are integrated. Of course, specific peripheral feedback can exist in certain cases—stimuli from contact with the eggs are specific to the activity of brooding, and stimuli from the penis, to copulation. In such cases, peripheral feedback may be important, but it is totally inadequate to account for all cases.

This point is stressed by Lorenz (*3*), and cases of independence of peripheral afferent control are quoted by him. Of these, the most striking is the vacuum occurrence of the whole complex sequence of movements involved in the binding of a length of grass into its nest by a weaverbird that had no nesting material available—a bird, in one instance, that had never even seen a blade of grass in its life. In this case, afferent feedback of any specific type is out of the question.

Here Prechtl again has some important suggestions. He points out that peripheral feedback is not the only known source of inhibitory influences and suggests that more attention be given to inhibition arising within the central nervous system. A considerable amount of information already exists both about specific inhibitory pathways emanating from the cortex and more generalized ones from the reticular formation. An instinctive center could turn itself off by activating a pathway to a specific inhibitory center, which would then relay back and inhibit the original center. One must assume either a high threshold for the pathway to the inhibitory center or, more probably, that it is opened only by the performance of the closing phases of the specific activity of the center concerned; a parallel with the "off effects" that originate in the sensory pathways at once suggests itself (*13*). A hypothesis of this type is (in theory at least) experimentally verifiable. If the location of a center is known, then the effects of operative elimination or stimulation of pathways which might possibly be inhibitory may be studied.

Consideration of the central interconnections of the relevant center may also provide the answer to another of the problems raised by Lorenz (*3*)—namely, the nature of internal reward. In nest building, correct performance seems to be its own reward, and this is of importance in some species in learning to select the right type of material, in others, in learning where to build. How does it happen that correct performance does act as a reward, to reinforce itself? Some experiments of Olds (*14*) on rats, and of Sidman *et al.* (*15*) on rats and cats, may provide an answer. Certain regions have been located in the septal area, lateral amygdala, and anterior hypothalamus whose stimulation can be used as a reward in training experiments; moreover, if given the opportunity to stimulate themselves by pressing a lever, the animals will do so with great frequency. Here, then, are brain areas whose stimulation is sought by the animals, and this stimulation can function as a reward in learning. If such a center acts as a relay station between an instinctive center and an inhibitory center, turning off the activity after correct performance, then we have the necessary condition for correct performance acting as reward. The animal may be expected to learn the correct performance, as the rats learned to reward themselves by pressing the stimulating lever.

Although a reflex interpretation of the action of instinctive centers, as has been outlined, thus seems possible, this is not necessarily the only possible explanation in terms of known physiological processes. Other rhythmically active systems are known, which function in a nonreflex manner, and these must also be considered. Although, in the vertebrates, there is no unequivocal evidence for the existence of spontaneous, centrally initiated rhythms, there are indications that these may exist in invertebrates. Von Holst (*16*) recorded a spontaneous central rhythm that corresponded to the normal locomotory rhythm in the isolated nerve cord of the earthworm, and Wells (*17*) has shown that the rhythm that governs the irrigation cycle in *Arenicola* also originates in the nerve cord. Peripheral automatisms are also known, both in vertebrates and in invertebrates; the vertebrate heart and gut muscles provide examples, and the esophageal pacemaker system that is responsible for initiating the feeding cycle in *Arenicola* (*17*) appears to be very similar. The exact method by which the activity is initiated may vary in different cases, but whether it depends on two sorts of cell, one producing an excitant, the other responding to it, or on a single cell type producing its own excitant does not affect the conclusion that there do exist systems which are rhythmically active without external excitation, either in the form of nervous input or alterations in blood composition.

Seeking New Evidence

It is thus clear that no new type of nerve function has to be postulated to account for the action of the centers that are responsible for endogenous behavior patterns. Our present knowledge of neurophysiology is sufficient to provide two possible models, the one depending on reflex excitation by way of intracentral receptors, the other on locally produced excitants. The difficulty is to devise experiments that will enable us to decide between the two possibilities. The difficulty arises from the fact that, even if they are basically self-excitatory, the centers that are concerned with endogenous patterns must be subject to some modulating influences exerted by blood composition serving to correlate and integrate their activities. One might, for instance, be tempted to conclude that if vacuum sexual activities never occur in a castrated animal, then there can be no autoexcitant production in the relevant centers. This does not follow, since clearly there would have been selection, in the past, to limit the production of any such autoexcitant to a level which remains subliminal in the absence of the appropriate hormone; otherwise the animal will waste its energies in behavior which is inappropriate, or which it is incapable of carrying to its functional conclusion.

A direct attack, by excising centers and finding out whether an excitant is extractable from a center that was just about to discharge at the moment of death but not from one which was not ready to react, is feasible but has not yet been attempted. In view of the variety of substances that are extractable from the central nervous system, this is probably a type of experiment in which the chance of getting a meaningful answer is small.

A second method of investigation lies in further exploitation of the technique of stimulation of brain centers with implanted electrodes. With this technique it has already been possible to locate areas whose stimulation results in the performance of normal patterns of behavior. A full "mapping" of any one species would make it possible to study such things as the variations in threshold, in relation to previous activity, of any particular center, the effects on it of removal of its connections with other areas, or the effects of simultaneous stimulation of other centers or of alterations in blood composition, to name only the most obvious possibilities. Until such investigations have been made, it is premature to assume that the types of behavior that are studied by the ethologists cannot be based on the same sort of nervous functioning that simpler reflex forms of behavior are based on, or to abandon the view that the complexities of the central nervous system are based on complexities of arrangement and interconnection. At the same time, it must be recognized that, although the idea of centers' generating their own excitation may not be attractive to physiologists, autoexciting systems are not unknown in their own domain of physiology. The fact that, in vertebrates, such systems have been clearly demonstrated only in peripheral organs like heart and gut does not prove that they cannot exist within the central nervous system.

It is unfortunate that the use by ethologists of such descriptive expressions as "accumulation of action-specific energy" has, in the past, tended to repel physiologists and conceal from them the fact that the work of the ethologists has brought to light phenomena of extreme importance for the understanding of behavior—phenomena which demand analysis not only on their own level, by the methods of ethology, but simultaneously by physiological techniques. Prechtl concludes his paper by expressing the hope that it will not only serve to bring to the notice of ethologists some of the more recent developments in neurophysiology but will also draw to the physiologists' attention problems raised by ethology which only physiological techniques can solve. "'Tis a consummation devoutly to be wished." (*18*).

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W. C. Mendenhall, Geologist

Walter Curran Mendenhall devoted his life to service in the U.S. Government. It appears that even when he was attending college at Ohio Normal University (now Ohio Northern University) he was attracted to geology and, after his first field work with the U.S. Geological Survey, decided to make a career in that organization. Except for several short absences—a year at Harvard University and another at Heidelberg—he was employed continuously on the survey from 1894 until his retirement in 1943. During those 49 years, he rose from geologic aide to assistant geologist, to geologist, to chief of section, to chief of two branches (now divisions), and to director.

His first assignment to field work was with M. R. Campbell in studies of Appalachian coal fields in West Virginia, Tennessee, and Kentucky during 1895, 1896, and 1897. Following this, he was one of the small group who did pioneer exploration in Alaska, during four seasons between 1896 and 1902, with a diversion for one season in the Cascade Range with G. O. Smith. Those not familiar with frontier conditions, especially as they existed in Alaska 60 years ago,