

K. Lorenz Evolution and Modification of Behavior The University of Chicago Press. Chicago and London 1965 p. 4/5

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Clearly distinct from the behaviorist's attitude, yet superficially somewhat similar, is that taken by Tinbergen and a great number of other modern ethologists. Although they have dropped the word "innate" for the terminological reasons already mentioned, they are, of course, fully aware that there really are two entirely independent mechanisms affecting adaptation of behavior: the process of phylogeny which evolves behavior as well as any other structural and functional organization, and the processes of adaptive modification of behavior during the individual's life. In spite of agreeing, on principle, with this "dichotomy," these scientists take the attitude that practically all behavior, down to its smallest units, owes its adaptedness to both of the above adaptive processes and that the types of behavior which we formerly described as "innate" and "learned" represent only the two extremes in a continuum of gradation in which all possible mixtures and blendings of

the two sources of adaptation can be found. That these two extremes actually occur and do so with a surprising frequency is fully recognized but explained by the tentative and rather arbitrary assumption that the extremes, being of particular survival value, are favored by selection pressure more than the intermediate forms.

1. Tinbergen, N. 1955 Some Aspects of Ethology, the Biological Study of Animal Behaviour. Advan. Sci. 12: 17-27
2. " 1963 On Aims and Methods of Ethology. Z. Tierpsychol. 20: 404-33.

K. Lorenz: Evolution and Modification of Behavior, The Univ. of Chicago Press. Chicago and London 1965 p.8

Campbell has called attention to the fact that the procedure by which a species attains information about its environment is virtually identical with that of pure induction and is devoid of the deductive processes which guide human experimentation. The information thus gained is stored in the genes, which for this reason have been aptly described as "coded information" by geneticists.



K. Lorenz: Evolution and Modification of Behavior, The Univ. of Chicago Press, Chicago and London 1965 p.8.

The organization which achieves all this obviously must have been evolved on our planet at a very early stage in the history of life. We know that all higher animals and plants are descended from organisms which had already "invented" a nucleus with chromosomes performing these functions. With the advancement of biochemical knowledge concerning analogous processes in the very lowest organisms, in bacteria and viruses, we are seriously confronted, however, with the question whether the origin of these mechanisms for acquiring information might not be identical with the origin of life itself.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.8/9

The second way by which information on the environment can be fed into the organic system is the interaction between the individual and its surroundings.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.9

Among all the mechanisms serving the gain of immediately exploited information, those achieving orientation in space stand apart insofar as they determine not only at what moment but also in what direction a motor pattern is to be discharged. These mechanisms imparting instantaneous temporal and spatial information are, in their more highly developed forms, largely identical with what is called intelligence in common parlance. Subjectively, their successful function is accompanied by the experience of "insight." They very often produce "learning" and frequently are its prerequisite. They are, however, totally independent of learning; they function even in the lowest unicellular organisms which do not learn.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.9

Particularly on the basis of one constitutive property, these mechanisms must be conceptually distinguished from learning. This has been pointed out by Russell¹. The processes that are under discussion here achieve an instantaneous adaptation of behavior to the environmental requirements of the moment; they do not cause a modification in the mechanism of the response but are themselves the function of the highly differentiated, phylogenetically adapted mechanisms, which, incidentally, are largely identical with what Pavlov called unconditioned reflexes.

1. Russell, W.N. 1958-61. Evolutionary Concepts in Behavioural Science: I-III General Systems (Year Book of the Society for General Systems Research), 1958, 3: 18-28; 1959, 4:45-73; 1961, 6: 51-92.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.9/10

Learning, on the other hand, is closely akin to the phylogenetical processes already discussed in its all-important function of not only acquiring, but also of storing, information. We do not know as yet how this storing is achieved. It might be done by adaptively modifying neural structure, or, as some biochemists tentatively like to assume, by coding information in chain molecules in the way phylogenetical information is retained. But whatever the mechanism, adaptive modification of a function cannot take place without corresponding modification of the structure underlying it. The enormous difference in their respective time scales and in their physiological mechanisms notwithstanding, the functional analogies between the phylogenetical and the individual processes of acquiring and storing information are such that Russell seems well justified in creating a concept encompassing both.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.11

Although well aware of all this, I propose, for the purposes of this book, to define learning in a much too comprehensive way, including all adaptive modifications of behavior. Any workable definition of learning must unconditionally contain, as its most indispensable part-constitutive property, the character of survival value or adaptiveness, as Thorpe pointed out in 1956.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.11/12.

Whatever else learning may be, it certainly is an adaptive modification of behavior, and its adaptiveness, that is, its ability to adapt behavior, needs a causal explanation. There is an infinitesimally small chance that modification, as such, is adaptive to the particular environmental influence that happened to bring it about.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.12.

Blithely assuming that "learning" (whatever that may be) automatically achieves adaptive improvement of behavior mechanisms implies neither more nor less than the belief in a prestabilized harmony between organisms and environment. The amazing and never-to-be-forgotten fact is that learning does, in the majority of cases, increase the survival value of the behavior mechanisms which it modifies. The rare instances in which this survival function miscarries serve to illustrate rather than to negate this -- but this fact itself demands an explanation.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.13

The indubitable fact that every learning mechanism is phylogenetically evolved is in no way contradicted by the other fact that a learning mechanism is evolved to exploit individual experience. Both facts together inescapably raise the question of how this learning mechanism achieves the task of choosing among innumerable possibilities of behavior those for reinforcement which develop positive survival value, and, for extinction, those which are detrimental to the individual or the species.

Food selection

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.14/15

The function of a very generalized "illness receptor" could perhaps furnish a tentative explanation for the amazing results which Richter¹ obtained when he supplied his experimental animals with foodstuffs disintegrated into their component parts and left it to the subjects to resynthesize a balanced diet. Even when the amino acids of the necessary proteins were offered separately, the rats, as subsequent weighings showed, took just the right percentage of each constituent. Animals deprived of the adrenal cortex proved to be able to compensate for the disturbance which the operation caused in their salt metabolism by eating a correspondingly increased amount of NaCl.

The most intriguing question posed by these findings is: from whence does the organism obtain the information telling it what chemicals are needed in

its metabolism at a given moment, and how are these to be recognized when encountered in the environment. We know of one case at least in which a special releasing mechanism achieves the recognition of a needed chemical: birds lacking calcium will peck at and eat any white, hard, and crumbling substance, regardless of its chemical composition, obviously guided by visual and tactile stimuli rather than chemical ones. I have known birds to poison themselves by eating carbide. It is, however, enormously improbable that similar phylogenetically evolved perceptual organizations are lying in readiness for each of the very special needs selectively supplied in Richter's experiments. His rats were, in all probability, the first ones in the evolutionary history of their species to synthesize protein from its component amino acids. It is a tempting, if untested, hypothesis that the animal tentatively eats just a little of each substance offered to it and forms an engram of "how it feels

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afterwards." This provisional assumption is supported by the fact that omnivorous animals invariably at the first encounter eat very little of any unknown food. Similar considerations might apply to the compensation of salt intake by adrenalectomized rats.

1. Richter, C.P. 1954. Behavioral Regulators of Carbohydrate Homeostasis. Acta Neurovegetativa 9: 247-59.

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K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.18

On the other hand, it is, for the reasons already expounded, an inescapable logical necessity to assume that learning, like any other organic function regularly achieving survival value, is performed by organic structures evolved in the course of phylogeny under the selection pressure of just that survival value. All observational and experimental evidence goes to confirm this assumption. None contradicts it.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.19/20

Physiologically, however, it is an entirely different process when, on the one hand, a species "experiments" by mutation or Mendelization and "records" results by one animal surviving and the other dying, and when, on the other hand, an animal "experiments" by doing this and that successively and "records" by forming a neural engram of what has brought about a reinforcing stimulus situation and what has not. For one thing, the amount of time needed for each of these processes are different by quite a few powers of ten. In addition, the coded information stored in the genes, and also its decoding in ontogenetic development, is different from the information stored in the nervous system and its decoding by whatever happens in the releasing of a conditioned response. No similarity of results and no difficulty in the practical task of

analysis can ever give us exemption from the scientific duty to trace back, to one or to the other of the two sources of information, any single point in which behavior can be shown to be adaptively molded to a corresponding point in the environment of the animal.

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K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.20.

There are also practical reasons which make the distinction important. For instance, the belief that human aggression is based not on phylogenetic adaptation but on learning implies a tremendous underassessment of its dangers. Hitherto this belief has only led to the production of thousands of intolerably aggressive non-frustrated children, but it may lead to much worse things.

14
K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.21.

We certainly do not believe that there is just one process into which learning does not enter. Even if we adhere to the superlatively comprehensive definition of learning which I proposed on p.11 and which includes all adaptive modification, we still know dozens of very complicated behavior mechanisms whose adaptedness is entirely based on phylogenetically acquired information. The computing mechanism which enables a starling to deduce the points of the compass from the motion of the sun across the sky (a sun which the bird has never seen; Hoffmann, 1952) the complex feedback mechanism which enables a mantid to aim its grabbing movement unerringly at the prey (Mittelstaedt, 1957)², the unvarying inherited courtship movement of a drake which releases a specific answer³ in a duck of the same species, the

"internal clock" which prescribes rhythmical recurrence of activities in so many animals⁴, all optomotor responses, and so on are all "nervous processes or mechanisms which are different from those into which learning enters." They are as different from each other as a tooth is different from a bone or a kidney and exactly for the same reasons. We do not know how many more such mechanisms or processes do exist - all different from and independent of each other.

1. Hoffman, K. 1952. Die Einrechnung der Sonnenwanderung bei der Richtungsweisung des sonnenlos aufgezogenen Stares. Naturwissenschaften. 40:148
2. Mittelstaedt, H. 1957. Prey capture in Mantids. Recent Advances in Invertebrate Physiology. University of Oregon Publ. 51-57.
3. Heinroth, O. 1910. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden, Verhandl. Ver. Intern. Ornithol. Kong. Berlin, 589-702.
4. Aschoff, J. 1962. Spontane lokomotorische

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Aktivität. Handbuch der Zoologie 10 (11).
Berlin: De Gruyter.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.24

Thus, paradoxically, the notion that the organism could, within the egg or in utero, learn behavior specifically adapted to later environment implies preformationism. An amusing double paradox lies in the fact that this preformationism is the penalty which some American psychologists incurred by trying to avoid, at all costs, the concepts of survival value and phylogenetic adaptation for no other reason than that they regarded them as "finalistic." Of course, they are not finalistic in the least. If a biologist says that the cat has crooked, pointed claws "with which to catch mice," he is not professing a belief in a mystical teleology, but succinctly stating that catching mice is the function whose selection pressure caused the evolution of that particular form of claws.

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K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.27

The naive ethologist's assertion that they are "completely innate" is indeed less inexact than the statement that a steam locomotive or the Eiffel Tower are built entirely of metal. In other words, it attains an exactitude rarely reached by biological assertions.

6

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.29

What I propose to discuss here is mainly the assumptions already mentioned in the introduction: that "what we formerly called innate" and what we formerly called "learned" represent only the extreme ends of a continuum of insensibly graduated mixtures between the two, and that all behavior, down to its smallest elements, owes its adaptedness to both processes. I think I can show that this assumption is not only bad strategy of research but completely unfounded and in all probability false.

7

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.29

In discussing the first behavioristic argument, I have attempted to demonstrate the fallacy of treating the "innate" and the "learned" as opposed, mutually exclusive concepts. I tried to show that, while all learning is performed by mechanisms which do contain phylogenetically acquired information, no reasons exist for assuming that individually acquired information "enters into" every kind of phylogenetically adapted behavior.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.30/31

The notion that learning or any other change of
behavior achieving survival value could possibly be
the function of a non-specifically organized and
programmed aggregation of neural elements, is
absolutely untenable.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.32

There is not and there cannot be any argument about
the fact that the Kuenzers' young Apistogramma
responded selectively to the configurational key
stimulus of a yellow and black pattern by the
specific activities of following the parent and that
a mother Apistogramma is indeed striped black and
yellow. Nor is it a matter of argument that a
stickleback responds to the key stimulus "red below"
by performing the motor patterns of rival fighting
and that a male stickleback is indeed red on the
ventral side. Only if we should forget these
central facts of adaptedness, and only then, should
we have to resort to the desperate strategy of
research which Jensen recommends to us, unless we
should prefer to give up as hopeless any further
attempt to analyze behavior.



1. Kuenzer, E. and Kuenzer, P. 1962. Untersuchungen zur Brutpflege der Zwergcichliden Apistogramma reitzigi und A. borrellii. Z. Tierpsychol. 19: 56-83.

9

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.33

Instead of being faced, as Jensen's proposal would make it seem, with a Herculean task promising only uninteresting results, we have before us a program of practically feasible experiments which simply cannot fail to give interesting results one way or the other. All we have to do is to rear an animal, as perfectly as we can, under circumstances that withhold the particular information which we want to investigate. We need not bother about the innumerable factors which may cause "differences" in behavior as long as we are quite sure that they cannot possibly relay to the organism that particular information which we want to investigate. If our baby Apistogrammas, who have never seen an adult female of their species, selectively respond to a certain black and yellow pattern by following it and staying with it

(as they would with their real mother) or if our stickleback responds to an object which is red below with the highly specific motor patterns used in fighting a rival, we are justified in asserting that the information which these fishes possess concerning these two objects is fully innate.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.34

The experimental embryologists, while trying to gain insight into the physiological causality of development, have always acted on the knowledge that any structure which is elaborately adapted to functions and environmental givens to be faced only much later in individual life must be blueprinted in the genome. They also know that adaptive epigenetical regulation can only be expected on the basis of such information that one part of the embryo can receive from another. The ectoderm must have all the information about how to build a neural tube. What the ectoderm can "learn" from the organizer emanating from the chorda is only where to do so. If investigators never put this into words, it was because all this was a matter of course to all of them, but they certainly would not have gained the results they did had they allowed their approach to be narrowed by the attitude

exemplified in Jensen's paper.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.36

At present, one example is sufficient to illustrate the point. The behavior by which an inexperienced turkey hen responds to her first brood of chicks is dependent on a single phylogenetically adapted¹ receptor mechanism. As Schleidt and Schleidt¹ have conclusively shown, she treats every moving object within the nest as an enemy, unless it utters the specific note of the chick. A deaf hen invariably kills all of her own progeny immediately after hatching. A hen with normal hearing accepts and mothers any stuffed animal, if it is fitted with a small loudspeaker uttering the correct call notes. Under natural circumstances with a young turkey hen hatching her own young, the one phylogenetically adapted auditory reaction effects so rapid a conditioning of maternal responses to other stimuli emanating from the baby birds that after a few hours



if not sufficiently used. The faculty of point discrimination, probably performed by the ganglion retinae, is lost to a large extent if not practiced, even if diffused light and unfocussed images do impinge on the retina. If a person's vision is impaired for a long period by purely optical deficiencies of the eye, point discrimination remains seriously damaged even after correction of the optical apparatus, a state of affairs termed amblyopsia ex anopsia by oculists.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.38/9

It is a matter of taste whether or not one chooses to call it learning when an activity is necessary to prevent atrophy and disintegration of a physiological mechanism, but it can be regarded as adaptive modification and it may well involve ontogenic acquisition of information. Much the same is true of the effector side of the reaction. Orientation mechanisms, motor patterns, etc. functioning in a stickleback fighting a rival or in an Apistogramma baby following its mother may also be elements of behavior that occur in other contexts as well. Among them, too, there may be some that need an inflow of individually acquired information for their full functional development.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and
London 1965, p.39/40

It must not be thought that the learned prerequisites for the proper functioning of innate information are only made up of the primitive types of adaptive modification of behavior. True conditioning does figure among them. A good example of this is furnished by the copulatory response of some geese. Greylags (Anser anser), Greater snow geese (Anser hyperboreus atlanticus), and probably many others possess perfectly good phylogenetic information about how a fellow member of the species behaves when inviting copulation, but they have to learn what a fellow member of the species looks like. The genetic information may be verbalized as follows: copulate with a conspecific who is lying low in the water and is stretched out along its surface. Hand-reared greylags, usually born in the first days of

May, usually do not meet their human foster parents swimming in the water earlier than June (in our climate). They then regularly attempt to tread them. As a human swimmer is much longer than any goose and also is lying much lower in the water, he represents a supernormal object for the copulatory response of all those geese which regard him as a conspecific. Even in very young fledgling geese and also in females, which normally never show any copulatory movements, attempts to tread can reliably be released by this supernormal stimulation. These phenomena definitely are not a consequence of imprinting. The geese behaving thus remain otherwise quite normal in respect to their sexual objects and do not persist in trying to copulate with humans. Nor do they ever attempt copulation with any other randomly chosen object that happens to be elongated and lying low in the water. These configurational properties are effective as key stimuli only if they pertain to an object which the goslings have learned to know as a fellow member of their species, and this learning is achieved by all the many conditioning processes which attach the gosling to its parents and ^{its siblings}.

12

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.41/2

The formulation that it is not characters but differences between characters which may be described as innate is, in my opinion, an unsuccessful attempt to arrive at an operational definition..... It seems to me that the opposite formulation is at least as workable: calling innate the similarities of characters developing under dissimilar rearing conditions. If we observe that all mallard drakes - and many other male dabbling ducks - whether reared in the wild or in captivity, by their own mothers or by a human keeper, under good or under highly unnatural conditions, perform the grunt-whistle in very nearly the same way, the breadth of variability being almost negligible in the confines of one species, our assertion that this similarity is innate, that is, based on genetical information, has at the very least the same likelihood of being correct as

the opposite one, that dissimilarities in identically reared organisms are innate.

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K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.44

The modern English-speaking ethologists are generally agreed that the concept of the "innate" is valuable and valid only if defined as "not caused by modification." This cautious definition, although of course quite true as far as it goes, states only the less important side of the problem. The important one is that the phylogenetically adapted structures and their functions are what effects all adaptive modification. In regard to behavior, the innate is not only what is not learned, but what must be in existence before all individual learning in order to make learning possible. Thus, consciously paraphrasing Kant's definition of the A Priori, we might define our concept of the innate.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.46

After carefully reading and rereading Mittelstaedt's paper¹ on the complex feedback mechanism enabling a mantid to aim a precise stroke at its prey, my own understanding of that mechanism is insufficient to permit sensible suggestions for its improvement. So I find it difficult to believe that the insect should be superior to myself in that respect, unless, of course, it possesses special built-in calibrating or adjusting mechanisms. I argue that this type of complicated neural mechanism must be highly refractory to random change by individual modification. The complexity and precision with which the processes of evolution have endowed these mechanisms would be destroyed immediately if individual modification by learning were allowed to tamper with them.

1. Mittelstaedt, H. 1957. Prey capture in Mantids. Recent Advances in Invertebrate Physiology. University of Oregon Publ. 51-57.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and London 1965
p. 47/8

In other words, the old and allegedly naive theory of an "intercalation" of phylogenetically adapted and of individually modifiable behavior mechanisms, far from having been refuted by new facts, has proved to agree with them in a quite surprising manner. Scientists working on entirely different problems, such as the selectivity of innate releasing mechanisms, bird navigation, feedback mechanisms of aiming, circadian rhythms, etc. have one and all found that if modifiability existed at all, it was restricted to one particular link in the chain of neural processes determining behavior. To demonstrate my point, I shall discuss a few examples of "circumscribed" learning. As we know, practically nothing about the physiological processes underlying the different types of learning, these examples can be classified only from a functional point of view.

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and London 1965
p.48

Thorpe has defined this phenomenon, which is generally called habituation, as "the relatively persistent waning of a response as a result of repeated stimulation which is not followed by any kind of reinforcement." While this definition justly stresses the size order of duration as a point discriminating habituation from fatigue and/or sensory adaptation, it implies, on the other hand, a close physiological relationship between habituation and the conditioned extinction of a response. I use this rather unorthodox phraseology advisedly because I want to emphasize that not only conditioned responses but also "unconditioned" ones can be extinguished by a conditioning process.

16

K. Lorenz: Evolution and Modification of Behavior,
Univ. of Chicago Press, Chicago and London 1965
p. 49/50

A bird whose escape responses are released primarily by anything that moves, as well as by anything new, would never come to rest at all, if it were not for its habituation to constantly recurring stimuli of this kind. These advantages of habituation would be counteracted by severe drawbacks, if the response to all other stimuli which also elicit it would suffer a decrement as well. The really surprising function of habituation, and the one in which its survival value lies, is the elimination of the organism's response to often recurring, biologically irrelevant stimuli without impairment of its reaction to others. A hydra is thus able to disregard water turbulence, while its responses to all other stimuli eliciting contraction remain as finely triggered as they ever were. The bird ceases to be frightened by moving branches and falling leaves without becoming, even in the slightest degree, less responsive to other movements that might spell danger.

K. Lorenz: Evolution and Modification of Behavior, 17
Univ. of Chicago Press, Chicago and London 1965
p.50

I suggest, as a definition of habituation, a combination of the two given by Thorpe: habituation is the relatively persistent waning of a response to certain stimuli caused by their repeated impinging and not affecting the threshold of the response in respect to any other than the habituated stimulus situation. This characterizes well enough what we know about the survival value of the process, and, as long as we know as little as we do about its physiological causation, it is advisable to confine ourselves to a purely functional definition which includes those cases of habituation in which conditioning takes a part as well as those in which it does not.

18

K. Lorenz: Evolution and Modification of Behavior, Univ.
of Chicago Press, Chicago and London 1965 p.52/3

Another interesting possibility, to which Hinde was the first to draw attention, is that an abnormally quick waning of response is caused by the great uniformity of circumstances accompanying the presentation of stimuli in the experimental setup, while, in wild life, no response is ever elicited even twice under exactly identical conditions. It has been the repeated experience of ethologists experimenting with dummies of all sorts that uniformity of place or of movement, regularity of rhythmically repeated sound, etc. cause a very fast waning of response. My own studies on the waning of the goslings' following response as well as of their reaction to the alarm note of the parents, Kühme's investigation (1962)¹ of the following response of young cichlid fish, and the Schleidts' research² on the turkey's escape reaction released by flying predators were in perfect agreement on this point.

1. Kühme, W. 1962 Das Schwarmverhalten elterngeführter Jung-
cichliden (*Pisces*) Z. Tierpsychol. 19: 513-38.



2. Schleidt, W. 1961. Reaktionen von Truthühnern auf fliegende Raubvögel und Versuche zur Analyse ihrer AAMs. Z. Tierpsychol. 18: 534-60.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.54/5

Immediately after hatching, a greylag goose will react to any object which in answer to its distress signals (lost piping) utters rhythmical sounds over a wide range of pitch. After the process of imprinting (p.55), on leaving the nest it will follow its mother or the dummy which has supplied sufficient stimulation for imprinting. At that time it can distinguish its mother from a man or from a dummy, but it is quite ready to follow any other goose. A few days later, it will follow its mother only and recognize her call at considerable distance, responding to it in preference to identical stimuli emanating from a much nearer mother leading goslings of its own age group. There is no evidence at all that conditioned extinction of the response takes part in these proceedings.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.55

In very many species of birds, the response of the parents to their offspring undergoes a similar increase in selectivity, also without any negative conditioning to other situations. Immediately after hatching their own eggs, they will accept any young of approximately equal age, but later they recognize their own chicks individually and refuse to take care of strangers. Under the abnormally uniform conditions of captivity, this increase of reactional selectivity can lead to the weirdest form of "pedantry." Old cage birds who have eaten from the same food tray for many years will often persistently refuse to eat from another tray or from the ground. In all these cases, the phylogenetically adapted releasing mechanism is supplemented by a great number of additional conditions which must be fulfilled in order to make it respond. This increase in selectivity takes place without any negative conditioning, as was well known to the classic investigators of the conditioned response.

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.56/7

After this process, which of course takes place in the same way between a gosling and its real mother, the following response is fixated on the object in question. This fixation is irreversible, at least insofar as any substitution of a different object results in a decrement of the response's intensity. Although indubitably coming under our definition of learning, this process is distinct from our accepted concept of conditioning in several interesting ways. The first, and probably most important, is that a response becomes conditioned to a highly specific stimulus situation without actually having been released. This is, particularly striking in many known cases of sexual "imprinting." The second, and still unintelligible, point is the generic quality of this fixation of the object of a certain response.

18

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.57

Similarly, a gosling's following responses become imprinted "to geese" or "to humans," but it is still an intriguing puzzle which particular stimulus situation represents each of these concepts. The human-imprinted gosling will unequivocally refuse to follow a goose instead of a human, but it will not differentiate between a petite, slender young girl and a big old man with a beard.

19

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.63/4

It is highly characteristic of the ontogeny of behavior in higher animals that a phylogenetically adapted motor pattern makes its first appearance in tolerably complete, or at least clearly recognizable, form but in a biologically inadequate situation. A puppy performs the shaking movement, adapted to the killing of prey, with its master's slippers for an object or the motor pattern of burying food remnants on the parqueted floor in the corner of a room. In his classic paper on appetites and aversions, Craig¹ has demonstrated in a masterly fashion that the phylogenetically adapted mechanism of the consummatory act itself is so constructed as to impart to the subject the "knowledge" of the environmental situation in which to discharge the motor pattern in question. Craig illustrated the principle by the graphic description of a young dove learning "to obtain the stimulation adequate for a complete consummatory reaction, and thus to satisfy its own appetites." The movements of the consummatory act itself are, as Craig repeatedly points out, wholly innate. Craig

held them to be true chain reflexes. He does not hesitate, nevertheless, to attribute to the bird highly pleasurable subjective experiences correlated with the performance of the consummatory act. When a young dove, sexually mature but inexperienced, is supplied with a nest for the first time, it does not recognize it at sight:

But sooner or later he tries it, as he has tried all other places, for nest-calling, and in such trial the nest evidently gives him a strong and satisfactory stimulation (the appetited stimulus) which no other situation has given him. In the nest, his attitude becomes extreme: he abandons himself to an orgy of nest-calling (complete consummatory action), turning now this way and now that in the hollow, palpating the straw with his feet, wings, breast, neck and beak, and rioting in a wealth of new, luxurious stimuli.

Much as a stickler for objective terminology might have to criticize in this representation, the fact remains that from now on this young dove is thus effectively conditioned to the nest.

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1. Craig, W. 1918. Appetites and Aversions as Constituents of Instincts. Biol. Bull. 34: 91-107.

20

K. Lorenz: Evolution and Modification of Behavior, Univ. of Chicago Press, Chicago and London 1965, p.64/6

The learning processes which Eibl-Eibesfeldt¹ investigated in rodents and small carnivora illustrate the same principle. Laboratory rats reared in such a manner that they could not gain any experience in the handling of solid objects and even deprived of their own tails (after it had been observed that they performed nest-building activities with this appendage for a substitute object) immediately displayed a number of complete motor patterns of nest building when Eibl-Eibesfeldt supplied them with suitable material. Long sequences of movements, such as running out, grabbing material, running back, and depositing it or arranging it in a circular heap around the prospective nest center, "upholstering" the inner wall by patting soft material smooth by alternating movements of the front paws, or manufacturing soft material by splitting coarse strands longitudinally, etc., were indistinguishable from those of normally experienced control animals, even in the analysis of slow-motion films. Yet the following learning processes proved to be indispensable to integrate these motor patterns into a functional whole.

If the cage was entirely devoid of structure which, by eliciting a phylogenetically adapted response, marked a preferable nesting locality, the rat had to decide by learning on the spot in which to deposit the nesting material it was carrying. Individuals which, in spite of the complete lack of structure within their cages, had formed a habit of sleeping in a certain corner started to build there at once when offered material without any preliminary trial and error. A tin screen about two inches square was sufficient to direct the inexperienced rat's very first acts of building to the cover it offered. The heaping-up movements and the upholstering movements were often observed when the rat had only carried in two or three paper strips which were lying flat on the ground. The movement was then performed, in perfectly normal coordination, an inch or so above the nest material without ever touching it. This never happens in a normally experienced rat. It will not adjust the movement to the height attained by the accumulated nesting material, but it will not perform it at all until the heap has attained the elevation necessary to bring it within the range of the fixed motor pattern.

2.

Obviously it is the reinforcing effect of the consummatory situation with all the proprio- and exteroceptor reafferences which arise under adequate environmental conditions which, in their joint effect, teach the animal what to do or, by their disappointing absence, what not to do, and particularly, in what sequence to use otherwise unchangeable fixed motor patterns. The information concerning the biologically "right" environmental situation is, in this case, not only contained in the organization of receptor patterns alone, but also essentially in the fixed motor pattern itself which produces the reinforcing reafferences only if very definite environmental conditions are fulfilled. I do not see how a complete study of the learning functions of a species can be accomplished without an investigation of its fixed motor patterns and the reinforcing consummatory situations pertaining to each of them.

1. Eibl-Eibesfeldt, I. 1955 Zur Biologie des Iltis
(*Putorius putorius L.*) Verhandl. Deut. Zool. Ges. Erlangen
304-23

Eibl-Eibesfeldt, I. 1955. Nestbauverhalten der Wanderratte. Naturwissenschaften 42: 633-34

1956. Über die Ontogenetische Entwicklung der Technik des Nüsseöffnens vom Eichhörnchen (Sciurus vulgaris). Z. Säugetierkunde 21: 132-34.

1961. The Interactions of Unlearned Behaviour Patterns and Learning in Mammals. Symposium on Brain Mechanisms and Learning. CIOMS Montevideo. Oxford: Blackwell, pp. 53-73.

1963. Angeborenes und Erworbenes im Verhalten einiger Säuger. Z. Tierpsychol. 20: 705-54.

K. Lorenz: Evolution and Modification of Behavior
Univ. of Chicago Press, Chicago and
London, 1966. p.66

Wherever trial and error followed by subsequent adaptive modification of behavior is observed, the assumption of Pavlovian conditioning is justified. Conditioned responses of the second and third order can be attached, forming chains of what purposivists would term means-end relationships. Learning processes of this type can thus accomplish survival functions of almost unlimited complexity.

K. Lorenz: Evolution and Modification of Behavior
Univ. of Chicago Press, Chicago and
London, 1966. p. 66

This specific function of learning is different from those described in the preceding chapters in one important point: it is dependent on a gradient of more effectively and less effectively reinforcing stimulus situations. Purposive psychologists, particularly Tolman, have always correctly emphasized that learning of this type can take place exclusively in the context of "purposive," or, as we should call it, appetitive behavior. Whether the latter is directed at the releasing of an instinctive movement or at a state of quiescence, in other words, whether it is an appetite or an aversion in Craig's terminology, is not essential for the present issue, because the conditioning effect or "reward" is different from that of "punishment" only in sign. The information on the adaptive optimal consummatory stimulus



situation itself is, of course, phylogenetically acquired. The mechanism which thus directs the learning process toward survival value is situated within the selective receptor processes constituting the afferent side of the "unconditioned reflex" which, as is known through the work of Pavlov, is the indispensable basis for the formation of any conditioned response.

1. Tolman, E.C. 1932. Purposive Behavior in Animals and Men. New York: Appleton-Century.

K. Lorenz: Evolution and Modification of Behavior
Univ. of Chicago Press, Chicago and
London, 1966 p.79/80

As has been explained in the critique of both behavioristic arguments, it is perfectly possible that a particular motor sequence may owe to phylogenetic processes all the information on environment underlying its adaptedness and yet be almost wholly dependent on individual learning for the "decoding" (p.20) of this information. This, indeed, is the important truth contained in the second behavioristic argument. The "decoding" of genome-bound information is, in such a case, achieved in two steps: first, by means of morphological ontogeny producing structure; and second, by means of trial-and-error behavior exploiting structure as a teaching apparatus. Processes of this kind are made to appear highly probable by the findings of Prechtl and Knoll on motor patterns and "reflexes" of children born in abnormal positions.

1. Prechtl, H.E.R. and Knol, A.R. 1958.
Die Fusssohlenreflexe beim neugeborenen Kind.
Arch. Psychiat. Z. Ges. Neurol. 196: 542-53.

21

K. Lorenz: Evolution and Modification of Behavior. Univ.
of Chicago Press. Chicago and London, 1966.
p.80

The fallacy of treating the "innate" and the "learned" as mutually exclusive concepts led the old ethologists to make the same errors of which, from page 7 to 21, I have accused behaviorists. Like the behaviorists, the old ethologists took it for granted that the modification of behavior effected by learning invariably caused an increase in survival value. The fact that a phylogenetically evolved neurophysiological mechanism must lie behind this highly differentiated function obviously never occurred to them any more than it did to those of the behavioristic school.

22

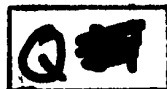
K. Lorenz: Evolution and Modification of Behavior. Univ.
of Chicago Press. Chicago and London, 1966.
p.80/81

It was Lehrman's¹ critique which, by a somewhat devious route, brought the full realization of these relations to me. In chapter 4 I have discussed the hypothesis that the passive movement imparted to the chick embryo's head by the beating of its heart might take part in teaching the bird to peck. As I have explained, this assumption neglects consideration of the necessity to explain the fact that the motor pattern fits environmental requirements only encountered later in life. In my first counter-critique I said rather satirically that this hypothesis, in order to circumvent the necessity of assuming an innate, that is, phylogenetically adapted motor pattern, unwittingly but unavoidably postulates the necessity of an "innate schoolmarm." In other words, it requires a phylogenetically adapted teaching mechanism. It soon dawned upon me, however, that this thrust against the preformationistic views on learning held by the behavioristic school recoiled with full force on the views



held by the older ethologists including myself. I came to realize rather late in life that "learning" was a concept illegitimately used by us as a dump for unanalyzed residue and that, no better than our criticized critics, none of us had ever bothered to ask why learning produced adaptation of behavior. All older ethologists, with the outstanding exception of Craig, had been confining their attention to the innate, while more or less neglecting all problems of learning, without realizing that in doing so they were neglecting one of the most important functions of the majority of phylogenetically adapted behavior mechanisms: the function of teaching!

1. Lehrmann, D.S. 1953. A critique of Konrad Lorenz' Theory of Instinctive Behavior. Quart. Rev. Biol. 28: 337-63.



15

K. Lorenz: Evolution and Modification of Behavior. Univ. of Chicago Press. Chicago & London 1966. p.81.

One of the worst repercussions which this complete neglect of the relations between the "innate school-marm" and individual learning had on the real understanding of phylogenetically adapted behavior mechanisms themselves was a one-sided and even physiologically erroneous view of the consummatory act. For a long time it was believed that the gradual rise and final critical drop of excitation typical of all consummatory acts was due to complete exhaustion of action-specific potentiality on the motor side. It has been conclusively demonstrated by experiments of Beach that in the case of the copulatory activities of the male chimpanzee, it is the effect of reafferent feedback which terminates the consummatory act. This proprio- and exteroceptor feedback is undoubtedly of enormous consequence for the reinforcing function of

most or all consummatory stimulus situations. In the case of higher animals, it is hardly an exaggeration to say that the special structure of a typical consummatory act is quite as much the result of the selection pressure exerted by its function of reinforcing appetitive behavior as of the one exerted by its primary function. The lack of appreciation of this fact hindered a true understanding of the processes discussed on p. 64, 65, particularly of the manner in which important information concerning the biologically "right" situation can be contained in the motor pattern itself and can be "decoded" by the animal itself, thus creating a maximum of adaptivity and economy of behavior, as illustrated by the experiments of Eibl-Eibesfeldt (pp. 64, 65). Only Craig gave, at least in his very vivid descriptions of consummatory activities and situations, a hint of the importance of these interactions between phylogenetical adaptation and adaptive modification of behavior (p.64).

2.

If these admittedly atomistic errors committed by my teacher Heinroth and myself did comparatively little damage to the initial progress of ethology, this is due to the fact that the all-important element of behavior, the fixed motor pattern or Erbkoordination, is an extremely invariable skeletal element which influences the system into which it is built far more than it is, in its turn, influenced or changed by the general systemic interaction.

1. Beach, F.H. 1942. Analysis of Factors Involved in the Arousal, Maintenance, and Manifestation of Sexual Excitement in Male Animals. Psychosomatic Med. 4: 173.

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K. Lorenz: Evolution and Modification of Behavior. Univ. of Chicago Press. Chicago & London 1966. p.105

It is not to be denied, however, that the embryo can indeed learn important elements of behavior before being born or hatched. Information contained in the genome can be doubly decoded, first by morphogeny and subsequently by trial-and-error learning while using morphological structure.

1. Prechtl, H.F.R. and Knol, A.R. 1958. Die Fussohlenreflexe beim neugeborenen Kind. Arch. Psychiat. Z. Ges. Neurol. 196: 542-53.