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Source: *The Quarterly Review of Biology*, Vol. 28, No. 4 (Dec., 1953), pp. 337-363

Published by: The University of Chicago Press

Stable URL: <http://www.jstor.org/stable/2813453>

Accessed: 23/01/2009 14:18

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THE QUARTERLY REVIEW of BIOLOGY



A CRITIQUE OF KONRAD LORENZ'S THEORY OF INSTINCTIVE BEHAVIOR

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BEGINNING about 1931, Konrad Lorenz, with his students and collaborators (notably N. Tinbergen), has published numerous behavioral and theoretical papers on problems of instinct and innate behavior which have had a widespread influence on many groups of scientific workers (Lorenz, 1931, 1932, 1935, 1937a; Lorenz and Tinbergen, 1938; Lorenz, 1939; Tinbergen, 1939; Lorenz, 1940, 1941; Tinbergen, 1942, 1948a, 1950; Lorenz, 1950; Tinbergen, 1951). Lorenz's influence is indicated in the founding of the *Zeitschrift für Tierpsychologie* in 1937 and in its subsequent development, and also in the journal *Behaviour*, established in 1948 under the editorship of an international board headed by Tinbergen.

Lorenz's theory of instinctive and innate behavior has attracted the interest of many investigators, partly because of its diagrammatic simplicity, partly because of its extensive use of neurophysiological concepts, and partly because Lorenz deals with behavior patterns drawn from the life cycle of the animals discussed, rather than with the laboratory situations most often found in American comparative psychology. These factors go far toward accounting for the great attention paid to the theory in Europe, where most students of animal behavior are zoologists, physiologists, zoo curators or naturalists, unlike

the psychologists who constitute the majority of American students of animal behavior (Schneirla, 1945).

In recent years Lorenz's theories have attracted more and more attention in the United States as well, partly because of a developing interest in animal behavior among American zoologists and ecologists, and partly through the receptive audience provided for Lorenz and his colleague, Tinbergen, by American ornithologists. The ornithologists were interested from the start, especially because a great part of the material on which Lorenz based his system came from studies of bird behavior, but the range of interest in America has widened considerably. Lorenz and his theories were recently the subject of some discussion at a conference in New York at which zoologists and comparative psychologists were both represented (Riess, 1949), and are prominently represented in the recent symposium on animal behavior of the Society of Experimental Biologists (Armstrong, 1950; Baerends, 1950; Hartley, 1950; Koehler, 1950; Lorenz, 1950; Tinbergen, 1950), and extensively used in several chapters of a recent American handbook of experimental psychology which will be a standard sourcebook for some years to come (Beach, 1951a; Miller, 1951; Nissen, 1951).

Because Lorenz's ideas have gained wide attention, and in particular because a critical discussion

of these matters should bring usefully into review Lorenz's manner of dealing with basic problems in the comparative study of behavior, a reconsideration of Lorenz's system and school seems very desirable at this time.

LORENZ'S INSTINCT THEORY

We may best represent the general characteristics of the theory under discussion in terms of a case analyzed by Lorenz and Tinbergen (1938). The many subsequent references to this case and the proffered analysis by these authors and their colleagues leave no doubt that the case and its treatment may stand as representative.

Egg-rolling in the Gray Goose

When a gray goose, sitting on its nest, sees an egg that has rolled out of the nest, it reacts in a characteristic fashion. It extends its head toward the egg and then, keeping its head and neck pointed toward the egg and its eyes fixed upon it, stands up and slowly steps forward to stand on the rim of the nest. Next the goose bends its neck downward and forward so that the egg rests against the underside of the bill. It then proceeds to roll the egg back into the nest by shoving it back between its legs, using the underside of the bill. At the same time that this movement of the head and neck is taking place in the sagittal plane, the goose performs side-to-side movements of the head which have the effect of balancing the egg against the under-side of the bill.

The instinctive act

The egg-rolling movement in the sagittal plane may be considered first, without reference to whatever side-to-side movements may occur, since these two types of movement are distinguished very sharply in the theory.

Lorenz and Tinbergen found that the goose's tendency to perform the sagittal movement can be "exhausted" by repeated elicitation, even though observations indicated that the muscles involved evidently are not themselves fatigued. The authors therefore concluded that what is exhausted is a central neural mechanism.

The form of the sagittal movement is always much the same, regardless of variations in the shape of the egg-object or irregularities in the path over which the egg is rolled. Furthermore, when the egg rolls away from its bill, the goose, instead of stopping the sagittal movement and reaching out

toward the egg, frequently continues the sagittal movement to completion much as though an egg were present. The longer one waits after "exhaustion," the easier it is to relicit the act.

In connection with certain other behavior patterns, Lorenz (1937b) has noted that, after long resting intervals, the animal may perform a complete act without any external stimulus. This performance "in a vacuum" is regarded by Lorenz as the extreme case of the lowering of the threshold of elicitation after long non-exercise of the act. He calls it "Leerlaufreaktion," or "going off in a vacuum" [translated by Tinbergen (1942) as "vacuum activities"].

The sagittal movement thus has the following characteristics: (1) it displays a reaction-specific exhaustibility; (2) although released by stimuli coming from the egg, once released it remains constant in form regardless of variations in stimulation from the environment and even of the presence or absence of the original releasing stimulus; and (3) the threshold for elicitation falls continuously during non-exercise of the act.

The movement in the sagittal plane, distinguished from lateral deviations, is a typical "instinctive act" (Erbkoordination) in Lorenz's system. This "instinctive act," of course, is only a part of the total behavior pattern of egg-rolling. However, Lorenz maintains that every "instinctive" behavior pattern has as its focus such an "instinctive act" or "consummatory act" (Craig, 1918), the performance of which serves as goal for much of the rest of the pattern.

To Lorenz, the instinctive act is a rigidly stereotyped innate movement or movement pattern, based on the activity of a specific coordinating center in the central nervous system. In this coordinating center, there is a continuous accumulation of excitation or energy specific for the act. When the animal comes into the appropriate external situation for the performance of the act, stimuli provided by that situation release the energy, the instinctive act is performed, and some or all of the excitation is used up. The center specific for the act thus is able to coordinate the instinctive act completely independently of the receptors, so that once the act is released (i.e., elicited) its performance occurs in complete form, coordinated by impulses from the center and without any chain-reflex character. The function of the stimulus is to release or elicit the act. Once released, the act no longer depends for its form on

anything outside the central nervous system. When the animal happens *not* to be in the appropriate stimulus-situation, this reaction-specific energy is presumed to be accumulated, or dammed up. Also, the greater the amount of reaction-specific energy which has accumulated, the more easily may the act be elicited and the more complete will be its form when elicited.

This picture is regarded by Lorenz as a representation of the neurophysiological basis of the above-described functional characteristics of the instinctive act. In particular, accumulation of energy in a neural center capable of determining the form and order of performance of the various movements of the act, independently of the receptors (except for a trigger-like elicitation), is postulated to explain the reaction-specific exhaustibility (using up of the specific energy), the presumed independence of the form of the act from concurrent external stimulation (reaction-specificity of the energy), and the lowering of the threshold during a non-exercise interval (i.e., when an accumulation of reaction-specific excitation is presumed to occur).

The innate releasing mechanism

If energy specific for the instinctive act can accumulate continuously in the neural center specific for that act, why is the act not continuously performed? Tinbergen (1948a) concludes that each coordinating center is normally held under inhibition by another center which functions to block impulses from the coordinating center, save under specific conditions of external stimulation. This postulated inhibiting center is called the "innate releasing mechanism." The effect of an external stimulus which elicits an instinctive act is to release the instinctive center from this inhibition.

For example, the sagittal component of the goose's egg-rolling movement is not performed continuously, even though energy specific for it is being produced continuously in the central nervous system. The movement is only performed in a particular stimulus-situation: i.e., when a smooth-outlined hard object is present near the nest. (In non-experimental situations, such an object in such a place will almost always be an egg that has rolled out of the nest.) This combination of stimuli, which is considered capable of releasing the particular instinctive act from the inhibition under which it is held by the innate releasing mechanism,

is called the "innate releasing pattern." According to Lorenz and Tinbergen (1938), "The innate releasing pattern . . . [is] . . . the innately-determined readiness of an animal to respond to a particular combination of external stimuli with a particular behavior. It thus consists of an innate receptor correlate of a combination of stimuli which, despite its relative simplicity, characterizes a certain biologically-significant situation sufficiently uniquely so that the animal will not normally perform the appropriate reaction except in that situation."

The view, then, is that the innate releasing mechanism holds the instinctive act under inhibition until there appears a specific innate releasing pattern of stimuli capable of switching off the inhibition and "triggering" an outflow of impulses from the instinctive center to the peripheral effectors.

Also, the higher the level reached by the accumulation of reaction-specific energy in the center, the more difficult is presumed to be any inhibition of the act by the releasing mechanism. Consequently, the less completely does any stimulus-combination need to fit the innate releasing pattern as a whole to elicit the act. This explanation is offered by Lorenz for the fact that the instinctive act is easier to elicit, the more time has elapsed since it was last performed. The *Leerlaufreaktion* thus is a breaking of reaction-specific energy through the inhibiting barrier, when such energy reaches a very high level.

The taxis

Side-to-side movements of the head, by which the goose keeps the egg balanced against the underside of the bill, unlike the sagittal movement, lack the character of centrally-preformed movement patterns. The side-to-side movements are believed to be elicited independently by contact stimulation of the underside of the bill by the egg being rolled. Whenever the egg rolls off center, a bill movement toward the side of the deviation restores the egg to the path. If the egg happens to roll free so that the bird may continue the sagittal movement without any egg, there are no accompanying side-to-side movements. When the bird is permitted to roll a cylinder, there are usually no side-to-side movements, since a cylinder is unlikely to roll from side to side in its path.

Thus the side-to-side movement is not only *elicited* by external stimuli like the sagittal movement, but is also continuously *oriented* with respect

to external stimuli while being performed. In this respect lateral deviations differ fundamentally from the instinctive act, the form of which is determined centrally so that the external stimulus acts as a trigger only.

Movements like the side-to-side movements, which are continuously oriented to stimuli during their performance, are called by Lorenz orienting movements, or *taxes*. A taxis may occur simultaneously with an instinctive act (as in the case of the goose's egg-rolling), or may occur interspersed with instincts in a behavior-chain.

The stimuli releasing the act (innate releasing pattern for the instinctive act), according to Tinbergen (Tinbergen and Kuenen, 1939; Tinbergen, 1942) are not necessarily the same as those guiding it (i.e., the innate receptor pattern for the taxis). In the case of egg-rolling, for example, the instinctive act is released by a combination of visual stimuli and tactual stimuli related to the hardness of the egg, as felt by the tip of the bill in tapping. The (side-to-side) taxis, on the other hand, is released by tactual stimuli on the underside of the bill.

Appetitive behavior

The first part of the goose's reaction to the egg outside the nest is a stretching of the neck forward and downward, toward the egg. This act, according to Lorenz, has a different character from the instinctive act itself. It serves the purpose of getting the animal into the particular situation in which a specific instinctive act can be released. The act thus is truly goal-directed, according to Lorenz, who terms it "appetitive behavior" (Appetenzverhalten). He regards *all* goal-directed behavior as appetitive, in the sense that such acts are directed toward getting the animal into a situation in which some instinctive act can be released. For him, appetitive behavior can be of enormous complexity, involving instincts, taxes, and learned behavior of various kinds. Such behavior normally occurs when the level of excitation in the central nervous system for any instinctive act becomes high enough. This causes the animal to become restless and active. What specific kind of activity may occur depends on the kind of animal, and on which instinct is the source of the appetitive restlessness. For example, a rat set into activity by a high level of energy specific for the instinctive act of eating (i.e., he wants to eat) may turn toward a corner of the cage, walk toward it, pick

up a piece of food in its paws, bite at it, and chew it. Now, the whole sequence of behavior in this hypothetical example would be regarded by Lorenz as appetitive to the instinctive act of chewing. For him, turning toward the corner is a taxis, the walking is an instinctive act, picking up the food might be an instinct, turning the head toward the food held in the paws is a taxis, and the chewing an instinct. Which corner the rat turns toward depends on his past experience—the taxis is thus partly learned. The turning of the head toward the food in the paws, however, might be innate. [Tinbergen (1942) points out that some taxes may be learned, others innate. According to Lorenz's system, however, all instinctive acts (as distinct from taxes) are innate.]

For Lorenz, the whole complex of behavior in this example, involving instincts and taxes, learned and innate elements, has at its core the act of chewing, and is motivated by the excitation set up by the neural center for chewing. The appetitive behavior continues until the instinctive act is performed, and the specific energy is thus used up. It is important to note that according to Lorenz the goal of the appetitive behavior is the *performance* of the act, not its biological result. That is to say, in our hypothetical case, the need of which the appetitive restlessness is an expression is reduced not by the introduction of food into the stomach, but by the act of chewing. This is shown more clearly in the case of instinctive acts like courtship displays of birds, which form the goal of appetitive behavior (moving toward the female, orienting to the female, etc.) and which according to Lorenz are subject to *Leerlaufreaktionen* even though they do not (like chewing and swallowing) result in the satisfaction of an *apparent* peripheral tissue need.

PROBLEMS RAISED BY INSTINCT THEORIES

Even this brief summary brings to light several questions which ought to be critically examined with reference to the theory. These are questions, furthermore, which apply to instinct theories in general. Among them are: (1) the problem of "innateness" and the maturation of behavior; (2) the problem of levels of organization in an organism; (3) the nature of evolutionary levels of behavioral organization, and the use of the comparative method in studying them; and (4) the manner in which physiological concepts may be properly used in behavior analysis. There follows

an evaluation of Lorenz's theory in terms of these general problems.

"Innateness" of behavior

The problem

Lorenz and Tinbergen consistently speak of behavior as being "innate" or "inherited" as though these words surely referred to a definable, definite, and delimited category of behavior. It would be impossible to overestimate the heuristic value which they imply for the concepts "innate" and "not-innate." Perhaps the most effective way to throw light on the "instinct" problem is to consider carefully just what it means to say that a mode of behavior is innate, and how much insight this kind of statement gives into the origin and nature of the behavior.

Tinbergen (1942), closely following Lorenz, speaks of instinctive acts as "highly stereotyped, coordinated movements, the neuromotor apparatus of which belongs, in its complete form, to the hereditary constitution of the animal." Lorenz (1939) speaks of characteristics of behavior which are "hereditary, individually fixed, and thus open to evolutionary analysis." Lorenz (1935) also refers to perceptual patterns ("releasers") which are presumed to be innate because they elicit "instinctive" behavior the *first time* they are presented to the animal. He also refers to those motor patterns as innate which occur for the first time when the proper stimuli are presented. Lorenz's student Grohmann (1938), as well as Tinbergen and Kuenen (1939), speak of behavior as being innately determined because it matures instead of developing through learning.

It is thus apparent that Lorenz and Tinbergen, by "innate" behavior, mean behavior which is hereditarily determined, which is part of the original constitution of the animal, which arises quite independently of the animal's experience and environment, and which is distinct from acquired or learned behavior.

It is also apparent, explicitly or implicitly, that Lorenz and Tinbergen regard as the major *criteria* of innateness that: (1) the behavior be stereotyped and constant in form; (2) it be characteristic of the species; (3) it appear in animals which have been raised in isolation from others; and (4) it develop fully-formed in animals which have been prevented from practicing it.

Undoubtedly, there are behavior patterns which meet these criteria. Even so, this does not neces-

sarily imply that Lorenz's *interpretation* of these behavior patterns as "innate" offers genuine aid to a scientific understanding of their origin and of the mechanisms underlying them.

In order to examine the soundness of the concept of "innateness" in the analysis of behavior, it will be instructive to start with a consideration of one or two behavior patterns which have already been analyzed to some extent.

Pecking in the chick

Domestic chicks characteristically begin to peck at objects, including food grains, soon after hatching (Shepard and Breed, 1913; Bird, 1925; Cruze, 1935; and others). The pecking behavior consists of at least three highly stereotyped components: head lunging, bill opening and closing, and swallowing. They are ordinarily coordinated into a single resultant act of lunging at the grain while opening the bill, followed by swallowing when the grain is picked up. This coordination is present to some extent soon after hatching, and improves later (even, to a slight extent, if the chick is prevented from practicing).

This pecking is stereotyped, characteristic of the species, appears in isolated chicks, is present at the time of hatching, and shows some improvement in the absence of specific practice. Obviously, it qualifies as an "innate" behavior, in the sense used by Lorenz and Tinbergen.

Kuo (1932a-d) has studied the embryonic development of the chick in a way which throws considerable light on the origin of this "innate" behavior. As early as three days of embryonic age, the neck is passively bent when the heartbeat causes the head (which rests on the thorax) to rise and fall. The head is stimulated tactually by the yolk sac, which is moved mechanically by amnion contractions synchronized with the heartbeats which cause head movement. Beginning about one day later, the head first bends *actively* in response to tactual stimulation. At about this time, too, the bill begins to open and close when the bird nods—according to Kuo, apparently through nervous excitation furnished by the head movements through irradiation in the still-incomplete nervous system. Bill-opening and closing become independent of head-activity only somewhat later. After about 8 or 9 days, fluid forced into the throat by the bill and head movements causes swallowing. On the twelfth day, bill-opening always follows head-movement.

In the light of Kuo's studies the "innateness" of the chick's pecking takes on a different character from that suggested by the concept of a unitary, innate item of behavior. Kuo's observations strongly suggest several interpretations of the *development* of pecking (which, of course, are subject to further clarification). For example, the head-lunge arises from the passive head-bending which occurs contiguously with tactual stimulation of the head while the nervous control of the muscles is being established. By the time of hatching, head-lunging in response to tactual stimulation is very well established (in fact, it plays a major role in the hatching process).

The genesis of head-lunging to visual stimulation in the chick has not been analyzed. In *Amblystoma*, however, Coghill (1929) has shown that a closely analogous shift from tactual to visual control is a consequence of the establishment of certain anatomical relationships between the optic nerve and the brain region which earlier mediated the lunging response to tactual stimulation, so that visual stimuli come to elicit responses established during a period of purely tactual sensitivity. If a similar situation obtains in the chick, we would be dealing with a case of intersensory equivalence, in which visual stimuli, because of the anatomical relationships between the visual and tactual regions of the brain, became equivalent to tactual stimuli, which in turn became effective through an already analyzed process of development, which involved conditioning at a very early age (Maier and Schneirla, 1935).

The originally diffuse connection between head-lunge and bill-opening appears to be strengthened by the repeated elicitation of lunging and billing by tactual stimulation by the yolk sac. The repeated elicitation of swallowing by the pressure of amniotic fluid following bill-opening probably is important in the establishment of the post-hatching integration of bill-opening and swallowing.

Maternal behavior in the rat

Another example of behavior appearing to fulfil the criteria of "innateness" may be found in the maternal behavior of the rat.

Pregnant female rats build nests by piling up strips of paper or other material. Mother rats will "retrieve" their pups to the nest by picking them up in the mouth and carrying them back to the nest. Nest-building and retrieving both occur in

all normal rats; they occur in rats which have been raised in isolation; and they occur with no evidence of previous practice, since both are performed well by primiparous rats (retrieving may take place for the first time only a few minutes after the birth of the first litter of a rat raised in isolation). Both behavior patterns therefore appear to satisfy the criteria of "innateness" (Wiesner and Sheard, 1933).

Riess (pers. com.), however, raised rats in isolation, at the same time preventing them from ever manipulating or carrying any objects. The floor of the living cage was of netting so that feces dropped down out of reach. All food was powdered, so that the rats never carried food pellets. When mature, these rats were placed in regular breeding cages. They bred, but did *not* build normal nests or retrieve their young normally. They scattered nesting material all over the floor of the cage, and similarly moved the young from place to place without collecting them at a nest-place.

Female rats do a great deal of licking of their own genitalia, particularly during pregnancy (Wiesner and Sheard, 1933). This increased licking during pregnancy has several probable bases, the relative importance of which is not yet known. The increased need of the pregnant rat for potassium salts (Heppel and Schmidt, 1938) probably accounts in part for the increased licking of the salty body fluids as does the increased irritability of the genital organs themselves. Birch (pers. com.) has suggested that this genital licking may play an important role in the development of licking and retrieving of the young. He is raising female rats fitted from an early age with collars made of rubber discs, so worn that the rat is effectively prevented from licking its genitalia. Present indications, based on limited data, are that rats so raised eat a high percentage of their young, that the young in the nest may be found under any part of the female instead of concentrated posteriorly as with normal mother rats, and that retrieving does not occur.

These considerations raise some questions concerning nativistic interpretations of nest-building and retrieving in the rat, and concerning the meaning of the criteria of "innateness." To begin with, it is apparent that practice in carrying food pellets is partly equivalent, for the development of nest-building and retrieving, to practice in carrying nesting-material, and in carrying the young. Kinder (1927) has shown that nest-building ac-

tivity is inversely correlated with environmental temperature, and that it can be stopped by raising the temperature sufficiently. This finding, together with Riess's experiment, suggests that the nest-building activity arises from ordinary food (and other object) manipulation and collection under conditions where the accumulation of certain types of manipulated material leads to immediate satisfaction of one of the animal's needs (warmth). The fact that the rat is generally more active at lower temperatures (Browman, 1943; Morgan, 1947) also contributes to the probability that nest-building activity will develop. In addition, the rat normally tends to stay close to the walls of its cage, and thus to spend much time in corners. This facilitates the collection of nesting material into one corner of the cage, and the later retrieving of the young to that corner. Patrick and Laughlin (1934) have shown that rats raised in an environment without opaque walls do not develop this "universal" tendency of rats to walk close to the wall. Birch's experiment suggests that the rat's experience in licking its own genitalia helps to establish retrieving as a response to the young, as does its experience in carrying food and nesting material.

Maturation-vs.-learning, or development? The isolation experiment

These studies suggest some second thoughts on the nature of the "isolation experiment." It is obvious that by the criteria used by Lorenz and other instinct theorists, pecking in the chick and nest-building and retrieving in the rat are not "learned" behavior. They fulfil all criteria of "innateness," i.e., of behavior which develops without opportunity for practice or imitation. Yet, in each case, analysis of the developmental process involved shows that the behavior patterns concerned are not unitary, autonomously developing things, but rather that they emerge ontogenetically in complex ways from the previously developed organization of the organism in a given setting.

What, then is wrong with the implication of the "isolation experiment," that behavior developed in isolation may be considered "innate" if the animal did not practice it specifically?

Lorenz repeatedly refers to behavior as being innate because it is displayed by animals raised in isolation. The raising of rats in isolation, and their subsequent testing for nesting behavior, is typical of isolation experiments. The development of the

chick inside the egg might be regarded as the ideal isolation experiment.

It must be realized that an animal raised in isolation from fellow-members of his species is *not necessarily isolated from the effect of processes and events which contribute to the development of any particular behavior pattern*. The important question is not "Is the animal isolated?" but "*From what is the animal isolated?*" The isolation experiment, if the conditions are well analyzed, provides at best a negative indication that certain specified environmental factors probably are not directly involved in the genesis of a particular behavior. However, the isolation experiment by its very nature does not give a positive indication that behavior is "innate" or indeed any information at all about what the process of development of the behavior really consisted of. The example of the nest-building and retrieving by rats which are isolated from other rats but not from their food pellets or from their own genitalia illustrates the danger of assuming "innateness" merely because a *particular* hypothesis about learning seems to be disproved. This is what is consistently done by Tinbergen, as, for example, when he says (1942) of certain behavior patterns of the three-spined stickleback: "The releasing mechanisms of these reactions are all innate. A male that was reared in isolation . . . was tested with models before it had ever seen another stickleback. The . . . [stimuli] . . . had the same releaser functions as in the experiments with normal males." Such isolation is by no means a final or complete control on possible effects from experience. For example, is the "isolated" fish uninfluenced by its own reflection from a water film or glass wall? Is the animal's experience with human handlers, food objects, etc., really irrelevant?

Similarly, Howells and Vine (1940) have reported that chicks raised in mixed flocks of two varieties, when tested in a Y-maze, learn to go to chicks of their own variety more readily than to those of the other variety. They concluded that the "learning is accelerated or retarded . . . because of the directive influence of innate factors." In this case, Schneirla (1946) suggests that the effect of the chick's experience with its own chirping during feeding has not been adequately considered as a source of differential learning previous to the experiment. This criticism may also be made of a similar study by Schoolland (1942) using chicks and ducklings.

Even more fundamental is the question of what

is meant by "maturation." We may ask whether experiments based on the assumption of an absolute dichotomy between maturation and learning ever really tell us *what* is maturing, or how it is maturing? When the question is examined in terms of *developmental* processes and relationships, rather than in terms of preconceived categories, the maturation-versus-learning formulation of the problem is more or less dissipated. For example, in the rat nest-building probably does not mature autonomously—and it is *not* learned. It is not "nest-building" which is learned. Nest-building develops in certain situations through a developmental process in which at each stage there is an identifiable interaction between the environment and organic processes, and within the organism; this interaction is based on the preceding stage of development and gives rise to the succeeding stage. These interactions are present from the earliest (zygote) stage. Learning may emerge as a factor in the animal's behavior even at early embryonic stages, as pointed out by Carmichael (1936).

Pecking in the chick is also an emergent—an integration of head, bill, and throat components, each of which has its own developmental history. This integration is already partially established by the time of hatching, providing a clear example of "innate" behavior in which the statement "It is innate" adds nothing to an understanding of the developmental process involved. The statement that "pecking" is innate, or that it "matures," leads us *away* from any attempt to analyze its specific origins. The assumption that pecking grows as a pecking *pattern* discourages examination of the embryological processes leading to pecking. The elements out of whose interaction pecking emerges are not originally a unitary pattern; they *become* related as a consequence of their positions in the organization of the embryonic chick. The understanding provided by Kuo's observations owes nothing to the "maturation-versus-learning" formulation.

Observations such as these suggest many new problems the relevance of which is not apparent when the patterns are nativistically interpreted. For example, what is the nature of the rat's temperature-sensitivity which enables its nest-building to vary with temperature? How does the animal develop its ability to handle food in specific ways? What are the physiological conditions which promote licking of the genitalia, etc.? We want to

know much more about the course of establishment of the connections between the chick's head-lunge and bill-opening, and between bill-opening and swallowing. This does *not* mean that we expect to establish which of the components is learned and which matured, or "how much" each is learned and how much matured. The effects of learning and of structural factors differ, not only from component to component of the pattern, but also from developmental stage to developmental stage. What is required is a continuation of the careful analysis of the characteristics of each developmental stage, and of the transition from each stage to the next.

Our scepticism regarding the heuristic value of the concept of "maturation" should not be interpreted as ignorance or denial of the fact that the physical growth of varied structures plays an important role in the development of most of the kinds of behavior patterns under discussion in the present paper. Our objection is to the *interpretation* of the role of this growth that is implied in the notion that the *behavior* (or a *specific* physiological substrate for it) is "maturing." For example, the post-hatching improvement in pecking ability of chicks is very probably due in part to an increase in strength of the leg muscles and to an increase in balance and stability of the standing chick, which results partly from this strengthening of the legs and partly from the development of equilibrium responses (Cruze, 1935). Now, isolation or prevention-of-practice experiments would lead to the conclusion that this part of the improvement was due to "maturation." Of course it is partly due to growth processes, *but what is growing is not pecking ability*, just as, when the skin temperature receptors of the rat develop, what is growing is not nest-building activity, *or anything isomorphic with it*. The use of the categories "maturation-vs.-learning" as explanatory aids usually gives a false impression of unity and directedness in the growth of the behavior pattern, when actually the behavior pattern is not primarily unitary, nor does development proceed in a straight line toward the completion of the pattern.

It is apparent that the use of the concept of "maturation" by Lorenz and Tinbergen as well as by many other workers is not, as it at first appears, a reference to a process of development but rather to ignoring the process of development. To say of a behavior that it develops by maturation is tantamount to saying that the obvious forms of learning do not influence it, and that we therefore do not

consider it necessary to investigate its ontogeny further.

Heredity-vs.-environment, or development?

Much the same kind of problem arises when we consider the question of what is "inherited." It is characteristic of Lorenz, as of instinct theorists in general, that "instinctive acts" are regarded by him as "inherited." Furthermore, inherited behavior is regarded as sharply distinct from behavior acquired through "experience." Lorenz (1937a) refers to behavior which develops "entirely independent of all experience."

It has become customary, in recent discussions of the "heredity-environment" problem, to state that the "hereditary" and "environmental" contributions are both essential to the development of the organism; that the organism could not develop in the absence of either; and that the dichotomy is more or less artificial. [This formulation, however, frequently serves as an introduction to elaborate attempts to evaluate what part, or even what percentage, of behavior is genetically determined and what part acquired (Howells, 1945; Beach, 1947a; Carmichael, 1947; Stone, 1947).] Lorenz does not make even this much of a concession to the necessity of developmental analysis. He simply states that some behavior patterns are "inherited," others "acquired by individual experience." I do not know of any statement of either Lorenz or Tinbergen which would allow the reader to conclude that they have any doubts about the correctness of referring to behavior as simply "inherited" or "genically controlled."

Now, what exactly is meant by the statement that a behavior pattern is "inherited" or "genically controlled"? Lorenz undoubtedly does not think that the zygote contains the instinctive act in miniature, or that the gene is the equivalent of an entelechy which purposefully and continuously tries to push the organisms's development in a particular direction. Yet one or both of these preformistic assumptions, or their equivalents, must underlie the notion that some behavior patterns are "inherited" as such.

The "instinct" is obviously not present in the zygote. Just as obviously, it is present in the behavior of the animal after the appropriate age. The problem for the investigator who wishes to make a causal analysis of behavior is: How did this behavior come about? The use of "explanatory" categories such as "innate" and "genically fixed"

obscures the necessity of investigating developmental *processes* in order to gain insight into the actual mechanisms of behavior and their interrelations. The problem of development is the problem of the development of new structures and activity patterns from the resolution of the interaction of *existing* structures and patterns, within the organism and its internal environment, and between the organism and its outer environment. At any stage of development, the new features emerge from the interactions within the *current* stage and between the *current* stage and the environment. The interaction out of which the organism develops is *not* one, as is so often said, between heredity and environment. It is between *organism* and environment! And the organism is different at each different stage of its development.

Modern physiological and biochemical genetics is fast destroying the conception of a straight-line relationship between gene and somatic characteristic. For example, certain strains of mice contain a mutant gene called "dwarf." Mice homozygous for "dwarf" are smaller than normal mice. It has been shown (Smith and MacDowell, 1930; Keeler, 1931) that the cause of this dwarfism is a deficiency of pituitary growth hormone secretion. Now what are we to regard as "inherited"? Shall we change the name of the mutation from "dwarf" to "pituitary dysfunction" and say that dwarfism is not inherited as such—that what is inherited is a hypoactive pituitary gland? This would merely push the problem back to an earlier stage of development. We now have a better understanding of the origin of the dwarfism than we did when we could only say it is "genically determined." However, the pituitary function developed, in turn, in the context of the mouse as it was when the gland was developing. The problem is: What was that context and how did the gland develop out of it?

What, then, is inherited? From a somewhat similar argument, Jennings (1930) and Chein (1936) concluded that only the zygote is inherited, or that heredity is only a stage of development. There is no point here in involving ourselves in tautological arguments over the definition of heredity. It is clear, however, that to say a behavior pattern is "inherited" throws no light on its *development* except for the purely negative implication that *certain types* of learning are not directly involved. Dwarfism in the mouse, nest-building in the rat, pecking in the chick, and the "zig-zag

dance" of the stickleback's courtship (Tinbergen, 1942) are all "inherited" in the sense and by the criteria used by Lorenz. But they are not by any means phenomena of a common type, nor do they arise through the same kinds of developmental processes. To lump them together under the rubric of "inherited" or "innate" characteristics serves to block the investigation of their origin just at the point where it should leap forward in meaningfulness. [Anastasi and Foley (1948), considering data from the field of human differential psychology, have been led to somewhat the same formulation of the "heredity-environment" problem as is presented here.]

Taxonomy and Ontogeny

Lorenz (1939) has very ably pointed out the potential importance of behavior elements as taxonomic characteristics. He has stressed the fact that evolutionary relationships are expressed just as clearly (in many cases more clearly) by similarities and differences in behavior as by the more commonly used physical characteristics. Lorenz himself has made a taxonomic analysis of a family of birds in these terms (Lorenz, 1941), and others have been made by investigators influenced by him (Delacour and Mayr, 1945; Adriaanse, 1947; Baerends and Baerends-van Roon, 1950). This type of analysis derives from earlier work on the taxonomic relations of behavior patterns by Whitman (1898, 1919), Heinroth (1910, 1930), Petrunkevitch (1926), and others.

Lorenz's brilliant approach to the taxonomic analysis of behavior characteristics has had wide influence since it provides a very stimulating framework in which to study species differences and the specific characteristics of behavior. However, it does not necessarily follow from the fact that behavior patterns are species-specific that they are "innate" as patterns. We may emphasize again that the systematic stability of a characteristic does not indicate anything about its mode of development. The fact that a characteristic is a good taxonomic character does not mean that it developed autonomously. The shape of the skull bones in rodents, which is a good taxonomic character (Romer, 1945), depends in part upon the presence of attached muscles (Washburn, 1947). We cannot conclude that because a behavior pattern is taxonomically stable it must develop in a unitary, independent way.

In addition it would be well to keep in mind

that the species-characteristic nature of many behavior patterns may result partly from the fact that all members of the species grow in the same environment. Smith and Guthrie (1921) call such behavior elements "coenotropes." Further, it is not at all necessary that these common features of the environment be those which seem a priori to be relevant to the behavior pattern under study. Lorenz's frequent assumption (e.g., 1935) that the effectiveness of a given stimulus on first presentation demonstrates an innate sensory mechanism specific for that stimulus is not based on analysis of the origin of the stimulus-effectiveness, but merely on the fact that Lorenz has eliminated the major alternative *he* sees to the nativistic explanation.

Thorpe and Jones (1937) have shown that the apparently innate choice of the larvae of the flour moth by the ichneumon fly *Nemerites* as an object in which to deposit its eggs is actually a consequence of the fact that the fly larva was *fed* on the larvae of the flour moth while it was developing. By raising *Nemerites* larvae upon the larvae of *other* kinds of moth Thorpe and Jones caused them, when adult, to choose preponderantly these other moths on which to lay their eggs. The choice of flour-moth larvae for oviposition is quite characteristic of *Nemerites* in nature. In view of Thorpe and Jones' work, it would obviously be improper to conclude from this fact that the choice is based on innately-determined stimuli. Yet, before their paper was published, the species-specific character of the behavior would have been just as impressive evidence for "innateness" as species-specificity *ever* is.

Taxonomic analysis, while very important, is not a substitute for concrete analysis of the ontogeny of the given behavior, as a source of information about its origin and organization.

Levels of Organization

Levels of "Innateness"

Animals at different evolutionary levels show characteristic differences in the extent and manner of learning. In addition, within the same animal's behavior different activities may be more or less susceptible to the influence of learning, and may be affected in different ways by learning (Schneirla, 1948, 1949a).

Lorenz explains these facts in terms of the richness of the animal's instinctive equipment. As described above, his conception is that instinctive

behavior is sharply different from all behavior leading up to the performance of the instinct. This "appetitive" behavior is conceived of as the sole evolutionary source of all learned and intelligent behavior. Thus he says:

"... appetitive behavior, as the sole root of all "variable" behavior, not only is physiologically something fundamentally different from the automatism of instinctive behavior, but . . . the two different processes appear as "substitutes" (*vikariierend*) for each other, in that the higher (phylogenetic) development of the one makes the other superfluous and stops its development. The reaching of a higher psychic performance goes hand-in-hand with a reduction of the automatisms that take part in the action, leaving a behavior pattern with the same function as the one originally existing" (Lorenz, 1937a).

Again:

"It is a peculiarity of many behavior patterns of higher animals, that *innate instinctive elements and individually-acquired elements immediately follow each other*, within a functionally unitary chain of acts. . . I have characterized this phenomenon as instinct-training interlacement. Similar interlacements occur between instinctive acts and intelligent or insightful behavior. . . . The essence of such an interlacement is that, within a chain of innate instinctive acts there is a definite point, which point is innately determined, where a learned act is inserted. This learned act must be acquired by each individual in the course of its ontogenetic development. In such a case, the chain of innate acts has a *gap*, in which, instead of an instinctive act, there is a *'capacity to acquire'*" (Lorenz, 1937a). [All emphases are Lorenz's.]

It is apparent that Lorenz regards differences in the extent to which learning occurs as representing differences in the size of the gaps in the chain of innate behavior. He considers any given "component" of behavior as "innate" or not "innate." This is entirely consistent with his virtual identification of "innate" with "autonomously developing."

However, we have already tried to make it clear that behavior patterns classified as "innate" by *any* criterion do not all fall into the same category with respect to embryonic origin, developmental history, or level of organization. Lorenz notes that more or fewer of the components of behavior may be "innate." But nowhere does he recognize that *one* component may be more or less "innate" or "innate" in one or another *manner*. We may call attention to an important difference between the pecking of the chick and the nest-building of the rat, both behavior patterns which develop without specific practice of the patterns: a major part of the learning which appears to be antecedent to the emergence of pecking in the chick occurs before hatching, while

much of the learning which is antecedent to the emergence of nest-building in the rat occurs after birth.

Shall we call those behavior patterns "innate" which develop before birth and not those which develop after? This would be fruitless in view of the demonstrated existence of prenatal conditioning (Ray, 1932; Gos, 1933; Spelt, 1948; Hunt, 1949), and unsatisfactory in view of the problem of the so-called postnatal "maturation" of various "innate" behavior patterns (Grohmann, 1938). But we must recognize that different behavior patterns may involve learning at different ontogenetic stages to different extents, and in different ways. For example, much less of the behavior of the rat is *directly* a consequence of the specific characteristics of its structure than in the case of the earthworm (Maier and Schneirla, 1935). The involvement of learning in the development of the rat's behavior is different from and occurs at different developmental stages from that of the chick. Further, some responses of the rat (such as licking of a painful spot) are very much less subject to change by learning than others, such as care of young (Sperry, 1945; Uylert, 1946). These are not differences in the *number* of behavioral elements which are "innate," but rather in the *way* in which the structures are involved in the development of behavior at different evolutionary levels and for different behavior patterns.

Lorenz does not fully utilize the idea of levels of organization of behavior, apparently because his concept of "innateness" is not the result of analysis of the development of behavior; it is in part the result of a preconception that "innate" and "not-innate" are the two categories into which behavior logically falls. Consequently Lorenz and his school have classified behavior as "innate" and "not-innate" on the basis of criteria which when carefully examined appear to be arbitrary. Their category of "innate" therefore includes very different kinds of behavior, which involve learning in many different ways. Lorenz's concept of "innate" behavior represents a lumping-together of many different kinds and levels of behavior on the basis of an essentially phenotypic classification, and the imposition of preconceived categories upon that classification.

Evolutionary Levels

Since Lorenz does not discuss the existence of qualitative differences with respect to modes of

development within his category of "innate" behavior it is not surprising that his conception of the evolution of behavior lacks any notion of qualitative change. Lorenz maintains at all levels a sharp distinction between "instinctive acts" and "appetitive behavior" (which includes all oriented, goal-directed, and variable types of behavior at all levels). He says:

"If we consider the unbroken series of forms of corresponding modes of behavior, which extends in a smooth progression from protozoa to man, we must determine that we cannot distinguish between taxis, on the one hand, and, on the other, behavior guided by the simplest intelligence (Einsicht). We cannot here distinguish between taxis and, in the case of our frog, an intelligence which might (anthropomorphically speaking) be limited to the knowledge: 'There sits the fly'" (Lorenz, 1937a).

This is restated in a later paper (Lorenz, 1939): "No sharp line can be drawn between the simplest orienting-reaction and the highest 'insightful' behavior."

It might be pointed out that whether we can distinguish various levels of behavioral organization depends in part on our assiduity in *attempting* to distinguish them. Preconceptions about the number and kind of categories into which behavior ought to fall naturally has an important effect on the kind of examination we make of behavior patterns and the kinds of distinctions we find ourselves able to make among them.

In the quotation above we have translated as "smooth" (progression) Lorenz's word "stufenlose," which might be more literally translated "without steps" or "without levels." This is a gratuitous and very misleading oversimplification on Lorenz's part. The transition from protozoa to man is *not* "step-less." There are *characteristic* structural differences between phyletic levels, and these differences are responsible for *characteristic* differences in the organization of behavior. A protozoan is not like a simpler man. It is a different kind of organism, with behavior which depends in different *ways* on its structure. The analysis of behavior mechanisms at different levels (Schneirla, 1946) shows that it is frequently misleading to speak of *behavior* patterns or elements as homologous when they seem to serve similar (or the "same") functions and have superficially similar characteristics. Analysis of structural organizations out of which the specific behavior patterns emerge shows that similar behaviors at different phyletic levels often are end-products of evolutionary selection leading to the similar behavior, but deriving from different

structures so that the underlying processes and mechanisms are not the same.

Lorenz's application of the concept of evolutionary change does not consist of analyzing the different ways in which behavior patterns at different evolutionary levels depend on the structure and life of the organism. It consists rather of abstracting aspects of behavior, reifying them as specific autonomous mechanisms, and then citing them as demonstrations of "evolution" in a purely descriptive taxonomic sense. Taxonomically, this procedure is often extremely valuable, but by its implicit assumption that "elements" of behavior maintain their nature regardless of change in the organization in which they are embedded (more properly, we should say from which they emerge), it hinders rather than helps analysis of the behavior patterns themselves.

Levels of Neural Organization

Lorenz characterizes each instinctive act as depending on a specific center in the central nervous system which continuously produces a type of excitation specific to the act, and which is partly "used up" when the act is performed. He uses the concept "used up" quite literally, even suggesting the existence of act-specific *substances* (Lorenz and Tinbergen, 1938). One of the principal types of evidence used by Lorenz to support this conception is the lowering of the threshold for release of the act as a function of lapse of time since performance of the act. That is, the longer the animal has gone without performing the act, the easier it is to elicit. This is taken by Lorenz as evidence of accumulation of the reaction-specific energy in the central nervous system. Lowering of the intensity of performance upon repeated elicitation is taken as further proof, since it may indicate the using up of the excitation faster than it can be produced.

Lorenz and Tinbergen offer observations along these lines on mammals, birds, fish, and insects. The hunting behavior of the dog (Tinbergen, 1942), food-begging of a young bird (Tinbergen and Kuenen, 1939), fighting in a fish (Tinbergen, 1942), courtship flights of a butterfly (Tinbergen, Meeuse, Boerema, and Varossieau, 1942) are all offered as examples of instinctive acts having this kind of physiological basis.

Lorenz and Tinbergen adduce as physiological evidence for this interpretation a series of studies by von Holst (1935-1937), on the mechanisms of locomotion in fishes. Von Holst observed that

almost completely deafferented fishes show some of the coordinations of locomotion. He concluded that the basic movement patterns of locomotion are the result of the accumulation of locomotion-specific energy in the central nervous system independent of peripheral activity, and are the result of a central (non-reflex) coordination.

In his original consideration of von Holst's work, Lorenz (1937b) stated that it would be premature to make positive assertions about the direct relevance of that work to his instinct theory. Lorenz and Tinbergen (1938), at about the same time, stated that the conception of locomotion as an example of instinctive coordination in Lorenz's sense might be a very rough simplification of the facts.

However, over the years since then, the relevance of this kind of evidence in their writings seems to have increased, although some doubt has been thrown on the validity of von Holst's conclusions. One might question the direct relevance of the neural mechanisms of locomotion in fish and amphibians to the explanation of the origins of complex "instinctive" behavior in birds and mammals. Tinbergen is aware of the dangers inherent in the procedure of using physiological evidence from lower evolutionary levels, lower levels of neural organizations, and simpler forms of behavior as analogies for the support of physiological theories of behavior mechanisms at higher and more complex levels. For example, after a description of this aspect of Lorenz's theory, Tinbergen (1948a) says: "These formulations are supported by the entirely independent investigations which have been conducted during the last ten years on the central nervous mechanisms of locomotion. Here, *to be sure on a lower level of integration* [my emphasis—D. S. L.], we are brought to a fundamentally similar position by the researches of von Holst, Weiss, Gray, Lissmann, and others."

In this case, Tinbergen's mention of the fact that the physiological evidence comes from a lower level of integration is actually embedded in an *expanded* use of these data to support theories based on observations at higher levels. This is merely a formal bow to the concept of levels, which appears to strengthen the form of the argument while actually weakening its content.

In point of fact, it is now doubtful whether even so simple a behavior pattern as locomotion, in so simple a vertebrate as a fish, is really organized in the way that Lorenz's instinct theory demands.

Gray and Lissman (1940, 1946a, 1946b; Gray, 1939, 1950; Lissmann, 1946a, 1946b) have studied the effect of deafferentation on locomotion in fish and amphibians. Both regard their evidence as being against the probability of automatic-rhythmic production of coordinations in the central nervous system, even at the fish level, and even for locomotion. Lissmann, in fact, designed his experiments specifically in view of von Holst's observations, and explicitly in view of the use made of the latter by Lorenz. He concluded, on the basis of a *complete* afferent isolation of the central nervous system, that there was no central automatic production of excitation. It should be noted that the experiments of Weiss (1936, 1937a-d, 1941, 1950) support the conclusion that spinal centers in amphibians are so organized that the coordination of locomotor patterns is dependent upon characteristics of the centers. Gray and Lissmann's experiments, however, show that proprioception actually plays a major role in the normal ambulatory rhythms, even of these animals.

Tinbergen (1942) has expanded Lorenz's concept of neural organization to include higher levels of physiological and behavioral organization than the stereotyped "instinctive act" or consummatory act. Tinbergen conceives of instinctive behavior in general as being hierarchically organized in the individual. For example, in the reproductive behavior of the stickleback Tinbergen sees three main levels of organization, hierarchically arranged. The highest level represents the reproductive drive in general. This corresponds to a center at a high level in the nervous system which when activated (by external conditions, hormones, or autonomous cyclicity) sends impulses to a whole group of intermediate centers, making the latter capable of activity. Each of these intermediate centers corresponds to a behavior pattern involved in reproductive activities: fighting, nest-building, courting, parental behavior, etc. Each of these intermediate centers, in turn, activates (or contributes to the disinhibition of) a group of lower centers each of which coordinates a particular act which is released by an innate releasing pattern. For example, the fighting center, when activated by external stimulation (which can only occur when its threshold is lowered by activity in the superordinated center for the reproductive drive in general) puts the animal in "fighting mood" which makes possible the performance under proper stimulus-conditions of each of the acts

involved in fighting: biting, chasing, threatening, etc. The latter are the "consummatory acts" or "instinctive acts" of Lorenz. [N. B. The slight differences in terminology sometimes occurring between Tinbergen and Lorenz do not usually represent theoretical or conceptual disagreements.]

Tinbergen cites the work of Hess (1943, 1949) as demonstrating the reality of these autonomous centrally-coordinated centers of activity. By electrically stimulating various points in the hypothalamus, Hess was able to cause cats to perform sleeping, eating, and other behavior which was not related to specific external stimulation, and which ceased upon cessation of the stimulation. Tinbergen regards these observations, with those of von Holst, as demonstrating the reality of Lorenz's picture of centers of automatic-rhythmic production of action-specific excitation.

Hess found, however, that there was considerable variation in the responses to repeated stimulation of a specific spot in the hypothalamus. Stimulation of the same point might elicit quite different responses, depending upon the conditions of afferent inflow. This led Hess to conclude that there was not strict localization of function in the hypothalamus as (he assumed) there is in the cortex. [It might be pointed out that recent discussions of cortical function indicate considerable doubt about the reality of localized functions isomorphic with their behavioral expressions, even in the motor areas of the cortex (Lashley, 1923; Hines, 1947; Clark and Ward, 1948; Clark, 1948).]

Now, a strictly punctate localization of function is not necessary, either in cortex or in hypothalamus, in order that these organs be able to serve organizing and coordinating functions. In the light of Hess's work there is no doubt that the lower-level details and components of many behavior patterns are coordinated and integrated in the hypothalamus. But it is difficult to see how the shifting locus of this integration can be reconciled with the conception of a *center which produces an excitation* specific for the behavior patterns concerned. It is equally difficult to reconcile the fact that the function of a "center" depends partly on the type of afferent inflow present with the notion of the center as a place where excitation is produced for a particular kind of act.

Neither do the researches of Hess, nor those of Gray and Lissmann, support the idea that rhythmicity or cyclicity of behavior is a function of the periodic reaching of a threshold level of energy

produced in such centers. As suggested by Gray and Lissmann, rhythmicity of behavior is much more parsimoniously explained in terms of periodic shifts in balance between central and peripheral processes or interaction between different central processes, than in terms of the production of periodic impulses by a single "center" which, in Lorenz's treatment, has the character of a "thing in itself."

Lorenz (1950) describes in some detail a hydraulic model, or analogy, of the instinct mechanism, including a reservoir of excitation and devices for keeping it dammed up (innate releasing mechanism) until appropriate keys unlock the sluices. Hydraulic analogies have reappeared so regularly in Lorenz's papers since 1937 as to justify the impression that they are not really analogies—they are actual representations of Lorenz's conception of the origin and channelling of "instinctive energy." [The basic assumptions—of a special center producing a reservoir of energy specific for each instinct, and of devices for distributing the energy—are very similar to those of MacDougall (1923, 1930).]

There is no neurophysiological evidence for such hydraulics in the brain. Aside from the controversial aspects of the idea of automatic-rhythmic production of excitation, such hydraulic conceptions simply do not conform with what we actually know about the complexities of brain function (cf. Fulton, 1949).

The actual physiological relationships underlying behavior patterns must be *analyzed* for the different behavior patterns concerned. The assumption which underlies Lorenz's approach to the neurophysiological basis of behavior is that the neural events underlying behavior patterns must somehow be isomorphic with the behavior itself. He is thereby led to assume that behavior patterns having similar functional characteristics must be caused by identical neural mechanisms. Lashley (1942) has pointed out the erroneous nature of such reasoning. It is by thus abstracting phenotypic resemblances in behavior at different levels, and by gratuitously transferring physiological explanations from one level to another that Lorenz creates the impression that "instinctive" acts are grounded in a common type of mechanism which is the same at different evolutionary levels.

Levels of Behavioral Function

As already pointed out, a serious question facing all investigators of animal behavior is the extent to

which different mechanisms may be assumed to be identical because of the apparent similarities in the behavior patterns they underlie. By this I do not mean to imply that the similarities may be unimportant, but only that functionally similar behavior patterns may be effectuated through very dissimilar causal mechanisms. And if the causal mechanisms hypothesized in the case of one of the behavior patterns are conceptually reified and applied to other patterns or other animals, because of the fact that the similar behavior patterns are subsumed under the same term or included in the same category or concept, the analysis of the mechanisms actually operating in the different cases is seriously hampered. Rather than making a developmental analysis of the processes concretely underlying each behavior pattern, the predominant tendency is to carry out brief studies on a variety of *selected* examples assumed to demonstrate the validity of the a priori "principle" or the reality of the hypothesized structure or "center."

This practice may produce very fallacious results. For example, both the amoeba and the neonate infant will move toward weak stimulation and away from strong stimulation (the amoeba as a whole, the child locally). In both animals, this serves the biological function of bringing the organism into contact with food (and for the child, protection), and away from contact with harmful stimuli. This similar biological utility is a sufficient basis of explanation for the evolutionary development of the similar modes of behavior in the two organisms.

But the *mechanisms* underlying the response in the two animals manifestly must be very different. In the amoeba, the differential response to weak and strong stimuli is caused by the differential effects of the weak and strong stimuli on the sol-gel relationship in the protoplasm of the single cell (Mast, 1926). In the neonate child, the basis is more obscure. Schneirla (1939) has suggested that initially it is the result of differences in arousal-threshold between flexor and extensor muscles of the limbs, so that they respond optimally to different impulse-frequencies in afferent volleys, corresponding to different intensities of stimulation.

These two behavior patterns may seem functionally quite analogous. Can we say that they are homologous? This would obviously be absurd. They represent two totally different kinds of adjustment, both selected (in the evolutionary sense) because they serve the same kind of function. Nor is there a "smooth progression" between the pro-

tozoan response and the human. At each level, the *mechanisms* underlying this characteristic and widely-distributed response (Maier and Schneirla, 1935) are derived from the specific structure of the organism in question. The behavior patterns are not homologous, although they *may* in some cases be based to different extents and in different ways on more or fewer homologous structures. The *analysis* of the behavior at each level must be in terms of its emergence from the structure of organisms at that level, as indicated in the examples of the amoeba and the neonate child, and *not* on superficial comparisons of the behavior with similar behavior patterns at other levels.

Lorenz's concept of "instinct" represents, I think, precisely this kind of undesirable reification of a hypothesized mechanism. Lorenz's use of the term "instinct" does not denote merely a group of behavior patterns characterized by certain common functional characteristics; it denotes a definite class of things—a specific group of homologous structures underlying acts *whose characteristics are isomorphic with those of the structures*. And the nature of the structures is inferred from the behavioral characteristics, supported by physiological evidence the inadequacy of which has already been pointed out.

This reification of the concept of "instinct" leads to a "comparative" psychology which consists of comparing levels in terms of *resemblances* between them, without that careful consideration of *differences* in organization which is essential to an understanding of evolutionary change, and of the historical emergence of new capacities. Thus the lowering of intensity of response as a consequence of repeated elicitation, in the case of certain sexual activities of a butterfly (Tinbergen, Meeuse, Boerema, and Varossieau, 1942) and of a fish (Tinbergen, 1942) is taken in both cases as verifying Lorenz's assumption of the nature of the organizing center for an instinctive act. The fact that some behavior patterns of a butterfly may exhibit functional similarities to some behavior patterns of a fish is interesting as an indication that similar response characteristics may be species-preserving in both cases. But it is not very judicious, and actually is rash, in view of the very different types of organization involved in the structure and the behavior of the two animals concerned, to assume that the mechanisms underlying the two similar response characteristics are in any way identical, homologous, or even similar, or that there is any historical (evolutionary) con-

tivity between them *as such*. Yet this is precisely the basis of Lorenz's whole treatment of "instinct" and evolution.

In addition to distorting comparative study and the study of evolutionary change, this reification of "instinct" has unfortunate effects on the study of ontogenetic development. The development of an "instinctive" act inevitably appears to Lorenz to be the self-differentiation of a preformed, autonomous thing. Thus Lorenz sees the developing behavior of the animal as progressing *toward* the full-blown "instinct" rather than as developing *out of* interactions among processes present at that stage. This is a teleology which is inherent in Lorenz's approach, and which cannot be eliminated by his formal attempt to deny teleological and purposive procedures and to exclude the terminology.

For example, Lorenz mentions the development of fighting behavior in ducks. When fighting with another drake, an adult drake will grasp its opponent's neck in its bill and strike at him with a wing. Lorenz noted that ducklings whose wings had not yet feathered would perform the same movements even though the stubby, unfledged wing was not yet long enough to strike the opponent. Lorenz's interpretation (1937a) is that the instinctive act had matured before the full maturation of the structure which was used by it. This interpretation does not explain what the *duckling* is doing; rather, it prevents the investigator from seeing the problem of what it is about the duckling and its situation (and its ontogenetic history) which gives rise to this kind of behavior. This type of theory apparently causes the investigator to look at the process of development in such a way that the problem of the *origin* of this behavior, and its cause and role *in the duckling* are not considered by him at all. In the light of our previous discussion, it would appear that these are the crucial problems, and that a theory which makes them appear as relatively irrelevant to the explanation of the development of fighting behavior must be seriously lacking.

This conceptual merging of very different levels on the basis of superficial similarities permeates the system. For example, the concept of "taxis" as a meaningful class of behavior elements seems to be based on such a procedure. Lorenz defines a *taxis* as a movement which is continuously oriented with respect to the stimulus (thus distinguishing it sharply from an instinctive act which, once started, is centrally coordinated, independent of the receptors).

Tinbergen (1942) further classifies taxes into several categories, based partly on Kühn's (1919) analysis: (1) tropotaxis, equivalent to Loeb's tropisms, in which the animal turns until the relevant stimulus is equally intense on both sides; (2) telotaxis, a visual orientation based on fixation movements so that either eye can serve as the sole receptor; and (3) menotaxis, like telotaxis except that the orientation, instead of being toward the stimulus, is at a constant angle from it. To these categories of Kühn, Tinbergen added a fourth: pharotaxis, in which the animal is oriented to a part of the visual field defined in terms of its relation to the rest of the field, irrespective of the animal's orientation to the field.

This classification of "taxes" solely in terms of a highly restricted definition of the receptor processes inevitably lumps together many very different processes. For example, our amoeba and newborn infant both show a "turning-to" reaction to mild stimulation. What possible category, based on the characteristics of the turning, could properly include both of these movements as examples of one kind of process? To say that the movement of the child and of the amoeba are both a *taxis* is to admit that the word "taxis" does not define a group of behavior patterns which have common mechanisms.

Tinbergen (1942) makes this explicit when he says: "... in the concept of pharotaxis the part played by mnemonic processes is not taken as a criterion, because in tropo-, meno-, and telotaxis the criterion upon which the 'distinction' is based also leaves this topic out of consideration... Menotaxis, for instance, can be innate or learned."

What then remains of Tinbergen's classification? Tinbergen himself is aware that the members of any of his *taxis*-categories probably differ widely in ontogenetic origin and central mechanism. How can the classification be justified? A preliminary classification has heuristic value only if the members of a given class are thought to be representative of similar dynamic processes which can be investigated. That, in fact, is the purpose which Tinbergen assumes for his classifications. But in the case of taxes, the classifications are known to contain different levels of organization and different processes. In this case the classification is based on the analogizing which appears to be basic to the Lorenz approach.

Lorenz (1939) and Tinbergen (1942) have both pointed out that, under the influence of natural selection, widely divergent species may develop

similar characteristics which should not be assumed to be homologous. Tinbergen (1948) gives an example of this "convergent evolution": "The most striking example of how far convergencies can go in these phenomena, is given by L. Tinbergen (1939) in his study of the mating behavior of the cuttlefish *Sepia officinalis*. Parallel with the development of eyes in cephalopods (convergent to those of fish) the courtship of the cuttlefish has evolved into a typically visual one closely resembling the courtship of certain sexually dimorphic fish, lizards, and birds. . . . This state of affairs closely resembles that found by Noble and Bradley (1933) in [the lizard] *Sceloporus*. In both species the male's display is primarily a means of threatening other males. . . ."

It will be noted that Tinbergen specifically notes that the resemblance is caused by convergence, rather than homology. However, his treatment of the behavior patterns involves the implicit assumption that the convergence is one of *mechanisms*. Actually, as far as we know, the convergence is only of *outcomes*. The assumption that the mechanisms underlying these similar outcomes are equally similar is both characteristic and gratuitous.

The Human Level

This analogizing and confusion of levels becomes patently shallow when either Lorenz or Tinbergen discusses human behavior.

For example, Tinbergen (1942) says, "The activation of other drives, too, leads to searching behavior. Classical examples are the searching for a nesting site in birds, for a house in man, etc." It is difficult to see what valid explanatory purpose can be served by such an inappropriate juxtaposition, based on the mere fact that the *outcomes* are similar *from the human point of view*.

Tinbergen (1942), speaking of "instinctive" acts which appear without external stimulation, as the result of extreme lowering of the threshold because of long non-elicitation, says, "Lorenz . . . discovered that various activities may occur in cases, where neither proprioceptive stimuli nor hormones could possibly be the driving causes. The simplest instance of this kind of vacuum activity is the hunting behavior of the well-fed dog. As every dog-owner knows, a dog can by no means be prevented from making hunting excursions by supplying it with ample food. Other instances of a similar kind are familiar to us by introspection. Sports,

science and so many other activities certainly have connections with internal factors of this kind."

Here the implication seems to be that, because both are "spontaneous" and neither is mainly caused by proprioceptive stimuli or hormones (itself a gratuitous assumption), therefore the causes of hunting activity in the dog are the same as (or belong to the same class as) those of scientific activity in human beings! It is obvious that this argument is based on the most casual and un-analytical kind of comparison, and a lack of concern with the specific origins of the behavior patterns at issue.

Lorenz (1937b), speaking of the evolutionary relation between instinctive and learned acts, says:

"The presence of an instinctive act also seems to be detrimental to the development of an intelligent process having the same function. At least, it is true of humans. To be convinced of the correctness of this statement, one has only to consider the behavior of highly intelligent men who have otherwise good critical faculties, when they 'fall in love' to carry out the undoubtedly instinctive reaction of mate-selection. The already-mentioned example of the ravens and jackdaws shows that higher psychological development may occur without any reduction of the instinctive, innate members of a behavior chain. . . ."

I include the last sentence to show how very easily Lorenz switches from man to bird without any apparent awareness that he is discussing phenomena which may be very different. The point of Lorenz's statement seems to be that men fall in love irrationally because "falling in love" is an instinctive reaction released by an innately-determined situation. In this case the unreality of the concepts used is apparent to any student of *human* behavior, although it may not be so to one of bird behavior—a fact which itself indicates that the source of the unreality lies partly in Lorenz's merging of different levels on the basis of superficial similarities.

Many other examples of Lorenz's interpretation of human behavior could be cited. For example (Lorenz, 1940), he interprets the relative attractiveness to women of several breeds of dog in terms of the degree to which they fit the innate perceptual pattern releasing instinctive maternal behavior in the human individual! This, again, is entirely derived from a too facile analogy with less complex kinds of animals. Recent work with chimpanzees reared in darkness (Riesen, 1947) and with congenitally blind human beings whose sight had just been restored by surgery (Senden, 1932) indicates

that, at least at these phyletic levels, any response to or perception of visual shapes, proportions, sizes, and relationships can only occur as the result of a long and complex learning process. Under these circumstances it is most difficult to assign any meaning whatever to Lorenz's assertion that these responses are based innately on perceptual characteristics of shape and proportion (Hebb, 1949). [Lower mammals apparently require less learning for the establishment of some of their characteristic modes of response to the visual field (Hebb, 1937a, 1937b; Lashley and Russell, 1934).]

The interpretation of human behavior in terms of physiological theory based on lower levels is carried one step further when Lorenz (1940) equates the effects of civilization in human beings with the effects of domestication in animals. He states that a major effect is the involution or degeneration of species-specific behavior patterns and releaser mechanisms because of degenerative mutations, which under conditions of domestication or civilization are not eliminated by natural selection. He presents this as a scientific reason for societies to erect social prohibitions to take the place of the degenerated releaser mechanisms which originally kept races from interbreeding. This is presented by Lorenz in the context of a discussion of the scientific justification for the then existing (1940) German legal restrictions against marriage between Germans and non-Germans.

The directness of Lorenz's application of the concept of innate releasers to human social relations may be gaged by the following quotation (1940): "The face of an Asiatic is enigmatic to us because the physiognomic characteristics to which our innate perceptual patterns respond are not connected with the same behavioral characteristics as in our race. . . . In all likelihood, this function (of recognizing facial characteristics) cannot be substituted for by experience, as has been determined by many people who are acquainted with foreign races."

Social psychologists will all agree that the various degrees of difficulty which different people have in learning to recognize and respond to facial expressions in a culture different from their own is at least partly dependent upon the attitude with which they approach the strange culture to begin with.

The Sources of Motivation

Lorenz states that as the level of action-specific energy in the central nervous system rises the

animal is set into activity. He says (1937b), "It is one of the most important and most remarkable features of the instinctive act, that the organism does not wait passively for its release, but *actively seeks these stimuli*." This active seeking is called "appetitive behavior" (Craig, 1918). It may range from simple turning movements ("taxes") to the most complicated kinds of intelligent behavior. As has already been pointed out, Lorenz regards these as being continuous with each other, both being (at different stages of evolutionary development) means of bringing the animal into a situation containing the stimuli which will release an instinctive act (viz., eating, copulation, etc.).

Lorenz recognizes a few instances of motivation the source of which is peripheral (viz., hunger, defecation, etc.). But he adopts the characteristic procedure of lumping together all "goal-directed" (i.e., adaptive) behavior which does not have an immediately obvious peripheral motivation under the rubric of "appetitive behavior." His conception of "peripheral sources of motivation" is practically limited to the examples just given. I do not recall any reference in any of the writings of either Lorenz or Tinbergen to the autonomic nervous system, or to the possibility of qualitatively different roles of the autonomic nervous system at different phyletic levels, or to the possibility of complex peripheral changes caused by hormones, as sources of motivation (cf. Beach, 1948). One result is that the referring of motivation to the action-specific "centers" in the central nervous system is often like the concept of "innate behavior" itself, simply a substitute for actual analysis of the biology of the specific case. For example, Tinbergen (1951) says that injection of prolactin into a dove has two effects: (1) it causes development of the crop gland, and (2) it causes brooding behavior. It is thus more or less taken for granted that the behavioral effect of the hormone is somehow a specific one; developmental analysis of relationships between broodiness and crop-gland or brood-patch stimulation is excluded by the nature of the instinct theory, and of the consequent theory of motivation. In the case of "dominance" behavior in the chimpanzee Birch and Clark (1950) have shown that behavioral effects of hormones may actually be mediated by peripheral structures in situations where it is not at all apparent a priori that "proprioceptive stimuli" can play a role.

Lorenz regards all purposive (adaptive) behavior as being directed toward the performance of the instinctive acts. For Lorenz, it is the *performance of*

the *instinctive act itself* which serves as the animal's goal. Thus he says (1937a):

"... in a man working with the motive of getting food, the behavior directed toward this goal includes many of the higher psychic performances of which he is capable; the 'motive' (goal)—the instinctive act of 'biting and chewing'—has become drawn back to the end of a long series of acts, without, however, thereby in any way denying its fundamentally instinctive nature."

Thus to Lorenz, the statement "man works in order to be able to have released [by food] the instinctive act of biting and chewing" is the *same* kind of statement as "the frog turns to the right in order to be able to have released [by the sight of a fly in front of him] the instinctive act of flipping out his tongue." He regards these two goal-directed behavior patterns as being (in the evolutionary sense) continuous with each other, and both as having the same kind of relationship to the instinctive act which is the end-member of the behavior chain. However, such a formulation is misleading and of little heuristic value. The actual complexity and variety, and situational relevance, of the sources of human motivation make such statements meaningless, not merely because human motivation is more complicated than that of the frog, but because it is qualitatively different in organization and development.

Tinbergen's equation of the causes of sports and scientific activity with those of hunting in the dog, because both appear to be internal and "self-exciting," is perhaps an extreme example of the result of analogical methods of approach, and of the belief that every behavior must have some center isomorphically corresponding to it in the nervous system.

HYPOTHESIS AND OBSERVATION

The "Innate Releasing Mechanism"

It may be instructive to examine some ways in which Lorenz's theoretical approach is expressed in an investigation of behavior.

Tinbergen and Kuenen (1939) studied the stimulus situations eliciting and directing the gaping (food-begging) movements of young thrushes. The gaping movement consists at first of vertically directed stretching of the neck, and opening of the mouth. The birds are blind at hatching; their eyes do not open until about 9–10 days of age. During this first blind phase gaping can be most easily elicited by tapping or jarring the substrate. When the eyes first open the bird

normally lies with its eyes closed, and opens them only when it is gaping. Tinbergen and Kuenen state that the bird will gape in response to a moving visual stimulus as soon as the eyes open, and that the innate releasing pattern for gaping therefore includes visual stimulation. For the first day or so after the eyes open gaping is not *directed* toward a visual stimulus; even though the stimulus will elicit gaping, the gaping is still directed vertically upward. However, after about one day the gaping begins to be directed toward certain defined parts of the visual stimulus (highest, nearest, break in outline, etc.).

Tinbergen and Kuenen's conclusions are that the "centrally-coordinated" instinctive act and the (continuously-directed) taxis mature at different rates, the taxis not maturing until 10 days or so of age while the instinct is fully mature at hatching. In addition, they conclude that the adequate stimulus-situations for releasing and for direction of the act are different, and are both innate.

First, a word about the "maturation of the taxis." It is not clear why the animal's experience during the first day after its eyes open is not an adequate reason for its development of orientation toward the visual stimulus. Tinbergen and Kuenen maintain in their discussion that some of the specific features of the stimulus toward which orientation occurs are not learned by direct experience. However, it is not clear that the *orientation* toward the visual stimulus is not a result of experience. Even their limited discussion of possible learning is based on inferences from incidental observations, indicating that Tinbergen and Kuenen's orientation toward Lorenz's theory led them to discount the serious possibility of learning being involved.

The "innateness" of response to moving visual stimuli is quite ambiguous. It will be recalled that the birds lie with their eyes closed for much of the time just after their eyes have first opened. I quote from Tinbergen and Kuenen's protocols:

"5/26/36. Black Thrush, 9–10 days. Lifting and moving back and forth of the wooden covers evokes no reaction. They gape immediately to a tap on the nest. When the gaping subsides, we move our hand back and forth over the nest, and the birds instantly beg strongly.

"Later on the same day: Tap on the closed box releasing gaping. Subsequent lifting of the cover does not; the eyes are closed. Tap causes gaping. After cessation of the reaction, the animals remain lying with open eyes. We hold over the nest, one after the other: a black disc, a white wooden rod . . . and a black wand. . . . All the objects are reacted to by violent gaping.

"5/10/36. Song Thrush, 10 days. Preliminary lifting

of the cover causes no reaction; light tap does. After the birds begin to calm down, a finger shown over the nest immediately releases gaping."

It is apparent that normally the *first times that young thrushes see visual stimuli they are already in a state of gaping excitement*, since at first their eyes are open only when they gape.

I have verified these findings on young red-winged blackbirds (*Agelaius phoeniceus*), on which I could repeat all of Tinbergen and Kuenen's observations. However, I was able by watching the birds for several consecutive hours to note several occasions on which one or another of the birds was lying quietly with its eyes *open*, when it had not recently gaped. Such birds would *not* gape in response to a moving finger above the head, although they might move their heads to fixate the finger. If I tapped the nest, thus causing gaping, and then moved my finger over the birds when gaping was subsiding, or shortly thereafter, the bird would gape instantly and vigorously. What is meant then by the statement that the birds gape "innately" to visual stimulation? It would be easy to produce ad hoc assumptions about temporary changes in threshold of the innate releasing mechanism as a result of tactual stimulation. But these must be recognized as ad hoc. The possibility should be recognized that any stimulation to which the bird is sensitive will increase the activity of the bird when it is already gaping, and may become associated with gaping, so that the later-apparent specificity of response to visual stimuli may be a consequence, not of innate connections, but of the conditions under which visual sensitivity normally first becomes possible. In addition, these birds must be fed almost every hour, and the possible relevance of association of visual stimulation with food reinforcement should not be overlooked. In this connection we may note the experiments of Padilla (1930), who found that chicks that were kept in the dark and force-fed for the first twelve days of life, so that they had no opportunity to associate pecking behavior with visual stimuli or with food, would when placed in a normal feeding situation starve to death without ever giving any sign of the allegedly "innate" pecking behavior.

It should be noted that the conditional nature of the effectiveness of visual stimuli is indicated by Tinbergen and Kuenen's own protocols, but that evidently these authors have not really considered these facts. This, I think, is because they are

a priori convinced that the developmental process is a maturational one, and that they therefore do not have to analyze its conditions. The Lorenz theoretical approach tends to restrict the recognition of significant details and to obscure possibly relevant features of developmental processes.

Many cases of "innate releasing mechanisms" seem to suffer from a similar approach. It will be recalled that the innate releasing mechanism is regarded as a "preformed neural mechanism" (Lorenz and Tinbergen, 1938) for the release of the instinctive act. Tinbergen refers to the releasing stimuli as "sign stimuli" because they "represent" the biologically appropriate object of the instinctive act. One might ask "Sign of what? Sign to whom?" There is a subtle anthropomorphism about the concept of innate releasing mechanisms which is not at first apparent. For example, Lorenz and Tinbergen (1938), in discussing the egg-rolling of the gray goose, speak of an innate releasing pattern corresponding to the situation "egg outside the nest." Now, "egg outside the nest" is *not* the perceptual situation to the bird—it is the perceptual situation to the human observer. When Lorenz and Tinbergen investigate the effective features of the situation, they are looking for a pattern of stimuli corresponding to a "pattern" which they presume to exist in the central nervous system. Consequently, there is never any analysis of any possible *specific* relationships between effective stimuli and the structure or physiology of the organism concerned. Thus the described stimulus-situations become structured in human terms (bird of prey, vegetation, the parent's head, etc.) instead of in terms indicative of the problems of specific relationships between the structure and function of the animal being investigated. This approach, again, derives from Lorenz's identification of every behavior pattern with a specific hypothetical "center," rather than with the coming into play of specific structural-functional relationships, which may be very different in different kinds of organisms and for different behavior patterns.

For example, Tinbergen (1948b) says: "The escape reactions of many birds from passing birds of prey are a response to a type of movement and to a special characteristic of shape, namely, 'short neck.'" Now, it is certainly true that many birds perform "escape" movements at the sight of a "short-necked" bird flying overhead (Krätzig, 1940). But Tinbergen says "short-necked" rather

than, for example, "having a short and long projection at opposite ends, and moving so that the short projection is anterior." His usage is, of course, more convenient, as he makes clear. But in addition it derives from, and in turn reinforces, the Lorenzian notion that the "short-neckedness" is a perceptual "sign" or "sign stimulus" (Tinbergen, 1939) which corresponds innately to a preformed neural "releasing" mechanism. Instead of leading to an analysis of the specific patterns of excitation of sensory elements in the bird's eye which are required for the elicitation of the response, and a further consideration of the effect of such patterning on central nervous activity in the nervous systems of these birds, Tinbergen's terminology requires the identification of the bird's readiness to perform "escape movements" with a preformed "conception" of the short-necked character of hawks. Thus, "the partridge runs for cover from an overhead object with a short neck," and "the goose rolls back to the nest an object lying near the nest which is smooth-contoured and hard-surfaced," become not *definitions* of the problem of how the structure of the various birds makes it possible for them to react to their environment, but rather *solutions* to the question: "What are the characteristics of these two members of the class of innate releasing mechanisms?" The essential assumption of Lorenz's approach is that these two types of behavior are related to environmental stimuli by means of mechanisms that are basically identical except for the perceptual details themselves. When extended (as it is) to the whole animal kingdom, this approach becomes profoundly anti-evolutionary, in spite of Lorenz's concern with "comparative" studies.

Lashley (1949) has noted with some approval Lorenz's studies of releaser patterns. For example he has said:

"A study of complex instincts requires a detailed analysis of the exact stimulus or combination of stimuli which call forth the behavior, combined with descriptions of the behavior elicited. This has been attempted under controlled conditions only for some instinctive behavior of birds (Lorenz, 1935)."

However, a closer examination of Lashley's concepts and those of Lorenz will show that the subsequent development of Lorenz's approach was not at all in the direction anticipated by Lashley. Lashley (1949) says:

"The nesting tern seems to notice no difference

when her eggs are dyed... but is... disturbed if their... contour is altered by sticking on a bit of clay or putty... smoothness of outline is the essential character of the egg. This is the sort of property that can be most easily interpreted in terms of the inherent tendencies to functional organization in the nervous network.

"I do not mean to imply by this that the geometry of the web of the spider is exactly represented in the spider's brain... The angle of radii may be determined by the angle at which the legs are held (Peters, 1937); the completeness or incompleteness of the orb may depend upon the readiness with which certain postures are assumed in relation to gravity... The simple nest of the rat is piled and pushed about until it satisfies certain sensory requirements of reduced heat loss. The orb of the spider is perhaps a composite of such sensory requirements combined with some specialized geometrical perceptions such as are illustrated by the rat's more ready recognition of a... circle than of irregular ink blots."

In contrast to this approach, Lorenz (1935) has used the analogy of a key unlocking a lock, to describe the function of the releasing pattern in releasing an instinctive act. To pursue this analogy, Lashley would regard it as the task of the locksmith-investigator to investigate all the characteristics of lockopening devices, including keys, picklocks, and any other means of opening the locks; and to consider these characteristics together with what he knows of the structure of locks, the conditions of their use, their history, etc., in order to gain an understanding of how the functions of the various kinds of locks are related to their structure. To Lorenz on the other hand, all the locks are basically alike, so that investigations of the characteristics of the keys required to open them reveals nothing about internal differences among lock mechanisms, but only about the specific arrangement of tumblers in each lock.

All of this should not be taken to mean that we do not recognize that relatively simple stimuli may sometimes lead to the appearance of quite complex behavior. As a matter of fact, some of the best studies of stimulus-conditions eliciting various types of animal behavior have been carried out by Lorenz and Tinbergen and their associates (e.g., Tinbergen and Perdick, 1950). The point is not to deny the existence of simple stimuli which under some conditions lead to complex behavior. Rather, it is that the assigning of the locus of activity to a hypothetical center in the brain, with characteristics predeterminedly and isomorphically corresponding to those of the stimulus situation, represents an unphysiological way of thinking disguised in physiological terms.

"Vacuum Activities"

The so-called "vacuum activities" or Leerlaufreaktionen are regarded by Lorenz and Tinbergen as evidence of the accumulation of reaction-specific energy in the instinctive center until it "forces" its way through the inhibiting innate releasing mechanism and "goes off" without any detectable external stimulus.

Lees (1949) has cited the example of the cyclical colony activities of the ant *Eciton hamatum* (Schneirla, 1938) as an example of "something akin to 'vacuum activity.'" Colonies of this army ant pass regularly through *statory* and *nomadic* phases, each lasting about 20 days. As Lees points out [based on Schneirla's (1944) description]:

"During the statory phase the bivouac, to which the single queen is confined, remains *in situ* and raiding activities are minimal. During the nomadic phase the position of the bivouac is changed each nightfall and strong raiding parties emerge from the colony. This activity is in no way related to the abundance or scarcity of food in the neighborhood. . . ."

This cyclic behavior thus appears to Lees to have the character of a "vacuum activity," in that it occurs periodically without any noticeable change in the external stimulus-conditions. This is very misleading, for Schneirla's (1938, 1944) analysis of this behavior has shown that the change from statory to nomadic behavior is a consequence of the growth of a great new brood of ants. When the callow workers emerge from their cocoons, their movements stimulate the adult workers to great activity. As the callows mature and cease to be dependent on the adults, their energizing effect is lessened. At this point, the emergence of wriggling larvae from the eggs supplements the diminishing activating effect of the callows on the adults. When the larvae pupate, and become inactive, the adults are no longer subject to trophallactic (Wheeler, 1928) stimulation, and the colony changes to its statory period.

The point that is relevant to our discussion is that Schneirla's analysis leads to a conception that is the *opposite* of that implied by the notion of "vacuum activity." The periodic recurrences are *not* the result of the building up of energy in any animal's nervous system. They are the result of the periodic recurrences of inter-individual stimulating effects. The behavior is not represented "in advance" in *any* of the animals in the colony; it emerges in the course of the ants' relationships with one another and with the environment. There

is no "reaction-specific energy" being built up. The periodicity is a result of the periodicity of the queen's egg-laying, which is *not* a "center" having *any* characteristics corresponding to the behavior. And even this is not a *direct* relationship. If the number of larvae in a colony is experimentally reduced by 50 per cent, thus reducing their total stimulating effect, a normal nomadic phase cannot occur. Recent findings (Schneirla and Brown, 1950) have in fact confirmed the hypothesis that each of the regular large-scale egg-delivering episodes in the queen's function basic to the cycle is a specific outcome of her over-feeding, due to a maximal stimulation of the colony by the brood. This event, occurring inevitably at the end of each nomadic phase, is a "feed-back" type of function, not at all related to the implications of "vacuum activity."

The restrictive nature of such categorical theories as that of Lorenz is very well illustrated by Lees' remarks on *Eciton*. The actual development process leading to the periodic performances of this ant are well understood, and are *known* to have no essential relationship to any "reaction-specific energy" in any nervous system; further they are *known* not to be "innate" as such (Schneirla, 1938). The processes leading to this behavior surely have nothing to do with the processes leading to "vacuum activities" in a fish. Yet the superficial similarity is sufficient to cause Lees to cite the ant's behavior as an example of a type of behavior described for vertebrates. This is a good example of the tendency encouraged by such theories to look for cases fitting the theoretical categories in many types of behavior, rather than analysis of the processes involved in the development of any one behavior pattern.

CONCLUSION

We have summarized the main points of Lorenz's instinct theory, and have subjected it to a critical examination. We find the following serious flaws:

1. It is rigidly canalized by the merging of widely different kinds of organization under inappropriate and gratuitous categories.
2. It involves preconceived and rigid ideas of innateness and the nature of maturation.
3. It habitually depends on the transference of concepts from one level to another, solely on the basis of analogical reasoning.
4. It is limited by preconceptions of isomorphic

resemblances between neural and behavioral phenomena.

5. It depends on finalistic, preformationist conceptions of the development of behavior itself.

6. As indicated by its applications to human psychology and sociology, it leads to, or depends on, (or both), a rigid, preformationist, categorical conception of development and organization.

Any instinct theory which regards "instinct" as immanent, preformed, inherited, or based on specific neural structures is bound to divert the investigation of behavior development from fundamental analysis and the study of developmental problems. Any such theory of "instinct" inevitably tends to short-circuit the scientist's investigation of intraorganic and organism-environment developmental relationships which

underlie the development of "instinctive" behavior.

ACKNOWLEDGMENTS

I am greatly indebted to Dr. T. C. Schneirla (who originally suggested the writing of this paper) and to Dr. J. Rosenblatt for many stimulating and helpful discussions of the problems discussed here. Dr. Schneirla in particular has devoted much attention to criticism of the paper at various stages.

The following people also have read the paper, in part and at various stages, and have made many helpful suggestions and comments: Drs. H. G. Birch, K. S. Lashley, D. Hebb, H. Klüver, L. Aronson, J. E. Barmack, L. H. Hyman, L. H. Lanier, and G. Murphy. Since these scientists differ widely in the extent of their agreement or disagreement with various points of my discussion, I must emphasize that none of them is in any way responsible for any errors of omission or commission that may appear.

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