

The Innate and the Learned: The Evolution of Konrad Lorenz's Theory of Instinct*

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Introduction

The character of instincts and the part they play in behaviour have long been controverted in American psychology. Undoubtedly the scepticism with which the topic has been discussed and often dismissed is kindled by the spirit, if not the letter, of Watsonian behaviourism. In the last forty years, however, a theory of the instinctually innate has been developed which has met many of the empirical and conceptual challenges of behaviourism and in doing so has established the theoretic beginnings of the now burgeoning science of ethology. I refer to the work of Konrad Lorenz.

Lorenz's importance in this regard is twofold. He has, first, focused the attention of psychologists on the issue of innate components of behaviour¹; and second, he has done this by offering substantive empirical and conceptual studies of the subject. The continued influence Lorenz will wield in directing the discussion of behaviour is, of course, dependent upon the merit and achievement of his own investigations. But here a problem arises. For in assessing Lorenz's accomplishment one must deal, not with one carefully defined theory of instinctual behaviour, but rather with an evolving conception of the determination of behaviour by innate and learned components. Both to facilitate and contribute to this assessment I propose in this paper to analyse the evolution of the concept of the instinctually innate as it develops through Lorenz's early work, receives the impact of telling criticism, and is modified through its own internal logic and the force of critical objection.

1. *The early period (1935-1952):² the mechanisms and distinctiveness of instinctive behaviour*

Demonstrations of instinctually innate behaviour. Typical of the experiments Lorenz has conducted on the instinctual and heritable aspects of animal behaviour are these three. In the spring of 1937 he tested the young birds of his reserve with fake predators moved along a rope stretched between

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two tall trees. The grey geese started to react spontaneously to the shadow of the predator from about their eighth week; up to that time they reacted only to their parents' warning call. 'Although they had a chance to learn the mechanism of the predator, the reaction matured at a certain time, unaffected by experience or parents' example.'³ On another occasion Lorenz used a young female mallard duck to demonstrate innate recognition and courtship behaviour. The female was raised in the company of pintail ducks yet never showed the slightest sexual reaction to drakes of that species. But when a mallard drake was first sighted the female exploded with an elaborate display of courting activity.⁴ Lorenz has also used breeding experiments to show the innate and heritable features of animal behaviour. By cross-breeding of ducks of different species new patternings of courtship behaviour, often combining the distinctive traits of both parents, have been produced. This and similar experiments appear to demonstrate the heritability of certain stereotyped behaviour patterns.⁵

Theoretical aims in the study of innate behaviour. Before considering Lorenz's analysis of experiments such as those just cited, it is important to clarify his purposes in conducting these studies. Throughout his career Lorenz has kept before him three principal theoretical aims: taxonomy, explanation, and evolutionary understanding. He contends that instinctive action is particularly conservative in species and therefore has great taxonomic value. For instance, there are no distinguishing morphological traits that all pigeons share; but if one turns to behavioural classification, then a trait can be found which characterizes all members of the family of pigeons: namely, when drinking all pigeons pump water by peristaltic movements of the oesophagus.⁶ Secondly, the category of innate behaviour can be used to explain certain sequences of animal activity. Why, for example, does a stickleback attack a plump wax model of a fish which lacks all structural resemblance to a rival stickleback? Because the model has a red underside, and it is the 'red below' which releases innately directed attack behaviour.⁷ Finally, the taxonomic and explanatory enterprises find their value and significance by being placed within the broader perspective of evolutionary understanding. To comprehend the development of patterns of innate behaviour and their controlling mechanisms is to engage in a comparative investigation of the evolutionary history of species. On the other hand, by neglecting to place taxonomic and explanatory procedures within the evolutionary context one renders them sterile and invites the kind of objections brought against the instinct theory of William McDougall. An analysis of the logical structure of the evolutionary-explanatory use of Lorenz's doctrine of instinct will be offered at the end of the third section of this paper.

The three components of instinctive behaviour. According to Lorenz instinctive behaviour has three components:

First, appetitive behaviour motivated by internal accumulation of readiness for a specific action. Second, activation of an IRM (innate releasing mechanism), which disinhibits the innate reaction. Third, discharge of the 'consummatory act' . . . which is the purpose of behaviour.⁸

Let us first consider Lorenz's conception of the *innate releasing mechanism* (*der angeborenen auslösenden Mechanismen*). Within his theory of instinct the IRM has the status of a theoretical entity, postulated to explain 'the innately determined readiness of an animal to respond with a certain action to a certain set of environmental stimuli'.⁹ Thus the stimuli of swollen abdomen and characteristic posture in the female stickleback act as a key unlocking the IRM of the male and releasing his mating behaviour. The postulated reality of the IRM is that of an innately determined neurosensory correlate to a specific stimulus complex; and its function is to release action, which, as it were, is dammed up in the organism. Lorenz, however, has never investigated the neurostructure of any organism to anatomically define the IRM's for its instinctive patterns.

The stimuli which unlock the IRM for a given behaviour are usually few in number, even in the highest vertebrates.¹⁰ Geese and ducks, for instance, show an escape reaction to a silhouette of a model simply if the shadow moves across the ground at a certain speed; the precise form of the model has no significance. The turkey, however, seems to demand more complexity; for it shows a more pronounced reaction to a short-necked model at the given speed.¹¹ The reaction of the turkey provides an example of what Lorenz calls, following his colleague Seitz,¹² 'the law of heterogeneous summation'. This is an additive law for simple releasing stimuli which states that no component of a releasing stimulus complex is indispensable, but that the total effect is the result of additive co-operation.¹³ Thus, though the turkey reacts to a certain speed, its full escape reaction is released only when the silhouette is that of a short-necked bird.¹⁴ Later in his early period Lorenz amends the law of summation with the observation that by using dummies displaying exaggerated stimuli it is often possible to produce a more energetic reaction than that effected by the biologically normal situation.¹⁵

There is an evolutionary parsimony shown in the requirement of only few stimuli to unlock an IRM. A selective advantage is accorded a species if its innate responses depend on stimuli which are relatively unique to the appropriate situation but simple and obvious of perception.¹⁶ Yet it would be uneconomical if an animal continued to display innate patterns to relatively constant releasing stimuli. To avoid this the IRM is endowed

with the ability to become selectively habituated to such stimuli in biologically neutral environments. The hydra, for example, adapts to the contraction producing movement of a swift current, yet remains responsive to contraction producing stimuli of other kinds. This phenomenon appears similar to conditioned extinction. Lorenz, however, distinguishes it from this latter in two ways:¹⁸ (a) since the extinguished response is not learned to begin with, the waning of response is not the result of withholding reinforcement; and (b) habituation is stimulus specific—there is no generalization gradient of extinction.¹⁹

The evolutionary perspective taken by Lorenz directs his empirical investigations to precise environmental situations which have led to the selective development of particular IRM's and corresponding fixed action patterns. His examinations into the character of instincts are thus significantly different from those of William McDougall.²⁰ McDougall's instincts are global. They are constituted by a general motivational aim and a large repertoire of plastic responses. For example, McDougall groups all the motor patterns we call parental care into one class. Then using this anthropomorphic category he labels the class 'parental nurture' and has ready-made the explanation for these different patterns of behaviour—they are the result of 'parental instinct'.²¹ Lorenz, on the other hand, examines each motor pattern separately and views it as the evolutionary result of specific environmental pressures toward selection of a particular adaptive behaviour. As a consequence of this theoretical perspective and refined method of investigation Lorenz concludes that there are no overarching instincts such as a parental instinct. That a duck, for instance, will display a series of innate motor reactions of care for its young does not mean it is guided by a single purposive instinct; rather the group of motor patterns are expressed only because the releasing cues are found together in ducklings of its own species. Careful experiment allows us to disjoin the patterns, permitting the manifestation of, for example, both protective and hostile patterns toward the same gosling. Functional unity is achieved only because of the unity of the object displaying the cues, not because of the unity of a global instinct.²²

Lorenz's evolutionary assumptions articulate another way in which his analysis of instinct differs from the generally discredited position of McDougall. In McDougall's view instincts are not only energizers but are also cognitively purposive. They direct the animal to a perceived goal and continue their channelled urgings until the goal is reached.²³ The attribution of a cognitively perceived instinctual goal to the individual animal organism is foreign to Lorenz's analysis. If purposiveness is to be predicated in this case, its proper subject according to the Lorenzian view is the species, not the individual. For the individual organism instinctual behaviour has no

perceived biological goal other than the activity itself. The finality of the individual's behaviour is determined solely by the causality of its organs.²⁴

Two phenomena which Lorenz has investigated convince him of the lack of cognitive purposiveness of the individual's innate behaviour patterns: intention movements (*Intentionsbewegungen*) and vacuum activities (*Leerlaufreaktionen*).²⁵ The grey-lag goose, for example, will perform incomplete nest-building actions all year round; but the biological end of such activities can be achieved only during a certain time of the year. Intention movements of this kind, some only perceptible to the trained—some might say tainted—eye of the ethologist, are executed without chance for biological success. At other times an organism will display the complete motor pattern associated with normal instinctual behaviour, though the goal of the activity is absent. Vacuum activity of this sort can be seen in the case of the young, hand-raised starling, a pet of Lorenz, who having never in its life caught a flying insect suddenly broke forth in fly-catching patterns, including the killing and swallowing of a non-existent prey.²⁶ In both of these instances, intention movements and vacuum activity, we have examples of instinctual behaviour which can have no individually perceived biological goal.

Intention movements and vacuum activities reveal continua of threshold and reaction levels possible for instincts. Thus, the partial to complete expression of reaction patterns in the absence of normal stimuli indicates one pole of the continuum of threshold values, that at which they are minimal. The continua may be affected by external stimulus conditions in three ways. First, as has been noted, exaggerating the releasing stimuli can produce an increased level of reactivity. The second way has also been mentioned: when there is a constant elicitation of the instinctual behaviour by adequate releaser stimuli decreased intensity, or habituation, of reaction occurs. Finally, when releaser stimuli which have been withheld for long periods of time are introduced to the organism a decidedly stronger reaction intensity can be expected.²⁷ These latter two ways of affecting threshold and reaction levels may produce rather bizarre activity on the part of the organism. A mallard female, for instance, may treat the same dummy one time as a bird of prey and another as a male of her own species, depending on whether the threshold for defensive behaviour or courting behaviour is particularly low at the time.²⁸

Early in his career Lorenz contrived a theoretical explanation of intention movements and vacuum activities which seemed to provide a key for our increased understanding of the neurophysiological substrate of instinct. Inconstant reaction levels can be explained, he argued,²⁹ by adopting an hypothesis of automatic-rhythmical generation and central co-ordination of impulse similar to that authored by Von Holst.³⁰ The latter had suggested

that the nervous system continually produced and accumulated reaction-specific excitational potential. The amount of this potential rises in proportion to the time during which there is an absence of discharge of the corresponding motor pattern. Lorenz took up the hypothesis and proposed an 'as if' model, one whose heuristic value compensated for its obvious fictional status. The model indicated that when requisite releasing stimuli for instinctive activity are present the IRM opens sluice gates and accumulated excitational substance flows to activate the appropriate motor pattern. Vacuum activities occur when the dam bursts, and intentional movements when it leaks a bit.

Later on in his first phase of development Lorenz abandoned the Von Holstian explanation of internal motivation. He had two reasons for doing so, and should have had a third. First, there was no neurophysiological identification of any of the multitude of action specific substances that would be required even for one species. Second, the phenomenon of 'allochthonous' or displacement activity convinced him that whatever accumulated within the organism was not action specific.³¹ Displacement reactions occur, for example, when a cock which is in a situation of conflict between attack and escape suddenly pecks at the ground as if he were feeding, or a heron in a similar situation preens itself, or a sparrow whets its bill. Though these displaced activities are usually not as intense as they ordinarily would be in their own proper setting, nonetheless when blocked 'autochthonous' drives are particularly strong, the displaced activity will be proportionately so. In recognition of this proportional shunting of energy Lorenz concluded that what was action specific was the 'reservoir' in which the excitational substance accumulated. Under certain conditions, so the theory now ran, a reaction different from the one normally expected could be fed from this 'pot'.³² But even in this amended version there is an unrecognized conflict with his views on habituation: if habituation to one set of stimuli occurs through dissipation of action potential, how is the animal able to run-off the same reaction to a newly introduced but different pattern of stimuli? Albeit, problems of this kind are later ameliorated by what appears to be the abandonment of, or at least diminished enthusiasm for, energetic models of the specific kind mentioned. Thus in his more recent work Lorenz admits instances of terminated activity through reafferent feedback, rather than simply through depletion of the reserve of action potential.³³

In Lorenz's conception instinctive activities are not behavioural isolates; they occur within the complex of learned and other kinds of innate behaviours. The complex may be likened to a chain, with the links being instinctive behaviours, learned behaviours, reflexes, taxes, and so on. In

other words, instinctive activities, while retaining their own unity, are strung along the line of behaviours exhibited by the organism.³⁴ An example of this 'instinct-learning intercalation' (*Instinkt-Dressur-Verschränkung*) is provided by the common raven. The raven, like the jackdaw, instinctively hides bits of food which it finds. But unlike the jackdaw it learns to hide the food while not under the watchful eye of competitors. The raven is able to forge a chain of learned activity and instinctive behaviour.

Lorenz's discussion of the instinct-learning intercalation presupposes another aspect of his general instinct theory which in his latest work is offered with more caution and less detail. In explaining the intercalation Lorenz argues that instinctive behaviour can be used as a 'tool' to achieve an individual goal of the organism. This goal is itself the release of instinctive behaviour. Implied by this explanation and made explicit by Lorenz in this early phase of his development is the notion that the organism 'desires' and finds emotionally satisfying the goal of releasing its instinctive action patterns.³⁵

Lorenz does not believe that terms like 'crave' and other commonly used emotion-aim words are naively anthropomorphic when applied to animal behaviour. There is no pathetic fallacy committed when we speak of the dog loving his master, the goose fearing the fox, or the blackbird taking pleasure in rain-worm boring. Lorenz maintains that animals subjectively experience emotions, indeed, as many emotions as they have autonomous instinctive activities.³⁶ His argument for ascribing emotions to animals rests on two supports: the close analogy which may be discovered between human emotional activity and similar activity in animals; and the postulated function of animal emotions in determining goal-directed behaviour. In fixing this latter support Lorenz assumes another analogy with human behaviour, this time looking to the motivational source of many human actions. Animals, he concludes, are driven to perform many of the deeds they do because of the pleasure associated with the release of instinctive acts.³⁷

Lest this description of Lorenz's theory of the instinct-learning intercalation appear to fade into McDougall's instinct theory—and certainly McDougall's contention that animals subjectively enjoy a variety of emotions helps smudge the boundary between the two—what Lorenz takes to be an essential feature of his position must be emphasized. Just as the characteristics of the fixed motor pattern and releaser stimuli are established through selective evolutionary pressures and are innately programmed into the genome of the species, so also is it evolutionarily determined in what positions in the instinct-learning chain the link of learning may be inserted. The phylogenetic history of the organism has arranged it so that gaps are present in potential chains; and into these gaps, instead of an instinctive act,

a 'faculty to acquire' is inserted.³⁸ This is the kind of evolutionary stance which distinguishes Lorenz's theory from McDougall's. The animal liberty espoused by McDougall is severely circumscribed by the innate constraints argued for by Lorenz. This feature of Lorenz's theory remains a constant in his theoretical development.

This section began with a quote from the end of Lorenz's first phase to the effect that instinct has three components: appetitive behaviour, activation of an IRM, and discharge of a consummatory act.³⁹ Lorenz's early treatment of instinct focused on the IRM, its releasing stimuli and their properties, and the rewarding release of patterned behaviour. And in most discussions of Lorenz's thought these are taken to constitute instinct. It is strange, therefore, that now appetitive behaviour, that is, learned behaviour, should be included under the rubric of instinct. In the paper from which the quote was taken Lorenz does little to indicate how we are to adjust our conception of instinct to include learned behaviour. But what Lorenz seems to be adumbrating here is a new conception of instinct built upon the instinct-learning intercalation. The full import of this anticipation will only be realized in his later works, which will be examined in the third part of this paper.

How instincts differ from learning. Lorenz's distinction between innate, instinctive behaviour and learned behaviour is one that some learning theorists have found most difficult to admit. Yet for Lorenz it was a distinction which virtually defined the ethologist's proper area of study: namely, behaviour which is innately determined, particularly instinctive behaviour. In the following I will sketch what Lorenz in this early period took to be the fundamental contrasts between instinctive and learned behaviour.⁴⁰

Most of the criteria which Lorenz uses to distinguish instinctive behaviour from learned behaviour have already been discussed in other contexts; but in order to illustrate the kind of argument which Lorenz employs to demonstrate the validity of the criteria, it is well again to list them. First, the patterns of motor activity and releaser selectivity for individual instincts can be found in all normal members of a given species; they are not subject to environmental modification or idiosyncratic adaption. Second, those patterns are inheritable and obey the laws of genetics. Third, unlike learned behaviour, instinctive activity is frequently displayed in the absence of conditions appropriate for its goal, for example, in intention movements and vacuum reactions. These criteria taken together seem to provide that conceptual cutting edge by which animal activity may be finely carved into instinctive behaviour and other kinds of behaviour. Yet the art is to carve at the joints, and even the sympathetic reader may wonder whether these criteria allow

us to do that. Could it not be that what began as instinctive behaviour becomes maintained through conditioning, or even from the start that fixed action patterns are the result of learning? Patterns universal in a species might then be the consequence of conditioning to environmental elements common in the development of its members. Concerning heritability, might it not be that certain dispositions are innate rather than actual behaviours and that in the proper environment these dispositions are realized? Finally, might not the pleasure Lorenz says is associated with the release of instinctive activity be a reinforcement for its acquisition? By trial and error the animal may discover that certain modes of behaviour are pleasurable and thus emit them in proper and sometimes improper circumstances. The answers which Lorenz provides for the difficulties besetting the first criterion will now be considered. Answers made to the remaining sets of questions mark the advance of his views in recent years and will be discussed in the third part of this paper.

Lorenz's response in this early period to the problems surrounding the first criterion is the assertion that both in the phylogenic history of the species and the ontogenic development of the individual, instinct and learning remain absolutely distinct. He offers two notes by which instinctive patterns of behaviour may be distinguished from learned patterns. The first is that the innate mechanisms which release the former respond to extremely simple stimuli, while the releasing stimuli for the latter are relatively complex. This is the case, he contends, because of the economic mechanisms of evolutionary selection on the one hand, and on the other because learned reactions, at least in the wild, occur in complex stimulus situations—hence the whole complex becomes the stimulus for releasing the learned behaviour.⁴¹ Unfortunately Lorenz offers no experimental evidence for this doubtful claim about learning.

The second way of distinguishing an innate from a learned pattern arises from the observation that individual experience is powerless to modify the structure of an instinctive pattern of motor activity. To be sure, releasing stimuli and the immediate past experience of the organism can affect the intensity with which an action is performed, or even what reaction a certain situation will evoke; nonetheless Lorenz insists in this early period that a 'new type of action, not predetermined and genetically established in one specific combination of movements never occurs'.⁴² To sustain this most fundamental thesis of his early doctrine of instinctive behaviour, Lorenz offers the experimental evidence of the 'deprivation experiment'.

The deprivation experiment is designed to prevent an organism from practising or otherwise acquiring a behavioural pattern through individual experience. If the subject still manifests the behaviour in question, this is

strong evidence for its origin in the phylogenic adaption of the species rather than the ontogenic adaption of the individual. Typical of this kind of experiment are the studies of Carmichael.⁴³ Carmichael kept developing tadpole embryos in a constant state of narcosis using a weak solution of acetone chloroform. The narcotic condition suppressed all movement but did not check organic development. When the animals were awakened in the late stages of maturation their swimming motions were the same as those of the normal controls which had been 'practicing' these motions for days. An example of what appears to be the ultimate in deprivation experiments is provided by the newly hatched chick: emerging from the isolation of the shell, it begins immediately to initiate the complex motor pattern of pecking for food.

2. *The critics of innate behaviour*

Some of us seem to have been constituted by nature with an anti-Platonic disposition, and any doctrine of innatism tends to evoke a predictable response. Lorenz's theory of instinct has stimulated a good many so disposed. There are, however, three objectors to the theory of instinct who, both by their general influence and by their specific effect on Lorenz's own thinking, deserve special attention.⁴⁴ These are Daniel Lehrman,⁴⁵ Frank Beach,⁴⁶ and Donald Jensen.⁴⁷

Fundamental criticisms of a theory of instinctively innate behaviour. The principal objection of Lehrman, Beach, and Jensen to a theory of instinctively innate behaviour is that the category of the innate is preconceived and imposes a classification on behaviour which tends only to obscure its analysis. Instead of focusing on the important question of how a particular behavioural pattern comes about, the disjunctive categories of innate and learned force us to lump together many different kinds and levels of behaviour on the basis of an essentially misconceived phenotypic scheme.⁴⁸

Lehrman forms his objection by enumerating the criteria he sees Lorenz offering for innate behaviour and then showing how they force us in particular cases to neglect important possible determiners of behaviour. The criteria he specifies as being major for Lorenz's use of the term 'innate' are these:

(1) the behaviour 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.⁴⁹

What these criteria fail to take into account, according to Lehrman, is that an animal can never be isolated from features of the environment which might contribute to the development of a particular behaviour

pattern.⁵⁰ In other words, the deprivation experiment cannot exclude all possible environmental determiners of behaviour. As an illustrative case Lehrman asks us to consider the apparently perfect isolation experiment, the appearance of pecking behaviour in the newly hatched chick. Lorenz's criteria would force us to call this behaviour innate. Yet, observes Lehrman, there are the studies of Kuo⁵¹ which indicate that the pecking behaviour of the newly hatched chick develops through stages of conditioning while the chick is still ensconced in the egg. For instance, it is known that the neck of the embryonic chick is passively bent when the heartbeat causes the head, which rests on the thorax, to rise and fall. At about this time also the bill begins to open and close as the bird nods. After some nine or so days fluid forced into the throat by bill and head movements causes swallowing. Hence, suggests Lehrman, what appears according to Lorenz's criteria as innate may only be the result of conditioning. Another example of the importance of considering the effects of the embryonic environment is offered by Beach.⁵² He reports studies showing that the susceptibility of a certain strain of seizure-susceptible mice can be lowered by placing the fertilized eggs of the strain in females which are seizure-resistant. Here too is a case of an activity which normally would be considered innate, yet experiment demonstrates that its manifestation is not completely genetically determined.

Jensen focuses on the epistemological and methodological difficulties surrounding the concept of innate behaviour. He argues that the operational definition of learning allows us to empirically specify the question 'Is behaviour learned or innate?' Learning may be operationally defined as 'the demonstration of a reliable change in responding as a result of responses being closely followed by reward stimuli'.⁵³ This definition allows us to give empirical significance to the question by rephrasing it as, 'Has an effect of difference in training procedures been demonstrated or not?' The meaning of innate then becomes, according to Jensen: 'An effect of difference in training procedures has not been demonstrated'. The meaning of innate is thus negative and as a consequence suffers all the liabilities of such definitions: 'no effect demonstrated' can result either from no real difference produced by the training procedure *or* because the test made to detect the difference is insensitive, involves measurement errors, or is otherwise contaminated. Innateness, concludes Jensen, can be 'demonstrated' by a bad experiment in learning.⁵⁴

Yet Jensen recognizes that a positive meaning for innate is intended by those who use the concept. He therefore suggests an operational definition of innate in terms of differences produced by genetic selection. Defined as 'differences resulting from genetic selection' the innate is no longer

necessarily opposed to the learned, i.e., 'resulting from training'. We are now in a position to solve in an empirical way the problem of whether a given pattern is innate or learned.

Though the categories of the innate and the learned now have a precise empirical meaning, a consideration of evidence of the kind cited by Lehrman and Beach convinces Jensen that 'many behavioural differences are both learned and innate in that both selection and training are important'.⁵⁵ Moreover, such evidence also shows that behavioural differences may be attributed to effects and interactions which fall clearly into neither of the two categories. Hence, instead of asking the obfuscating question 'Is this behaviour learned or innate?' we should ask:

'To what antecedent difference can we attribute this difference in behaviour?' or simply 'What causes this difference in behaviour?' So asked, the question becomes a matter for research instead of argument.⁵⁶

Objections to a theory of instinctively innate behaviour of the kind mentioned here, though rebutted by Lorenz point for point, nonetheless forced him to change his theory significantly. His specific responses to the objections and the manner in which he was compelled to modify his views will be discussed in the next section of this paper. But before that discussion is undertaken it might be well briefly to consider some of the principal objections from a perspective other than that of Lorenz.

The logic of the category of innate. The objections lodged against a Lorenzian theory of instinct are of two kinds, epistemological-methodological and empirical. And as is usual in science the former determines the weight of the latter. So it is from the epistemological-methodological perspective that I would like to examine the objections.

The principal objection of Lorenz's critics is that the imposition of a two category scheme is damaging, for it forces us to overlook the multiplicity of factors governing behaviour. This objection fails to tell on three counts. First, it does not appreciate that the category of the innate is a generic one, and has several nomenclally related subcategories included under it. Hence, it is only a two-category classification scheme at the highest level of abstraction. And even then there is no claim that it is exhaustively descriptive of all behaviour. Second, the objection assumes that one can go to experience without organizing concepts—we are advised simply to look at animal behaviour and its environment and then detail the multitude of factors influencing it. What, the patient epistemologist may ask, are we to detail? To even begin to sort out the infinite array of impinging causal factors which affect even the smallest behaviours requires a classification system which already selects some influences as pertinent and rejects others that may be 'safely' disregarded. Indeed, to carve out independent causal events

from the processes of nature demands the possession of such categories before we come to particular experiences. Without any classification scheme we would be in danger of examining a universe of factors, most of which would be irrelevant for scientific purposes—and this only if we could conceptually and perceptually articulate them to begin with. Third, the objection assumes that to concentrate on two classes of behaviour is to make a thorough study of behaviour impossible. Why? The analysis of behaviour can go on at many theoretical and descriptive levels (e.g. chemical, physiological, behavioural, genetic, evolutionary, historical, etc.). It makes good procedural sense to concentrate efforts at one or two closely related levels and their interface. In fact the relations between levels and areas can be determined only after theories at different levels have been fairly well established. The strategy of investigating the instinctual ground of certain behaviours does not, therefore, preclude the study of physiological mechanisms producing those behaviours. On the contrary, instinct theory directs one to elaborate the mechanisms through which the results of natural selection are realized.

The objection that the definition of innate is essentially negative and means only that learning has not been demonstrated, perhaps because of defects in the experiment, is curious for several reasons. Particularly in his early period Lorenz's concept of learning is vague and ill defined, but that of instinct is carefully delineated—hardly possible if the instinctually innate were simply defined in terms of what learning is not. The objection seems designed to put the instinct theorist in the methodologically precarious position of proving a null hypothesis. The issues are too complex to be treated briefly here, and at the end of the next section they will be attended to again. But some limited observations may be apposite. A null hypothesis expresses the belief that the outcome of an experiment is due, not to relevant conditions, but to chance. However, what is declared to be the null hypothesis governing a certain situation depends on what statistical test is utilized. For instance, a high correlation between experienced and experimentally deprived groups of similar genotype on tests relevant to a putative instinctive pattern could be shown to be statistically significant beyond chance. This is a statistical design which could be used with the deprivation experiment to enable one to reject the null hypothesis, rather than awkwardly attempting to prove it. A final source of wonder at the objection is that it can so easily be turned against those employing it. The objection assumes that the concept of learning is secure, that it can be operationally defined by positive criteria. This is a dubious assumption at best. Further, since the concepts of innate and learned are supposed to be negatively related, one could just as logically maintain that the concept of learning is worthless because it can be defined

only in terms of what is not innate: the term 'learned' is to be applied only when the behaviour has been shown not to be innate. And surely, it is always possible that there are defects in any experiment. Again, it just may be the case that when we think we have demonstrated learning, actually the behaviour is innate, only we have made measurement errors or have failed to make sufficient observations.

Having made these responses to general epistemic objections we must now recognize a lingering difficulty: what, other than descriptive or theoretic convenience, will allow us to call one behaviour innate and another learned, especially when we admit that all behaviours are conditioned by both genetic and environmental factors? This admission, also made by Lorenz—if somewhat grudgingly—in his recent work, suggests that to retain the important concept of the innate we will have to relativize it. The necessary changes to be made in the logic of the concept will be discussed at the end of this paper.

3. Recent developments in Lorenz's theory of instinctive behaviour

Lorenz's response to his critics. In recent monographs⁵⁷ Lorenz has attempted to answer many of the objections of his critics, but at the same time he has been forced to accommodate some of his early views to the force of those criticisms. In a general orienting reply to the shared assumption of those antagonistic to a theory of innate behaviour Lorenz clarifies a position which he has always held, but not always emphasized. His long-held conviction is that the concepts of innate and learned behaviour are not necessarily antithetical, though for expository purposes they may be opposed. Rather, as he insists, the evolutionary point of view dictates that the ontogenic modification of behaviour called learning can be properly understood only as expressing an innate ability acquired through the selective process that formed the species. Learning can occur in animals only in those behavioural spaces and under those environmental conditions determined by the phylogenic programme of the species.⁵⁸ Lorenz even argues that if we are to explain the obvious adaptive function of learning, we must postulate an 'innate teaching mechanism'. Otherwise we are forced to accept the Leibnizian assumption of a preestablished harmony between organism and environment.⁵⁹ But let us turn to the specific responses which prepare the way for Lorenz's restructured position.

Should the category of the innate be dropped because behaviour is the result not only of innate features, but learned and a multitude of other environmental influences? Lorenz thinks that the categories of the innate and its traditional reciprocal, the learned, should no more be discarded than the concepts of phyletic and ontogenic adaption. Simply because phenotypic

patterns do not easily yield to these categories does not mean they are no longer appropriate. It means that we have to become more sophisticated in devising experiments to tease out the components of manifest patterns. It cannot be denied, of course, that several factors enter into the determination of any behaviour; Lorenz's critics have little difficulty forcing him to acknowledge this. However, as he points out, the ethologist is primarily interested in *adaptive* modifications:

As students of behaviour, we are not interested in ascertaining at random the innumerable factors that might lead to minute, just bearable differences of behaviour bordering on the pathological. What we want to elucidate are the amazing facts of adaptedness. Life itself is a steady state of enormous general improbability and that which does need an explanation is the fact that organisms and species miraculously manage to stay alive.⁶⁰

Hence, it seems entirely appropriate that the categories of the innate and the learned be maintained; for they are conceptually designed to articulate the characters of phyletic and individual adaptiveness.

Lehrman and Beach have argued that the deprivation experiment fails because it does not exclude the possibility of embryonic learning. In responding to this objection Lorenz considers only Lehrman's example of the chick's pecking behaviour and thus does not exclude the possibility of embryonic learning in other animals. The case of each species would require an individual analysis. But in the proposed illustration learning in the embryo must be denied. If the chick's acquisition of pecking behaviour were contingent, a by-product of anatomical development, we would be hard pressed to explain why the 'motor pattern thus individually acquired should fit the requirements of eating in an environmental situation which demands adaptedness to innumerable single givens as exactly as it does'.⁶¹ The evolutionary exigencies of the situation make Lehrman's proposal untenable in this case. Further, it would be difficult to explain why only certain birds peck after hatching, while others gape like passerines, or push their bill into their parent's mouth like pigeons, although all the embryos of the mentioned species have their heads passively moved while still in the egg.⁶²

Nonetheless it is undeniable—and Lorenz does not now mean to deny it—that the embryonic environment contributes to the final shape displayed by the patterned behaviour of the neonate. But to acknowledge the effect of the uterine or ovular environment does not render useless the concept of the instinctually innate. Those environmental influences could presumably produce their adaptive consequences only if the genome has programmed precise reactions to them. Hence, an innate substructure and the internal environment may work to produce an instinctual behavioural pattern, although in a manner not before suggested by Lorenz.

The task of translating his theory of instinctually innate behaviour to a new setting, the American psychological scene, with its emphasis on the environmental determinants of behaviour, has forced on Lorenz an adaptation of his theory to meet the requirements of scientific survival. Before uninterested and sometimes antagonistic to the notion of extra-innate sources of species specific behaviour, Lorenz now avers: 'No biologist in his right senses will forget that the blueprint contained in the genome requires innumerable environmental factors in order to be realized in the phenogeny of structures and functions'.⁶³ This avowal demands a recasting of the notion of the innate in behaviour. The innate is not simply what is not learned, but what must be 'in existence before all individual learning in order to make learning possible'.⁶⁴ And what that something is which must preexist and which can be inherited by the individual is not any 'character' or 'pattern of behaviour', but a 'limited range of possible forms in which an identical genetic blueprint can find its expression in phenogeny . . .'.⁶⁵ This means for Lorenz that we should strictly no longer use the term 'innate' to refer to behaviour, even if a given pattern has negligible possibility of modification. Rather, the term should be used to refer to that range of possible forms expressible in the phenotype, or if this be too metaphysical, to the *information* stored in the genes.⁶⁶

In this new conception, then, learning and the innate are not as opposed as Lorenz sometimes assumed them to be. It is possible, according to the reformed view, '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' of this information'.⁶⁷ This reformation resolves a problem suggested earlier, namely, that it was theoretically conceivable that certain motor patterns and sequences are found rewarding and thus engaged in because the animal has learned to display them in the proper circumstances. Lorenz now allows this very possibility.

The new perspective on the relationship between what is innate and what is learned in behaviour, that the message is innate though one may need to learn the required behaviours to decode it, shows itself most perspicuously in Lorenz's acknowledgement that even the IRM is subject to modification through learning.⁶⁸ This, of course, is in marked contrast to his earlier position. The modified stance also demands a new conception of what was formerly called the 'instinct-learning intercalation'. Before Lorenz spoke of this as an interlocking of discrete units of learned and innate behaviours. Now he construes it as a functional unity, one not having the serial unity of a chain, but of an integrated whole.⁶⁹ Some of the influences which determine the whole arise during ontogenesis, however others are provided

by innate information acquired in phylogenesis. No parts of the behaviour pattern itself are to be considered innate, only the information which underlies some of the features of the unified pattern is to be so considered. Lorenz's critics have left their mark.

The scientific employment of the concept of instinct. Given Lorenz's recognition of the multi-determination of the phenotypic patterns of behaviour, can he distinguish instinctual behaviour from other kinds in any meaningful way? Indeed, is the concept of instinct any longer scientifically useful? The answers to these two questions will conclude our examination of Lorenz's theory of instinct and will suggest what significance his views have for the contemporary psychologist.

The discernment of the sources of behaviour, a little like the discernment of spirits, is rarely easy; one cannot always be sure the agents responsible have been uncovered. The situation is no different, of course, in any of the other sciences. Any chemical event, for instance, is determined by virtually an infinite number of present and past causal occurrences. The origins of behaviour, however, are multiple not only in number, but also in theoretic kind: causes are conceptually articulated according to chemical, genetic, physiological, evolutionary, and psychological theories. Over-determination of this sort is less theoretically precarious, perhaps, for selection experiments than for deprivation experiments. But the problem of holding constant or eliminating factors other than those of interest (e.g. the instinctual) is one which all behavioural experiments and, indeed, all experiments in natural science share.

However, utilizing his reformed notion that it is not behaviour which is innate but information, Lorenz can offer a guiding principle for the deprivation experiment which is adequate for demonstrating certain invariances in patterns of behaviour to be due to innate information. The general principle is: 'If the information which is clearly contained in the behavioural adaptation to an environmental given is made inaccessible to the individual's experience and if, under these circumstances, the adaptedness in question remains unimpaired, we can assert that the information is contained in the genome'.⁷⁰ The principle recognizes that fixed action patterns are adaptive to particular environmental and biological situations; and if the organism is deprived of prior experience with those situations, it would rack scientific credulity unmercifully to believe the behavioural pattern at issue just happened to meet the requirements of adaption to the particular situation. The principle also redirects the question of instinct such that for Lorenz it now is not so much one of the causes of the fixed action pattern but of the sources of the information which the pattern expresses.

Lorenz has argued that the ability to acquire certain behaviour patterns

during ontogenesis is also genetically determined. How then are we to distinguish patterns which are to be designated 'expressive of instinct' from those to be called 'learned'? We can do this by first acknowledging that these terms are polar; they describe behaviour only at the extremes. Consequently there will be some patterns which could as easily be referred to by one as the other (e.g. imprinting). Yet, we can still give some definite empirical meaning to the relativized concept of the instinctually innate if we stipulate that those patterns are to be termed 'instinctive': (*a*) whose genetic base permits only one definite form of behaviour to be manifested in typical environmental situations; (*b*) which appear at a predictable stage in maturation; (*c*) which are commonly linked in the species with certain patterns of releasing stimuli; (*d*) which are displayed in their behavioural entirety the first few times they are released, with instrumental shaping required only to refine the pattern; and (*e*) which conform to the laws of heritability. That pattern will be called 'learned' if: (*a*) its genetic base permits a rather wide range of alternate motor patterns; (*b*) its releasing stimuli are effective at no definite maturational stage and only after some period of motor responding in their presence; (*c*) it is not commonly linked in the species with a definite releasing pattern of stimuli; and (*d*) it is developed by stages through a relatively lengthy process of shaping. Other traditional criteria for the learned would still be pertinent.

The relativizing of the concept of the instinctually innate is demanded in yet another sense, one which recognizes that in practice important scientific concepts are frequently applied on the basis of unstable and shifting criteria. This, of course, is not necessarily a happy situation. Nonetheless, theoretical and practical exigencies require we not abandon our concepts simply because they do not always neatly fit the situation. The concept of anxiety, for example, has served well the clinical psychologist—if not his academic brethren—but the reasons it is applied to one person are not always precisely similar to those for another. These same methodological considerations are relevant to the concept of the instinctually innate. The concept is to be applied when most of the several criteria specified by instinct theory are present. When some criteria are absent, however, the theory should indicate why this might be expected. The theory and the concept it defines will cease to be scientifically useful when the criteria for application are discovered to be actually few and ambiguous. As is usually the case in science, the death of an important concept is not swift; it occurs only when the critical supporting evidence slowly gives way. The concept of the instinctually innate is still relatively healthy, and the reports of its demise have been greatly exaggerated.

What kind of scientific explanations can be formulated using the instinct

as an organizing category? One, I would argue, which has the same logical features as others produced in the natural sciences. How, for example, do we explain the phenomenon of the male salticid spider's mating dance? We do it by noting the environmental releasing conditions in which it occurs (i.e. just after the final molting, in the presence of a female having this certain appearance, etc.) and producing a generalization to the effect that under these specific conditions the male salticid displays a certain motor behaviour whose pattern (i.e. a mating dance with thus and so movements) is expressive of instinctual information. From the statement of antecedent conditions and the appropriate generalization the description of the dance can be deduced. And this conforms to the logical structure of one of the principal kinds of explanation offered in the natural sciences.⁷¹ What is added by indicating that the pattern is instinctual is a conceptual link with evolutionary theory and the phylogenic development of the species. This link directs our further research to the history of the species, with the aim of discovering the adaptive value of the pattern within its particular natural and social environment. The conceptual indicator also suggests that we might trace out particular genetic and physiological structures of the species in order to determine the necessary conditions for the behavioural elements which express the instinctual information. Thus an explanation employing the concept of instinct not only meets the logical requirements of explanation in science, it also proves fruitful in directing further investigation into behavioural mechanisms.

The simple conclusions one may draw from this historical and critical analysis of Lorenz's theory of instinct are, I believe, that the theory is not speculatively dogmatic—it is amenable to modification in the face of the conceptual and experimental evidence—and that it remains profitable for the consideration of those scientists concerned with animal and human behaviour.⁷²

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NOTES

- 1 Even before Lorenz made his impact on contemporary psychology there were scattered studies to indicate that many kinds of animal behaviour can be attributed to innate mechanisms. G. McClearn reviews these early studies in his 'The Inheritance of Behaviour', in *Psychology in the Making*, edited by L. Postman, New York 1962.
- 2 Any chronological markers fixing the boundaries in the evolution of species or concepts must be imposed only with great hesitation. By 1935 Lorenz's theory of instinct achieved initial form; the origins of his theory and his methodological views prior to this period will be discussed in a forthcoming paper. 1952 is chosen as a convenient close for the early phase of Lorenz's thought, for in that year he published a theoretical retrospective of the preceding period of ethology's great advance. The article, 'The Past Twelve Years in the Comparative Study of Behaviour', along with several early pieces by Lorenz can be found included in the volume *Instinctive Behaviour: the Development of a Modern Concept*, translated and edited by C. Schiller,

- New York 1957. (The original reference is 'Die Entwicklung der vergleichenden Verhaltensforschung in den letzten 12 Jahren', *Verhandlungen der Deutschen Zoologischen Gesellschaft in Freiburg*, 1952, pp. 36-58. When possible reference will be made to Schiller's translations; otherwise translations from Lorenz's papers will be my own). The second or more recent stage in Lorenz's thinking has obviously arrived with his monograph of 1961, 'Phylogenetische Anpassung und adaptive Modifikation des Verhaltens' (*Z. Tierpsychol.*, 18, 139-87).
- 3 Lorenz, 'Comparative Study of Behaviour' in *Instinctive Behaviour*, p. 255. (Originally published as 'Vergleichende Verhaltensforschung', *Zoo. Anz. Suppl.*, 12, 1939, 69-102.)
 - 4 *Ibid.*, p. 260.
 - 5 Lorenz, 'The Evolution of Behaviour', *Sci. Am.*, 199, 1958, 67-78. Lorenz was of course not the first to conduct such genetic experiments. In 1929, for instance, W. Crozer and G. Pincus ('Analysis of the Geotropic Orientation of Young Rats', *J. Gen. Physiol.*, 13, 1929, 57-119) studied the inheritance of geotropic orientation in rats. They discovered that the angle of orientation adopted in climbing an inclined plane differed in three strains of rat. Through breeding experiments similar to Lorenz's they showed that the variability of behaviour was an inherited characteristic. Perhaps the most frequently cited study of the heritable features of behaviour was conducted by R. Tryon ('Genetic Differences in Maze-Learning Ability in Rats', *Yearb. Nat. Soc. Stud. Educ.*, 39, 1940, 111-19). Tryon selected from a large foundation stock of rats those which quickly learned to correctly run a maze and those which learned only slowly. From these two groups he developed two lines of rat, those which were 'maze-bright' and those which were 'maze-dull'. This experiment forcefully supports the thesis that learning ability is heritable. These two latter studies and others are discussed by McClearn.
 - 6 Lorenz, 'Comparative Study of Behaviour', pp. 240-1.
 - 7 Lorenz thinks much of human behaviour also amenable to explanation using the concept of instinct. He discusses several examples in his 'Die angeborenen Formen möglicher Erfahrung', *Z. Tierpsychol.*, 5, 1943, 235-409. This work is rather more speculative than his earlier studies. In this monograph his task is, he says, the same as that of Kant: to discover the innate forms of human experience. He differs from Kant, however, in maintaining that the forms of possible experience are adaptive modifications of the central nervous system to the real features of the environment. ('Merkwürdigerweise hat er [Kant] aber daraus nicht den Schluss gezogen, der dem heutigen Naturforscher so nahe liegt: dass nämlich die Kategorien und Anschauungsformen in gleicher Weise und aus gleichen Gründen auf die reale Welt "passen", wie das Auge zu den Lichtstrahlen', p. 237.)
 - 8 Lorenz, 'The Past Twelve Years in the Comparative Study of Behaviour', p. 290.
 - 9 Lorenz and N. Tinbergen, 'Taxis and Instinct', in *Instinctive Behaviour*, p. 290. (Originally published as 'Taxis und Instinkthandlung in der Eirollbewegung der Graugans', *Z. Tierpsychol.*, 2, 1938, 1-29.)
 - 10 Lorenz, 'Companionship in Bird Life', in *Instinctive Behaviour*, p. 86. (Originally published as 'Der Kumpan in der Umwelt des Vogels', *J. Ornithol.*, 83, 1935, 137-213.)
 - 11 Lorenz, 'Die angeborenen Formen möglicher Erfahrung', p. 254. This is a good example of the difficulty of performing reliable demonstrations of innate motor patterns unaffected by individual experience. When W. Schleidt ('Reaktionen von Truthühnern auf fliegende Raubvögel und Versuch zur Analyse ihrer AAM's', *Z. Tierpsychol.*, 18, 1961, 534-60) replicated Lorenz's experiment he found that naive turkeys did innately react to silhouettes passing at a certain speed, but length of neck was not a critical factor. He surmised (p. 536) that Lorenz's birds had become habituated to the long-necked geese of his preserve. Though Schleidt has indicated the difficulty of the deprivation experiment, he has also shown that defective experiments can be redesigned to produce significant results. Ethological demonstrations of innately directed motor patterns are not as hopeless as some critics have contended. But these problems will be further discussed at the end of parts two and three of this paper.
 - 12 A. Seitz, 'Die paarbildung bei einigen Zichliden I', *Z. Tierpsychol.*, 4, 1940, 40-84.
 - 13 Lorenz, 'Comparative Study of Behaviour', p. 261; and 'Die angeborenen Formen möglicher Erfahrung', p. 265. When the law is stated in this form it implies that the total magnitude of responses released by different parts of the stimulus complex taken separately is equal to the magnitude of response released by the whole. This seems to conflict with the Gestalt assumption that the patterned whole has properties above those of its parts separately considered. There is evidence that the additive principle governs less complex organisms, but that the Gestalt principle applies to more complex animals. For a further discussion of this problem see R. Hinde's *Animal Behaviour*, New York 1970 (2nd ed.), pp. 69-70.

- 14 The law of summation is operative in cases of responses released both by unexperientially affected IRM's and by learned cues. Stimulus integration thus obeys the same law whether phylogenetically or individually acquired. This is the conclusion of G. Baerends, K. Brill, and P. Bult, 'Versuche zur Analyse einer erlernten Reizsituation bei einem Schweinsaffen', *Z. Tierpsychol.*, 22, 1965, 394-411.
- 15 Lorenz, 'The Past Twelve Years in the Comparative Study of Behaviour', p. 293.
- 16 Lorenz, 'Companionship in Bird Life', p. 88: 'All social releasers represent a compromise between two biological needs: utmost simplicity and utmost general improbability'. For example, it is the relative uniqueness or 'general improbability' of the colourful markings of the nesting grosbeak which prevents the parents' innate feeding reaction from being released on other stimuli.
- 17 Lorenz, 'The Past Twelve Years in the Comparative Study of Behaviour', p. 294.
- 18 In his 'Factors Governing the Changes in Strength of a Partially Inborn Response, as Shown by the Mobbing Behaviour of the Chaffinch (*Fringilla Coelebs*): II The Waning of the Response' (*Proc. Roy. Soc. B*, 142, 1954, 331-58), R. Hinde has his own list of the differences between the waning of instinctive response and conditioned extinction; however, he is not ready to assert these to be fundamental. First, the habituated decrement of an instinctive response is often accompanied by a reduction in factors which influence the state of the underlying nervous mechanism: the stomach becomes full, the seminal vesicles are emptied, etc. Second, experimental extinction of a conditioned response is subject to the effects of disinhibiting stimuli, while this has not been shown to be the case for the waning of the instinctive response. Finally, extinction of a conditioned response often restores the original response to the conditioned stimulus; and, of course, the instinctive response is the original response to the releasing stimuli. Other theorists speculate that the mechanisms underlying habituation and conditioned extinction are identical. See, for example, R. Thompson and W. Spencer, 'Habituation: A Model Phenomenon', *Psychol. Rev.*, 73, 1966, 16-43.
- 19 Unfortunately the two criteria Lorenz suggests are not as clear as could be desired. In some cases reinforcement does seem to play a part in selecting adequate stimuli for the release of instinctive responses. W. Carr, L. Loeb, and M. Dissinger ('Responses of Rats to Sex Odours', *J. Comp. Physiol.*, 59, 1965, 370-7) found that experienced rats prefer females emitting an odour of receptivity, while naive males have no such preference; hence, differential instinctual responsiveness can be controlled in part through learning in some instances. Lorenz later admits that learning can influence an IRM, and, one would presume, habituation. The second criterion also meets some difficulty. Hinde's work on chaffinches indicates that decremental effects may be products of two processes, one stimulus specific, the other response specific. But as Hinde later acknowledges (in *Animal Behaviour*, pp. 290-5) the evidence for a two process model is not entirely clear.
- 20 See McDougall's *Outline of Psychology*, New York 1923. Lorenz's theory of instinct in this period may also be distinguished from the views of Morgan, Loeb, Watson, James, and other theorists who conceived instincts to be nothing but concatenations of simple reflexes. In the early 1930s Lorenz, too, conceived instincts generally as a species of reflex action (to be discussed in a forthcoming paper). However, he now observes three principal differences between instinctive behaviour and reflexes that make their identification untenable. First, once the IRM of an instinct has been triggered the course of the fixed motor pattern is quite independent of further receptor activity. (Die angeborenen Formen möglicher Erfahrung', pp. 247-8.) Second, the longer the time elapsed since an instinctive action has been released, the greater the intensity with which the organism responds to releaser stimuli, even to the point of releasing in vacuo. But the patellar reflex, for example, does not respond more readily if it has not been elicited for a time. ('Comparative Study of Behaviour', p. 246.) Finally, Lorenz contends that unlike reflex activities the animal frequently craves the discharge of instinctive behaviour. Intimate contact with animals and the purposeful way they attempt to place themselves in circumstances in which instinctive behaviours can be released suggested to him that they subjectively take pleasure in instinctive behaviour. ('The Conception of Instinctive Behaviour', in *Instinctive Behaviour*, pp. 171-2; first published as 'Über die Bildung des Instinkt-begriffes', *Naturwiss.*, 25, 1937, 289-331.) Yet, nothing suggests that the patellar reflex is desirously sought or rapturously enjoyed. For an instructive investigation of the early instinct theorists, see R. Herrnstein's 'Nature as Nurture: Behaviourism and the Instinct Doctrine', *Behaviourism*, 1, 1972, 23-52.
- 21 McDougall, *Outline of Psychology*, pp. 130-9.

- 22 Lorenz, 'Companionship in Bird Life', p. 87; and 'The Conception of Instinctive Behaviour', pp. 156-7.
- 23 Purposeful action is for McDougall (*Outline of Psychology*, p. 51) 'the most fundamental category of psychology; . . . Behaviour is always purposive action, or a train or sequence of purposive actions.' In the gregarious instinct, for example, the animal expresses the purpose of 'giving some signal which serves to warn its fellows, and to bring them together for defense of escape' (p. 151).
- 24 Lorenz, 'Induktive und teleologische Psychologie', *Naturwiss.*, 27, 1942, p. 137: 'Die Finalität des Systemganzen ist von der Kausalität seiner Organe . . .'. Lorenz in this article discusses the relation between his evolutionary-causal model of behaviour and vitalistic theories of teleology.
- 25 Lorenz, 'The Conception of Instinctive Behaviour', pp. 142-4; and 'Comparative Study of Behaviour', pp. 245-6.
- 26 Lorenz, 'Comparative Study of Behaviour', p. 247.
- 27 Lorenz, 'Induktive und teleologische Psychologie', p. 139.
- 28 Lorenz, 'Comparative Study of Behaviour', p. 249.
- 29 Lorenz and Tinbergen, 'Taxis and Instinctive Action', pp. 179-80; and Lorenz, 'Die angeborenen Formen möglicher Erfahrung', pp. 247-8.
- 30 E. Von Holst, 'Vom Dualismus der motorischen und der automatisch-rhythmischen Funktion im Rückenmark und vom Wesen des automatischen Rhythmus', *Pflug. Arch. ges. Physiol.*, 237, 1936, 356-78.
- 31 Lorenz, 'The Past Twelve Years in the Comparative Study of Behaviour', pp. 295-7.
- 32 While admitting the heuristic value of Lorenz's energy models of motivation, R. Hinde yet feels the experimental evidence demands their abandonment. He believes that a probability model of response, along with reference to external stimuli and hormonal level are sufficient to explain changes in responsiveness under constant environmental conditions. See his 'Changes in Responsiveness to a Constant Stimulus', *Brit. J. Anim. Behav.*, 2, 1954, 41-55; and 'Energy Models of Motivation', *Sym. Soc. Exp. Biol.*, 14, 1960, 199-213. Nonetheless, the energy model has not been rejected by all workers in animal behaviour. Research continues on the production and storage of endogenous excitatory potential. See chapters three and four of Eibl-Eibesfeldt's *Ethology: the Biology of Behaviour*, New York 1970, for a review of the literature.
- 33 Lorenz, *Evolution and Modification of Behaviour*, 1965, p. 81.
- 34 Lorenz, 'Companionship in Bird Life', pp. 99-100; and 'The Conception of Instinctive Behaviour', p. 137.
- 35 Lorenz, 'The Conception of Instinctive Behaviour', p. 139. There is experimental evidence that instinctive acts of aggression are at least reinforcing, if not pleasurable. A. Tellegen and J. Horn ('Primary Aggressive Motivation in three Inbred Strains of Mice', *J. Comp. physiol. Psychol.*, 78, 1972, 297-301) found that male mice were able to acquire a position response in a T maze when rewarded with the opportunity to attack a nonaggressive mouse. Strain differences were found, further indicating the innate features of instinct and its properties.
- 36 Lorenz, 'Companionship in Bird Life', p. 123.
- 37 Lorenz and Tinbergen, 'Taxis and Instinctive Action', p. 184.
- 38 Lorenz, 'The Conception of Instinctive Behaviour', p. 137.
- 39 Lorenz, 'The Past Twelve Years in the Comparative Study of Behaviour', p. 290.
- 40 Much of Lorenz's early work is also devoted to distinguishing instinct from what he takes to be the other forms of innate behaviour: taxes, reflexes, and imprinting. The contemporary discussion of Lorenz's work, however, has concentrated on the instinct-learning distinction.
- 41 Lorenz, 'Companionship in Bird Life', pp. 85-6.
- 42 Lorenz, 'The Conception of Instinctive Behaviour', p. 136.
- 43 L. Carmichael, 'The Development of Behaviour of Vertebrates Experimentally Removed from the Influence of External Stimulation', *Psychol. Rev.*, 35, 1927, 253-60.
- 44 There are of course other important critics of a Lorenzian kind of behavioural analysis. In addition to the three chosen, mention should be made of T. Schneirla ('A Consideration of Some Conceptual Trends in Comparative Psychology', *Psychol. Bull.*, 49, 1952, 559-97; D. Hebb ('Heredity and Environment in Mammalian Behaviour', *Brit. J. Anim. Behav.*, 1, 1953, 43-7); and R. Hinde (*Animal Behaviour*, pp. 424-34).
- 45 D. Lehrman, 'A Critique of Konrad Lorenz's Theory of Instinctive Behaviour', *Quart. Rev. Biol.*, 28, 1953, 337-63.

- 46 F. Beach, 'The Descent of Instinct', *Psychol. Rev.*, 62, 1955, 401-10.
- 47 D. Jensen, 'Operationism and the Question "Is this Behaviour Learned or Innate?"', *Behaviour*, 17, 1961, 1-8.
- 48 Beach, 'The Descent of Instinct', pp. 404-6.
- 49 Lehrman, 'A Critique of Konrad Lorenz's Theory of Instinctive Behaviour', p. 341.
- 50 Ibid., p. 343.
- 51 Z. Kuo, 'Ontogeny of Embryonic Behaviour in Aves', *J. Exptl. Biol.*, 61, 1932, 395-430, 453-89.
- 52 Beach, 'The Descent of Instinct', p. 407.
- 53 Jensen, 'Operationism and the Question "Is this Behaviour Learned or Innate?"', p. 3.
- 54 Ibid., p. 4.
- 55 Ibid., p. 5.
- 56 Ibid.
- 57 Lorenz, 'Phylogenetische Anpassung und adaptive Modifikation des Verhaltens'; *Evolution and Modification of Behaviour*; and 'Innate Bases of Learning', in *On the Biology of Learning*, edited by K. Pribram, New York 1969. These all appeared during the decade of the 1960s.
- 58 Lorenz, *Evolution and Modification of Behaviour*, p. 47.
- 59 Lorenz, 'Innate Bases of Learning', p. 48.
- 60 Ibid., pp. 32-3.
- 61 Ibid., p. 23.
- 62 Ibid., pp. 23-4.
- 63 Lorenz, *Evolution and Modification of Behaviour*, p. 37.
- 64 Ibid., p. 44.
- 65 Ibid., p. 1.
- 66 At the beginning of his *Evolution and Modification of Behaviour* (p. 1) Lorenz suggests that the term innate refers to the 'limited range of possible forms in which an identical genetic blueprint can find expression in phenogeny'. Later in the book, however, he confines use of the term to the information stored in the genome: 'It is obviously this information alone to which we have a right to apply the term innate' (p. 40). No harm accrues if we allow the term to apply to both 'limited range of forms' and 'information'—perhaps to the former in a less strict sense—as long as the relation between the two is clear.
- 67 Ibid., p. 79.
- 68 Ibid., pp. 35 and 58.
- 69 In his 'Phylogenetische Anpassung und adaptive Modifikation des Verhaltens', (p. 168) Lorenz confesses:
I myself on occasion have represented the 'intercalation' between phyletic adaption and learning too much as a mosaic and too little as a reciprocal function—a marked error of thinking atomistically. (Ich selbst habe mir viel zu mosaikhaf und viel zu wenig als Wechselwirkung vergestellt, ein ausgesprochen atomistischer Denkfehler.)
- 70 Lorenz, *Evolution and Modification of Behaviour*, p. 107.
- 71 The logic of scientific explanation is a topic of considerable dispute in the philosophy of science. However, the objections and counter-objections which range around this subject are not such that they affect our discussion here. For a detailed treatment of the topic consult C. Hempel's *Aspects of Scientific Explanation*, New York 1965.
- 72 I owe a debt to professors Donald Jensen and James Connor for offering invaluable critical help; however, I suspect they will judge I have not always profited from it.