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The Objectivistic Theory of Instinct

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The Objectivistic Theory of Instinct

I have been invited, by M. le professeur GRASSÉ, to talk about ehological theory. Lately, papers by Prof. HEBB, Dr. LEHRMAN and Dr. KENNEDY have appeared, which attack our theories rather severely. Though these papers are, in several respects, very helpful and revealing, their merit lies more in showing what facts we seem not to have sufficiently emphasized and in pointing out some faults in our reasoning than in actually suggesting improvements on our hypotheses. The critique of any hypothesis consists, throughout inductive science, in offering an alternative explanation for the same facts as underlie the criticised hypothesis. Such an attempt is justified, even if the new hypothesis is neither simpler nor better than the old one: the mere existence of an alternative explanation, hitherto unsuspected, is of importance. The attempt is more highly justified if it offers, for the same facts, an explanation which is more economical of thought. Lastly, the supreme, and, in inductive science, most usual justification for the critique of a hypothesis is that the critic, working in the same field himself, has found some new facts that will not fit with the old hypothesis. He then will have to evolve a new one that is able to cope with both the new *and* the old facts.

Now I hope you will pardon my stating baldly that none of the three criticisms I have mentioned is of this kind. Quite on the contrary, all of them are not only guilty of supression of facts, but of supression of the most important facts underlying our theories. Of course, I do not dream of accusing any of our critics of consciously or even unconsciously, in a psycho-analytical way, supressing facts. It must be assumed that we have not stated them clearly enough in our writings. For the very reason that these facts are so fundamental, and so much a matter of course to ourselves, we seem to have failed to «get them over» — if I may be pardoned this idiomatic term. Semantic difficulties may also have contributed to this failure. I feel very deeply that I should make the utmost of the present opportunity to expound those fundaments of ethological theory which, although they incontestably are observational facts, are still flatly ignored by our critics. The value of these facts is not subject to any doubt while that of our hypothetical interpretations certainly is. It is therefore my plain duty to get these facts generally accepted before I go into details concerning modern ethological theory.

At the beginning of this century two zoologists, WHITMAN and HEINROTH, have hit upon a new phenomenon. They investigated each a group of animals, WHITMAN Pigeons, HEINROTH Anatidae, with a view of getting their taxonomy in every detail. Now, for comparative studies, the taxonomists cannot get enough comparable characters. In tabulating taxonomic interrelations within groups you cannot have enough characters to compare because the value of each character depends on all others. And in this search for further characters, WHITMAN and HEINROTH, independently from each other. — WHITMAN about ten years earlier than HEINROTH — discovered the fact that behaviour patterns could be used as taxonomic characters, as characters that are not only characteristic of a species, but often of a genus, an order or even of one of the largest taxonomical group categories. The classical example of such a behaviour pattern is the drinking movement of Columbidae. Pigeons and Sand Grouse (Pteroclidae) have been put as two sub-orders into the one order of Columbidae by naturalists who were guided by morphology alone and not interested in behaviour. This classification finds a convincing support in the movement in question, which characterizes the group better than any single morphological detail. When you read the zoological diagnosis of Columbidae in any modern textbook, it is quite a paragraph and yet not an absolutely satisfying definition of the group. But if you say they drink water by sucking it up with a peculiar peristaltic movement of the oesophagus you have fully characterized the order.

The invariability of such movements by far exceeds what Prof. HEBB has aptly termed species predictability. They are predictable, not only for a species, but for a genus, an order, or even a larger taxonomic unit. It is, for instance, predictable with supreme certainty that any new species belonging to the order of Columbidae will drink in the manner just described or that any species of Anatidae will take oil from the oilgland by rubbing its head on it in a rotatory movement.

This remarkable distribution of motor patterns throughout the whole zoological system was the superlatively unexpected positive discovery whose tremendous inferences caused research to take that particular direction which Ethology has pursued ever since. Yet, Professor HEBB, 54 years after WHITMAN, very clearly stated the nature of his discovery, asserts that the concept of instinctive behaviour is not analytically valid because of its «consistently negative definition». He says: «Instinctive behaviour is what is not learned, not determined by environment and so on. There must be strong doubt about the unity of factors that are identified by exclusion».

It must be stressed that WHITMAN and HEINROTH never even tried to define «instinctive behaviour» at all! They found one element of behaviour which is certainly innate and which we call today «instinctive movement». Like genetics and many other branches of inductive science, ethology started from a real discovery and definitely not from a theory. This is a fact that we do not want to be forgotten.

Neither WHITMAN nor HEINROTH ever offered any opinion concerning the physiological nature of the motor patterns which they have discovered. They were much more interested in the taxonomical conclusions to be drawn from them. Thus, Ethology began as a purely descriptive and classifying science which, incidentally, was the best start possible. This way of proceeding resulted in the collection of such an amount of observational material concerning the newly discovered motor patterns that their common physiological properties became too apparent to be overlooked. The most important among these properties are the following. First: the modifiability is infinitesimal, at any rate much smaller than that of bodily characters which are unanimously considered as «inherited» by biologists. Second: the very same motor patterns which, in phylogeny, prove to be so extremely conservative, tend to appear, in ontogeny, with a demonstrable independence of individual learning. Third: they show a type of spontaneity and of a tendency to rhythmical recurrence peculiar to themselves. In the interests of the discussion which is, I hope, to follow, I must expound these three constitutive properties of instinctive movements in some detail.

a) ***Limited modifiability.*** — There is absolutely nothing in any organism's body or behaviour that is not dependent on environment and, to a certain extent, subject to modification through environment. Even the most direct and rigid effect of genes is dependent on environment in so far as it cannot appear if the organism's milieu is changed to such an extent, that the animal sickens and dies. What is inherited, is not the character itself, but the range of its modifiability. The question that we have to ask concerning the instinctive movements is obviously how broad their range of modifiability may be. Geneticists have no hesitation to apply the term «inherited» to gene effects whose range of modifiability is inconsiderable to the point of being negligible. The red colour of Mendel's pea blossom is «inherited» or «innate» for this reason, the same colour in *Primula sinensis* is a «modification» because in lower temperature no anthocyan is produced, so that the flower is white. What is innate in *Primula sinensis* is the range of modifiability between red and white. I want to ask any geneticist whether he deems it necessary to refrain from calling the red colour in Mendel's peas an inherited character because of the fact that one can, by creating an exceedingly unhealthy environment, cause the plant to produce only buds which shrivel and drop off before opening into bloom and showing the red colour? This question is pertinent because that is mutatis mutandis, all that environment can do to instinctive movements. Unless the changes of environment impinging on the animal during its individual development, are so radical as to impair its physical health in an appreciable degree, no change in its instinctive movements can be noticed at all. I may add in parenthesis that, if this were not so, MAYR and DELACOUR's fine taxonomy of the Anatidae would have come out all wrong. If the abnormal environment results in producing a sickly individual, all the changes in its instinctive movements concern their intensity: they may be dropped out altogether or may be represented by weak incipient movements only. A spurious change of quality may be produced only where quantitative differences in excitation normally result in different instinctive movements. Thus, in the drake Mallard, certain movements of courtship, the grunt-whistle, the down-up movement and the head-up-tail-up are activated by the same kind of excitation but possess different thresholds at which they respond to it. For this reason it is possible to produce, by an adequate dosage of environmental damage, a weakly bird whose level of courtship excitation just reaches the threshold of the grunt-whistle while not attaining that of the two other movements. This effect can be attained not only in a young bird, but just as well in an old one which, in his former life, has performed the two movements now lacking. All that environmental influence can do, is preventing some instinctive motor patterns from appearing at all. No qualitative change has ever been observed, and it seems worth mentioning that the nuptial plumage will have disappeared long before the movement does.

But there are some instinctive movements which surpass the red colour of Mendels pea regarding their independence from environment because, short of killing the animal, it is impossible to prevent them from appearing. The so-called prying movement characteristic of Sturnidae and Icteridae consists of sticking the bill into a cleft and then opening it with considerable force, thus prying the cleft open. In the Europaean Starling this movement is performed even by very sickly and dying birds, quite irrespective of whether there is a cleft to stick the bill into, or not.

I would emphasize again that this complete lack of modifiability is not characteristic of what ethologists call «instincts» or what other authors call, in a looser sense, instinctive behaviour. All I have said is true only for those particular motor patterns which show that particular distribution in the zoological system of which I have spoken, and which were discovered by WHITMAN in 1898. If Prof. HEBB thinks that ethologists assume, with too much assurance, that the inborn behaviour pattern with which they are dealing, are directly genetically fixed, I feel inclined to agree with him regarding many other elements of instinctive behaviour, especially taxes and IRMS, but not regarding instinctive movements. It is certainly true that real genetical evidence concerning them is meagre: Hybrids between *Xiphophorus* and *Platypoecilius* often show, in the F2 generation, a curious dissociation of an instinctive movement and the organ used by it. The so called «sword» of *Xiphophorus* is an organ whose function indubitably is to stimulate the female by a peculiar courtship movement of the male which swims rapidly backward, sword first, in the direction of the female. The F2 hybrids often show the normal combination of organ and movement, but just as often the movement without the organ or the organ without the movement. Exact figures concerning the frequency of the three possibilities have apparently not been attained. In Drosophila, wingless mutants often are still in full possession of the normal movements of cleaning wings. In Anatidae, hybrids very often possess instinctive movements which none of the parent species have, but which are characteristic of other and, in this respect, more primitive forms. I emphatically agree with Prof. HEBB that it is superlatively important to get real experimental evidence concerning the genetics of instinctive movement. The difficulty is to get a suitable object: Two races or species which are sufficiently closely allied to produce completely fertile hybrids and yet different in regard to some clearly definable pattern of innate behaviour. We have looked in vain for such species among our Cichlids, but we think that we have hit, a short time ago, on two ducks fulfilling all the requirements mentioned: The Bahama Pintail, *Anas bahamensis* L. and the Chiloe Pintail, *Anas spinicauda* L. We shall get F1 hybrids of the two species, we know they are fertile and we hope to report results in a few years.

For the present, I should like to relay Prof. HEBB's question regarding the innateness of instinctive movements to Prof. E. MAYR whom I consider one of the greatest living authorities on phylogeny and genetics combined. I would ask him to what extent he regards as genetically fixed any of the morphological characters he is using in the taxonomy of Anatidae, for example the black and white markings of the downy chick in Casarcinae. There are, to the best of my knowledge, no genetical experiments concerned with this character, yet I do not think that Prof. MAYR would hesitate to call it an inherited one. Whatever the answer may be, instinctive movements have exactly the same right to the term.

I think that Prof. HEBB considerably overestimates the influence of environment if not on instinctive behaviour, but certainly on what we call instinctive movements, when he says, in the paper repeatedly quoted: «Instinctive behaviour may be nearly as misleading, but might be kept as a convenient designation for species-predictable behaviour, *as long as it is not thought of as determined by an invariant heredity alone,* but also by an environment that is equally constant in most or all important matters (Italics mine).» These sentences, while being obviously true for what is often loosely termed instinctive behaviour, evidently cannot be applied to the motor patterns which we call instinctive movements and which certainly are neither a postulation nor a «reification» of a theory, as Dr. LEHRMAN asserts, but something very real, found more than half a century ago by C. O. WHITMAN. I should like to know what could be considered a matter in the animal's environment that could be more important to the development of a fly's wing-preening movements than the presence of wings, or to the development of a young starling's prying movement than the presence of a cleft to stick the bill into.

b) ***Independence of individual learning.*** — It must be stressed again that the very same motor patterns which have the above described distribution in the zoological system and which show the other two constitutive properties here discussed, are also the ones which have the peculiarity to make their appearance, in ontogeny, in such a manner as to indicate very clearly, to any unprejudiced person, that their form and coordination is not and could not be acquired by individual learning. All Passerines scratch their head standing on one leg, lowering the contralateral wing right down to the perch, then moving the other leg, over the top of the wing, forward and upward, finally scratching the plumage of the head and the corner of the mouth with the second toe. In coordination with these movements, the head is held sideways in a particular way, so as to meet the scratching toe at the right place in space. You will all know the homologous coordination of movements in the dog, as to details about its phyletic history I refer you to a paper by HEINROTH published 1910. Now in the ontogeny of young passerines well coordinated parts of this movement make their appearance, before the movement as a functioning unit has ever been performed. The first appearance invariably consists of the young bird lowering the wing, holding its head askew and not being able to get its foot off the perch because it is not yet quite able to stand on the other alone. The pre-existence of such motor coordinations in individual life becomes particularly clear, whenever the organ matures later than the movement, so that function is quite out of question at the time of the first performance of the motor coordination. I remind you of the young gosling holding the adversary with its bill in exactly that position in space where the wing would hit it if it already had its adult proportions. In very many cases, motor coordinations would never render their particular survival value if they were not completely finished and ready to function perfectly before ever having been performed once. There is any amount of observational evidence for all this.

Nevertheless, these views are regarded as «finalistic» and «preformationistic» by our critics. PAUL WEISS, in this dogmatism, has gone to the extent of transplanting crosswise the buds of the forelegs in the *Ambystoma* embryo, expecting them to perform the motor coordination preformed to fit to their original location, that is to say to walk backward. This they did, throughout the animal life. Or, to be more precise, each of the transplanted forelegs worked in the original coordination with the hind leg of the side from which it came, thus working backward when the animal tried to go forward and vice versa. It is the wildest carricature of scientific truth to reject all these facts, for purely dogmatic reasons, and then to accuse the men who found them out, of being dogmatists, as Dr. LEHRMAN has indubitably done. Consider the weight of the circumstantial evidence pointing to preformation of motor coordinations within the central nervous system, and then compare it with Dr. KUO's theory, desperately supported by Dr. LEHRMAN, that the domestic chick learns to peck by having its head moved up and down passively by the action of the heart. The facts found by Dr. KUO, are, in themselves, extremely interesting, but they are open to quite different interpretations. And in the supremely unlikely case that the theory mentioned should be correct, I should like to know why young Passerines, instead of pecking, gape, why Pigeons insert their bill into the corner of the mouth of their parent, why ducks dabble and also, how the heart action teaches unhatched birds to preen, to walk, and so on and so forth, all of which many of them do even before they start pecking, literally a few minutes after hatching. The existence of motor coordinations, ready for use, in organisms devoid of environmental experience opens an immense field of investigation to the physiology of development, I assure you that not even the youngest of our students is blind to the problems. But it is a dogmatic error to attempt the solution of these problems on the assumption that there is only one factor on whose basis they can be solved, that of learning, and desperately to uphold the monopol of this factor by trying to make it work where there is no room for it to work in. There you have the situation in a nutshell — or an eggshell.

That our critics do not draw into consideration the existence of instinctive movements becomes very clear when one considers their way of argumentation. In the paper mentioned, Dr. LEHRMAN extensively describes the maternal behaviour of the rat, showing in what way learning enters into it. No ethologist ever doubted that it did and none ever believed, as the author evidently implies that we do, that this extremely complicated set of widely differing behaviour elements was wholly innate, but we do contend that the motor patterns which we call instinctive movements are. And to disprove this, our critics must take one typical example of such a motor pattern, which possesses the typical wide distribution characteristic of a taxonomic unit and the typically high species-predictability already mentioned. Then they must proceed to show, that, as Prof. HEBB asserts, «an environment equally invariable in most or all important matters» is necessary to produce that species-predictability. Let me propose, for a suitable object, the movement with which Oscines (Song Birds) and Anatidae distribute oil from the oil gland over their plumage. All the Oscines which I know (and also all those that I do not) do this by taking oil from the gland with the tip of their bill and then executing the scratching movement already described in a peculiar manner, first touching the tip of the bill with the claw of the second toe and subsequently rubbing it all over the top of the head. All Anatidae bite their oil gland, not with the tip of the bill, but taking it far back between their mandibles, chewing it in a sort of milking movement, pressing oil into the feathers growing on and about the gland. Then they press their head against those feathers and rub it against them in a rather slow rotating movement which brings most of the head plumage into direct contact with the oil-soaked feathers which function rather like a wick. Now let our critics do their utmost, changing whatever they can change in environment, or even excising the gland altogether and see whether they succeed in making a song-bird do the Anatidae's movement and vice versa. I give them a free hand to use all the methods of animal training known hitherto, starting with the moment the bird hatches, or even before that.

*c) **Spontaneity***. We now come to the third and physiologically most interesting property of instinctive movements, to their so-called spontaneity. The same motor patterns which possess the properties of which I have already spoken show very peculiar phenomena concerning their readiness to go into action: this readiness is by no means constant, but fluctuating within extremely wide limits in a strictly lawful manner: the organism's readiness to perform a certain instinctive movement is dependent, amongst other factors, but very directly, on the question how often, with what intensity and how far back the animal has performed that particular motor pattern. If one keeps a Cichlid in isolation from conspecifics thus withholding all the stimuli normally eliciting the fish's fighting and courting activities, one will find the thresholds of all these stimuli considerably lowered after a period of a few days. If one now offers stimulation eliciting fighting and allows the fish to fight for a certain time, one will find subsequently that the threshold of these stimuli has gone up again. This is not surprising, but easily interpreted as «fatigue». What is surprising, however, is that this bout of fighting, though it may have quite evidently fatigued the fish who may be breathing heavily and leaning against a waterplant, has not affected the threshold of courtship activities. This particular «fatigue» is specific for one activity only.

This activity-specific fatigue has its even more interesting counterpart in a progressive lowering of the threshold of all releasing stimuli, going on more or less continuously as long as the activity remains quiescent. This results in the organism's reacting to non-adequate stimulation, to so-called substitute objects, after adequate stimulation has been withheld for a considerable period. Male Cichlids of many species — for instance *Etroplus maculatus* — will invariably accept their own females as substitute objects for another fighting male and kill her off, if the pair is kept alone in a tank for a period of time during which the male finds no «outlet» for his fighting movements. If two pairs are kept in a larger tank in which they can mark out territories, the males will fight each other at the boundary line and never attack their own females. The threshold lowering may, in certain cases, reach such extreme degrees that the activity «breaks out» apparently with no outward stimulation at all — and that is the much-discussed phenomenon of «vacuum» activity. It is worth noting that the instinctive movements appearing with this extreme independence of adequate stimulation are invariably such as are performed extremely often and continuously in the normal daily life of the animal in question, such as the insect-killing movements of the Bee-eaters and the Starlings, the prying movement of the latter, the pecking-and-swallowing movement of the African Ostrich, etc. etc...

I have used the comprehensive terms of «fighting» and of «activity» in describing the behaviour of Cichlids, without explaining in what way these concepts are different from that of instinctive movement. The activity of fighting includes a considerable number of the latter: erecting median fins, spreading the gill membrane, beating the tail laterally, ramming and some others. These single instinctive movements are linked together in a number of ways which are very suggestive of a physiological interpretation which really is a hypothesis and the first one I am going to mention. First: The thresholds of all these movements fluctuate parallel to each other, according to the «readiness to fight» in which the fish is at a given moment. If, in the beginning of an experiment, we find that our Cichlid will react very quickly and to a very slight stimulation by erecting median fins and distending the gill membrane, it is predictable that the other movements will be releasable with corresponding ease. Conversely, if we find that the Fish takes a long time and a rather strong stimulation to erect the median fins, it becomes predictable that not even optimal stimulation will succeed in exciting is to the point of giving the tail beat, still less the ramming thrust. Second: As has already been anticipated in the last sentence, there exists a very strict order between the single instinctive movements mentioned. Not only do they appear in a strict temporal order, in the sequence in which they were mentioned above, but the appearance of the preceding motor patterns is the condition for that of the subsequent ones, while not permitting any prediction whether the latter will be performed or not, on the contrary, the activity may fade out at any point. Third: The performance of any of these movements affects, e.g. raises, the threshold of all others.

No generalizations are possible as to what movements are linked by the common factors just described. Very often one single motor pattern has its own independent fluctuation of threshold, for instance the prying movement of the starling. Very often one biological function comprises motor patterns possessing thresholds which fluctuate quite independently of each other, such as those of killing the prey and of eating it in a weasel or a stoat. Conversely, movements of amazingly different function can be dependent of each other in the above-mentioned manner. DREES has shown conclusively that this is the case in the motor patterns of hunting and of courting in certain Spiders of the family of Attidae. Both activities commence with the same motor patterns of running towards and stalking the releasing object. By the exhaustion of one activity the threshold of the other is raised to the point of making it unreleasable. Yet the total exhaustion of the spider running at a prey and/or at a female has no influence on the animal's readiness to run photo-tactically towards light — and vice versa!

These are the facts which are described in an illustrative manner by the world-famous model of the flushing reservoir. Please believe me that none of our youngest students has ever believed for a moment that this object of ridicule is more than a parable or should be regarded as an attempt at explanation of facts. But now I do come, for the first time in this paper, to the point at which I have to deal, not with facts overlooked by our critics, but really with hypothesis, that is to say with our interpretation of facts.

The regular and strictly lawful relationship between such a «set» of motor patterns as, for instance, those of fighting in Cichlids, make it very probable that they are activated by one mutual excitatory factor to which they respond with different thresholds. This factor increases and vanes with the quiescence and the performance of the movements, it can be accumulated, under abnormal environmental circumstances, to truly abnormal levels. «Something» which I have termed in an old paper Action Specific Energy and which is much better described by R. HINDE's less prejudicial term Action Specific Potentiality is generated and discharged. This «something» may be anything, it may be humoral, perhaps a neuro-hormone, I am not quite disinclined to believe so even today, or it may be a neural process. And after all it is common-sense to look to neurophysiology as the most likely source of possible explanation; if we ask whether there are some neurophysiological processes known which might be akin to our crucial phenomena of spontaneous generation and rhythmical discharge of «something», we naturally hit upon those processes of endogenous, rhythmical generation of impulses which have been found in the sinus ganglion of the heart, in medusae, in the breathing centre, in the olfactory tract and in the central nervous system of many animals by SHERRINGTON, BETHE, ADRIAN, WEISS, VON HOLST and others.

Consider the facts found by VON HOLST concerning the automatic production and intra-central coordination of the impulses which, in the earthworm, control the movements of creeping. When the nervous system of this animal is not merely desafferentiated, but completely isolated from the body and suspended in Ringer's solution, it still goes on to produce these impulses, rhythmically and in perfect coordination. This was shown by simultaneously recording, on a series of instruments, the action currents emanating from every segment. When a critic doubted that the activity thus recorded was really identical with the one resulting in creeping movements in the intact organism, VON HOLST improved on the experiment by leaving a few segments intact and in connection with a preparation otherwise identical with the one first mentioned, and showed that these segments now performed real creeping movements keeping exact time with the beat of the instruments connected with the isolated part of the ganglion chain.

We do not know yet to what extent the characteristic properties of instinctive movements can and will be explained on the basis of these and similar processes found on lower levels of the central nervous system. (Contrary to what Dr. LEHRMAN thinks of us, we are very cautious in identifying analogous processes going on on different levels.) But it seems to me to be the most obvious kind of commonsense to seek for explanations in this particular direction and not in that of learning, conditioned responses or, still worse, «chain reflexes». And this last sentence comprises pretty much all the «theory» we have developed concerning instinctive movements.

And now let us hear what our critics have to say concerning the spontaneity of instinctive movements. Dr Kennedy says that the assumption of two different functions, viz. a) the endogenous generation of stimuli and b) their afferent control, is decidedly «dualistic» and, therefore, vitalistic. I do not mind being considered a vitalist in company with men like ADRIAN, WEISS and VON HOLST, all of whom certainly believe in the reality of both these functions.

Dr. LEHRMAN, on the other hand, in refuting the theory of an internal «build up» and of vacuum activity resorts to the same type of argumentation he used to disprove the «innateness» of instinctive behaviour. He cites an example which looks like a vacuum activity but is not and then thinks he has proved that vacuum activities — he does not bother about threshold fluctuations and other minor details — do not exist. LEES said in his paper on the ant *Eciton hamatum,* that the rhythmical recurrence of these animals preying expeditions are «akin to vacuum activities» because they are in no way related to the abundance or scarcity of food. SCHNEIRLA has shown conclusively that these excursions of Eciton are not vacuum activities but definitely released by the growth of a new brood within the colony. LEHRMAN concludes that this error of LEES shows «the restrictive nature of such categorial theories as that of LORENZ». I am sure that LEES never really thought that an army ant expedition was a vacuum activity. It needs a profound ignorance regarding the properties of those simple and rigid motor patterns that we call instinctive movements to think that any ethologist would ever consider the possibility that such a complicated behaviour as an army ant expedition should be one instinctive activity and, of course, only the latter can ever «break out» in a vacuum activity. And the few instinctive activities that ever do so, interesting as they may be concerning the independence of exteroceptor and proprioceptor control, are not at all the most opportune object to study those phenomena which really intrigue us because they may lead us to a causal explanation. The problems of endogenous «build up» of readiness, parallel threshold fluctuations etc, can be much better approached in much less spectacular objects, for instance in the fighting movements of Betta, investigated by LISSMANN many years ago and lately by PRECHTL, or in Cichlids, as we are doing at present, or in the classical object of the wiping «reflex» of the frog, on which FRANZISKET has lately done such very successful attempt at the quantitative analysis of exhaustion and accumulation of action specific potentiality. Our theories seem to be categorically restrictive indeed, as they seem to have restricted our critic from going to the next pet shop, buying some of these cheap animals and first questioning our facts before questioning our hypotheses.

Hitherto I have spoken exclusively about the fundamental observational facts which concern one innate element of behaviour, the instinctive movement. I have not spoken at all about that other element which may be regarded as the counterpart of instinctive motor patterns on the receptor side of the central nervous system and which really is much nearer to my heart: the IRM, the innate releasing mechanism. I have no time to do so. There are other particulate functions of the central nervous system. We do not know how many of them there are, still undiscovered. I thought it best to show the existence of particulate elements by expounding the facts concerning one of them, facts which still are not generally known, or generally disbelieved.

I have been defending facts and not theories. And now I have done enough of defending altogether and I am going to do some attacking of theories.

For some reason, which probably can be accounted for by the historical development of behaviour study, many authors, and among them our critics, hold the theory that there cannot be, within the central nervous system, any particulate structures controlling behaviour. It is on the basis of this dogma that every theory which recognizes the incontestable fact that such structures do exist, is branded as preformationistic, finalistic and what not. According to this dogma, the central nervous system is a so-called whole in which everything is in universal mutual interaction with everything else and which is modelled on WOLFGANG KOEHLER's concept quite particularly of «physikalische Gestalten», in respect to the one fallacious point that the whole must possess only one kind of element, just as KOEHLER's model of the electric charge on the spherical conductor, of the solar system and of the soap bubble. No organism is built that way and even the Amoeba has more structures than the dogma now criticised tends to concede to the human brain. Animals have bones and sinews and glands and any number of particulate structures which, in the interaction within the system, influence the whole far more than they are influenced by it in return.

It may be an error of mine, but I do think and I put it to the discussion that it is just this dogma, or attitude, that lies at the root of the two fundamental errors contained in the following sentence which I quote from Prof. HEBB's paper. He says: «I urge there are not two kinds of control of behaviour, and that the term «instinct» implying a mechanism or neural process independent of environmental factors, and distinct from the neural processes into which learning enters, is a completely misleading term and should be abandoned». The two afore mentioned errors are the following. First: Prof. HEBB obviously believes that the concept of «instinct», as it is defined and used by TINBERGEN implies one particulate neural mechanism independent of learning: we know about a dozen of such mechanisms and we do not know how many more there are, there may be another dozen, all of them being the functions of particulate and, on principle, structural organizations within the central nervous system. The second error is the dogmatic assumption that «learning» must «enter» into literally every function in the central nervous system, being the one and only «element» permitted by the theory sketched above.

If we try to make a short synopsis of central nervous functions which, on the basis of present knowledge, can be regarded as particulate and clearly distinct from each other, we find quite a good number. There is that complicated apparatus of optomotoric reactions, investigated with such spectacular success by WEISS and SPERRY and by VON HOLST and MITTELSTEDT in so different objects as Amphibia and Insects and yet with such conforming results. There are the functions of stimulus generation and coordination found and analyzed in the same institutes. There are the complicated navigating functions of birds, involving the existence of an «internal clock» as well as that of a mechanism able to compute where the sun is standing at any given hour of the day, and able to do so, as KRAMER has incontestably shown, in a Bird that never saw the sun moving in all its life. There are the wonderful functions of orientation in the Honey Bee which is able to compute the position of the sun on the basis of the direction in which the light is polarized at any given patch of blue sky visible to the insect. There are many more independent particulate functions and it is irrelevant whether or not I am allowed to add, in all modesty, the instinctive movement to this list. The point I want to make is just this: All these functions are different from each other for exactly the same reasons and in exactly the same manner, as the functions of a sparking plug, of a connecting rod and of a crankshaft are: In all these cases the differences of the function is intelligible only on the basis of the differences of the structures that are functioning. I concede that it is a tall order to approach analytically the structures underlying the functions I mentioned. But we have already one important hint how to approach this problem: This hint comes from cybernetics. And it is just the cybernetic analogies to some of the computing functions contained in our list, that make it so extremely unlikely that learning enters into them to an appreciable degree.

If our concepts of certain functions such as, for example, the IBM, are erroneous, the fallacy is not at all likely to lie in the fact that there is, in reality, no particulate structure in the central nervous system performing that function. The error will, in all probability, lie in the opposite direction: future investigation is very likely to show that, where we assumed one particulate mechanism, there are, in reality, two or more, performing analogous functions which we misleadingly united in one concept, I chose the IBM for an example because I have some shrewd suspicion about how this particulate mechanism will be split into at least two in the near future. We are ever ready to split up our concepts. The history of ethology is full of examples of concepts becoming ever narrower and narrower with every step of the investigation.

Conversely, we have good reasons to be extremely suspicious of all allegedly explanatory procedures which necessitate a widening of concepts. I am quite aware that it is, on principle, possible to assert that «learning» is «entering into» all the functions and, what is more, all the neural structures of all organisms. One only has to define the concept accordingly. But to explain structure, the point at which «learning» would have to enter, would obviously be that of all processes of embryonic development. In other words, the concept of learning would have to be widened to such a degree as to include all epigenetic factors taking part in the formation of structure. I think that there are, even today, some indications that such a widening of the learning concept is already beginning. But I strongly doubt that such an inflation would be of advantage to the analytical value of the learning concept. It would become a very big balloon with a very thin wall and very liable to collapse. I urge that we should not do that to a concept which at present does correspond to something very real. I urge that we should be profoundly grateful that organisms do have good hard particulate structures performing particulate functions, because these are the archimedic points from which analysis can start. I urge that we should be particularly grateful that the central nervous system is not just one big holistic jelly built up out of a single kind of element and possessing less structure than even an *Amoeba* but does have particulate functions such as innate behaviour patterns and learning.

DISCUSSION

J. HALDANE. — 1° M. Lorenz a eu raison de qualifier de classique la systématique des Oiseaux selon leur comportement. C'est Aristote (ou peut-être Théophraste écrivant sous son nom), et non HEINROTH ou WHITMAN, qui a noté le premier la façon spéciale de boire des Columbidae en citant 3 espèces.

2° Vu que j'ai fait la génétique de *Primula sinensis* pendant 12 ans, je nie formellement la doctrine de Baur que la couleur des fleurs des formes rouges de cette plante varie avec la température. La plupart sont presque invariables. II y a une forme hétérozygote peu stable, mais c'est exceptionnel. Dans mon livre *The Biochemistry of genetics,* j'ai donné des exemples d'interaction du génotype et du milieu mieux fondés.

3° Je doute que M. Lorenz ait le droit de se dire objectiviste tandis qu'il emploie des mots comme «prying, etc...» qui sont assez anthropomorphiques. Je ne suis pas d'ailleurs très hostile a l'anthropomorphisme, qui est une forme primitive de l'ethologie comparée.

4° Je crois que M. Lorenz exagère la stabilité des mouvements musculaires. Mon Collègue, M. Grüneberg, m'a dit qu'*à* peu près la moitié des mutations chez les Souris ont été découvertes par l'observation d'anomalies de comportement. Pour les Souris de Laboratoire, les mouvements de la nage sont des mouvements «innés» et non acquis. C'est en étudiant la nage que l'on peut le plus facilement classer de nombreuses anomalies innées du comportement.

5° Je ne crois pas que la phrase «portée de variation» soit très utile pour ce qui est hérité (ou selon moi, déterminé par voie génétique). Je préfère parler avec Lyssenko d'une détermination de besoins. Je préfère encore mieux dire que chaque génotype détermine un schéma de réactions à tout milieu possible.

6° Dans un mémoire tout récent, Gordon et ses collègues, ont montré que certains mouvements endogènes (gestes héréditaires) de Poissons de deuxième génération, hybrides de *Xiphophorus* et *Platypoecilus,* ne sont pas indépendants des caractères morphologiques. Les Poissons sans «glaive» peuvent bien faire des mouvements caractéristiques de *Xiphophorus*. Mais il existe une corrélation assez forte entre les mouvements des *Xiphophorus* et la présence de cette modification caudale.

7° L'attribution de la spontanéité à un mouvement est toujours difficile. La miction des Mammifères semble être assez spontanée. Mais Reynier vient de montrer que les Rats nouveaux-nés meurent de rétention urinaire s'ils n'ont pas reçu une stimulation des organes génitaux extérieurs, due, dans la vie normale, à un léchage naturel. Dans un tel cas, «learning» ou «apprentissage» me paraît encore un mot plus douteux que «l'instinct».

8° Quand on me parle des rythmes spontanés, surtout des rythmes respiratoires, je pense à l'expérience foudroyante de Thunberg, il y a 30 ans. En mettant des hommes dans une chambre où la pression était changée 15 fois par minute, il a supprimé complètement les mouvements respiratoires pendant 24 heures ou plus.

K. LORENZ. — I only want to state that the example I used is probably not the best that could be found. As regards the other questions, I think I had better come to that of spontaneity at once. No generalisation is possible about spontaneity or dependence on external or internal stimuli. Take, for instance, urination or defaecation, both of which are definitely dependent on proprioceptor stimulation in most higher animals. Yet, in very many young Mammals urination is dependent on being released by the mother's attention who massages the baby's abdomen with her tongue. We rear a lot of young Mammals artificially in Buldern and we know that young Polecats, Squirrels and other Mammals will die of uraemia if one fails to procure a substitute for this specific stimulation. But I think that the existence of such behaviour patterns which are absolutely dependent on external stimulation serves only to set off and emphasize the existence of the opposite, of behaviour patterns which are performed even if external stimulation is completely lacking. The rhythmical recurrence of such activities, as, for instance, the prying movements of the Starling, which were mentioned before, is very similar to activities whose rhythmicity is brought about by recurrent tissue-needs, whether working through the means of proprioceptors or acting directly on the central nervous system. Only, hitherto, we have no idea what the physiological mechanism that causes rhythmical recurrence of instinctive activities may be like. The most amazing examples of independence of external stimulation are afforded by those instinctive movements that look oriented at an object or a part of the animal's body and yet go on without any change when the object is lacking as in the case of HEINZ's Flies or wingless mutants of Drosophila all of which preened non-existent wings.

This brings me to the question of mutation. Of course, we have not yet studied behaviour mutations in domestic animals with anything like sufficient exactitude. Of course, I quite agree to what Professor HALDANE said about the Mendelian segregation of the Sword-tail and the courtship movement in *Xiphophorus X Platypoecilus* hybrids. But there is one thing I want to make clear: I did not say the instinctive behaviour patterns are particularly resistant to change through mutation in domestic animals, I said they were resistant to environmental influences, in other words, that their phenotypic modifiability was so small as to be negligible. As regards mutations, their occurance in behaviour patterns has even been actually observed. There are some indications, though, that single mutations can change innate behaviour in a noticeable manner. Comparative study of the courtship movement of very closely related Ducks shows convincingly that the latest steps in the phylogeny of their movements do not consist in qualitative changes of single motor coordinations but in a process through which single motor patterns are either coupled together or dissociated from each other. While these motor patterns are widely distributed throughout the subfamily, the way in which they are welded together in a single indivisible sequence, is characteristic of the species. Thus the «head-up tail-up» movement in the Mallard is invariably followed by «nod-swim» while in the Gadwall it is coupled with the socalled «down-up» movement. There are innumerable cases in which the species differences consist of different coupling of the same motor elements. That such a coupling or uncoupling may be effected by one or very few mutations is made very probable through a chance observation: Before the world war I had a strain of Kakhi-Campbell ducks (a domestic race of the Mallard) in which the «head-up tail-up» movement was coupled to a subsequent «down-up» movement, instead of «nod-swimming», as in the wild Mallard. Unluckily I lost sight of that strain of ducks, it would have been interesting to crossbreed them with Mallards and to see how this behaviour characteristic behaves genetically.

At present we have just begun to experiment on the genetics of instinctive movements. The difficulty is to find two species close enough to each other to produce fertile hybrids and yet different enough in their motor patterns. The Bahama Pintail, *Anas bahamiensis,* and the Chiloe Pintail, *Anas spinicauda,* seemed the most favourable species. In each of them one particular courtship movement is highly developed, while all others have disappeared, *Anas bahamiensis* does only the «tail-up» movement, *spinicauda* only the «grunt-whistle». PETER SCOTT has saved us three years by a free gift of nine Birds, F-l hybrids and recrosses of *spinicauda*.

MRS SPURWAY-HALDANE. — Geneticists use fixed action patterns (Erbkoordinationen, instinctive movements) in their experimental technique. May I explain why geneticists cannot use Lorenz's vocabulary?

Experiments can be performed during the lifetime of a given individual i. e. after the fertilization that resulted in that organism. Alternatively experiments can be performed to collect circumstantial evidence as to what happens before and at fertilization. These techniques have evolved different vocabularies. All the experiments made by LORENZ and his school have been on development of individuals resulting from zygotes, but this school have consistently attempted to describe their results in the vocabulary currently used for the processes preceding zygote formation. This has resulted in LORENZ being blamed both for making claims about genetic determination, and for ignoring developmental processes.

HEBB was not attacking Lorenz, but integrating the work of the latter with the hypotheses currently held about the genotypic contribution to the epigenetics of taxonomic characters.

The clause «not thought of as determined by an invariant heredity» refers to the repeated discovery (HARLAND, DOBZHANSKY, KIKKAWA) that different genotypes contribute to phenotypes which are indistinguishable. Neither the standardization of «wild types» on which the species concept is based, nor the phenomena called special homology are due to identity or even similarity of the relevant genotypes; i. e. taxonomic categories do not seem to be definable by a highest common factor of allels or even loci.

Similarly «an environment that is equally constant in most or all important matters» is a formal qualification necessary and usual in biological discussion to allow for the results of possible experiments with the environment, including embryological experiments. I believe that we will be able to make an Oscine preen like an Anatid. This may be prohibitively expensive like lifting a 5 ton weight a kilometer into the air, but it is a confession of vitalism to say that it is impossible. Being a Lorenzian I do not believe this change of movement will be achieved by conditioning.

K. LORENZ. - I am quite aware that our vocabulary is most insufficient from the geneticist's point of view. Of course, we do not know how much of what we call «innate behaviour» is directly genetically determined and how much is due to epigenetical processes. That is why I find Professor HEBB's conception of species predictability so enormously useful. The point I was trying to make was just this: It is actually our interest in the modifiability of behaviour through learning that impells us first to analyze the limits of variability, in other words, the degree of species-predictability of behaviour. In order to assess the modifiability by learning it is immaterial in what way the «rigidity of behaviour» is determined. We need not know, for this purpose, how much is really directly dependent on genes and how much is epigenetic. Also, for the purpose of phylogenetic comparison, this question does not interest us just as it does not interest the comparative morphologist or palaeontologist studying bodily characters.

Professor HALDANE said he did not like our term «objectivistic»: I agree and I want to emphasize that it is not meant as a boast of particular objectivity and exactitude. It is only meant to set us off against subjectivistic psychology which claims to know anything about the subjective experience of animals. We hold, for epistemological reasons, that no such attempt can be considered scientific. On the other hand, this position does not imply that we do not recognize the scientific value and justification of a subjectivistic human psychology.

T.C. SCHNEIRLA. — Let me refer first to the point Dr. LORENZ raised concerning cybernetics, to the effect that in an analytical approach to structural — functional relationships in «instinctive behavior», cybernetics analogies to such functions make it unlikely that learning enters to any appreciable extent.

I do not see how this follows, for even on cybernetic grounds, or other analogical thinking in terms of models, learning may be involved in stereotyped as well as variable forms. This reminds me of the statement that cybernetics brain models learn best when they are unaware of it.

There is no dispute of course about the fact that distinctive morphological and behavioral characteristics are all somehow related to genetic constitution. These characteristics, once we know their range, might even be described as «genetically fixed.» This is a convenience for the systematists, — the question is how, on different phyletic levels, genetic constitution is related to individual morphology and to individual behavior.

From an interest in the traditional background offered by WHITMAN's and related work, this has been a concern of mine from my graduate days. In 1932 I deliberately chose the army-ant behavior pattern as a subject for investigation, because in it there seemed to be a problem well worth investigating, concerning species biological make up as related to species behavior pattern. Interest in this investigation has always centered around species comparisons. What we are trying to get at in such research is the relationship between genetic constitution and behavior, characteristic of each animal type. There is no difference of opinion among us, as to this point.

From my own standpoint, as a psychologist, I find in the work of the LORENZ school a long sequence of fine and interesting observations, vividly reported; but in these reports it is often very difficult to distinguish hypothesis from factual evidence. An example is the term *releaser,* often used, which habitually colors the report of a stimulus-response relationship because it forcibly intrudes the observer's subjective conception of what is important in the situation for the animal. This, assumed to be effective as a schema, is presumed to be natively effective as meaningful for the animal.

Embedded in reports of stimulus — response relationships are found presumptions of an innately determined isomorphism, referable to postulations about the natively — determined role of the nervous system difficult to accept, unless on faith. The nub of the question, it seems, and foremost in my own theoretical difficulties with the LORENZ position, is in postulates concerning organization of key responses, the «instinctive movements» so-called, by virtue of innately constituted functions of hypothetical neural centers. In my own paper I shall try to bring out some further considerations with respect to natively given organization-determining properties of neural centers so conceived, with respect to the rest of the organism.

Now, as concerns learning, it is probable that if reliable evidence is found for qualitatively different types of modifiability in behavior ontogeny, we shall have to accept them. Against the background of our current indistinct understanding of behavioral ontogeny, I cannot share the confidence Prof. LORENZ has shown in previous publications, with respect to making a sharp distinction between the learned and the unlearned in development. Hut increasing attention is being paid to the possibility that qualitative levels exist in learning capacity, and the same principle may well apply to the role of extrinsic factors all through ontogeny. As I recall the last section of his paper, Dr. LORENZ says that it is possible to assert, on principle, that learning enters into all the functions of *all* organisms. This seems pretty sweeping, but not consistent with the way he dismisses KUO's work in the preceding section, although KUO's was one of the few attempts to analyze behavior in embryo. Something important to the developmental process may be lost when the question is posed, as Prof. LORENZ does, in terms of whether or not the heart «teaches» the unhatched chick to do something. What we do have is the indication of a relationship between head activities and the functions of other parts of the chick embryo, of apparent significance to adult pecking and very probably other characteristic activities as well. The word «teaching» does not seem valid for such relationships. Behavior modifiability here may be of a much simpler order than, say, even conditioning. As HEBB says, we do not know the nature of adult learning well enough to make categorical distinctions at this stage as to its influence in ontogeny. Rather, the question concerns the status of extrinsic — intrinsic relationships at progressive stages of development.

My difficulties with the LORENZ system center mainly around its deficient attention to the need for analytical investigation of ontogenetic processes. This is perhaps a matter of more serious concern to many American psychologists, against a background of interest in behavioral development, than to others. In Dr. LORENZ'S paper here, it seems that more than a gesture is being given to ontogeny, and that is good. But although the LORENZ group has been doing much work on early behavior, this is essentially descriptive in its approach, rather than analytical.

It is perhaps not necessary to stress the fact that analytical investigations, along comparative lines, are much needed on the ontogeny of behavior in various animals. This raises also the desirability of penetrating into species differences at progressive developmental stages on different phyletic levels. It seems likely that in such work, careful attention will have to be paid to the role of the species developmental context from early to late in ontogeny. Evidence on the relationship of the intrinsic to surrounding conditions is relevant from the first stage. A much simpler concept than learning, though related, may be required for the early stages of modifications appearing through such relationships. It is not a question of relative emphasis upon either of the agents implied in the traditional heredity — environment dichotomy. There seems to be no possible gain in reviving that controversy. But a realistic approach should discourage the habit of opposing these concepts sharply, as when «learned» is set against «unlearned» in development. At present we are not altogether groping in the dark with respect to desirable revisions in developmental concepts, although in many respects evidence is too scanty.

Another point here concerns what Dr. LORENZ says HEBB said: namely, that the «concept of instinctive behavior is not analytically valid because of it's consistently negative definition.» On this point, HEBB was quoting BEACH, who had offered this criticism in an earlier context. There is much truth in the criticism, I believe. One telling example is the common insistence that behavior appearing in «isolated» animals must be «innate», and not influenced to any important extent by developmental context. But can the acquired and the learned be so readily and cleanly separated from the «instinctive»?

This brings us back to the difficulty of distinguishing what the nervous system does, or does not do, on an innate basis. Of course, any theorist is justified in erecting hypotheses if he shows that they follow from his theory, and sets about testing them. But much of the LORENZian hypothesizing as to how the nervous system works on an innate basis seems wanting on both scores. It is even possible that the term «finalistic» may not be misapplied when used for these procedures. It is good to learn that Dr. LORENZ is not altogether adamant in these matters, although he still seems largely consistent with his earlier position as to how the nervous system works innately. Even now, I am not really too sure whether he takes the drainage hypothesis more or less seriously than do his students. — Neurologists offer us no clear orientation as to how the nervous system works in consecutive behavior, which means that concepts of innately given neural organizations must be considered highly tentative. It is not a foregone conclusion that «instinctive behavior» as organized behavior centers upon neural functions directly fixed as described through genetic constitution. Other central mechanisms, as well as peripheral, will have to be considered in the developmental picture.

These are some of the main difficulties that I have had in following the line of this theory, as a psychologist interested in animal behavior. The problem is to assimilate and make use of the rich content of data from this source, yet to remain sufficiently objective about the somewhat preformistic ideology as to what is innately given in behavior.

K. LORENZ. — I hope I have fully understood Professor SCHNEIRLA's intervention, but I still see no real contradiction between what he has said and what I say about Doctor KUO's theory that the heart-beat teaches a Chick peck and about the widening of the learning conception. I said that one can explain practically all behaviour by learning provided the learning concept is defined so widely as to include all epigenetical processes. I meant this statement as a warning against such an inflation of a concept, the value of which would certainly be entirely destroyed by such a proceeding. I don't think there is any real difference of opinion in that respect.

Now, secondly, regarding the morphology of behaviour, though the interest in it is common to both of us I think the difference in our opinion is the following one: you are inclined to think that the Morphology of a species influences its behaviour in an epigenetical way. I concede that you may be entirely correct as concerns your object. We, on the other hand, are quite sure that we know many instances in which the morphological structure and the behaviour patterns in which it is functioning are transmitted quite independently of each other. The Bearded Tit and the Golden Pheasant perform display movements where the feather structure necessary to its function have not yet been developed. JEAN DELACOUR observed that a Mandarin drake that did not develop a nuptial plumage persisted in «display-preening» the fan-feathers it had not got.

In answer to the accusation that we are not interested in ontogeny I may remark that pioneer work of ethology, the four huge volumes of HEINROTH's *«Die Vögel Mitteleuropas»* are exclusively dedicated to the ontology of birds reared from the egg and that by far the greatest part of what we know about behaviour is derived from watching its first appearance and further development in ontogeny. The vast majority of all birds and mammals kept in our department have been reared from earliest infancy. Ontogeny, far from being neglected, is actually one of the chief sources of our knowledge. In spite of this I do, of course, entirely agree that we do not know enough about the ontogeny of instinctive movements and that it is one of our most important tasks to study it.

MRS. SPURWAY-HALDANE. — Exactly in epigenetical vocabulary and ontogenetic vocabulary.

K. LORENZ. — I entirely believe that and TINBERGEN has been doing so since very long ago.

And now to the question of our alleged finalistic attitude: being phylogenists we are so far from being finalists that we are, may be, somewhat careless about our expressions. We may, perhaps, say something like: the cat has sharp falcated claws to catch mice with, when we mean to say that the selection pressure of this function has caused the evolution of the cats claws. This is exactly what I meant yesterday in my example of the pug having a curly tail «in order to» being selected by the judge for stud in a dog show. I think that Professor RUYER's paper about finality may give us occasion to go into finality in detail. I have already prepared my views about finality in order to bring it into the discussion then, so I think to leave these questions of finality to that paper.

D. LEHRMAN. — There are many points that I might raise in discussing LORENZ's paper which I'll have better opportunities to say when I present my own paper on Saturday. I will therefore restrict myself to, I hope, a few brief comments.

First I must say that I think Dr. LORENZ has misunderstood what Dr. SCHNEIRLA meant by the study of ontogeny. For example, I am sure Dr. SCHNEIRLA is very far from believing that an epigenetic approach implies that the bearded tit raises the feathers. This is not the point. The alternatives are *not* simply: *either* the bird raises the feathers reflexly because of some stimuli provided by the feathers, *or* the feathers are there, and there is also, independently, a center in the central nervous system which sends impulses appropriately to the muscles which erect the feathers. There are other possibilities.

The histology and physiology of this skin area, the arrangement of the muscle fibers, the arrangement of the sensory and motor neurones of the area, all might be relevant to the problem of the origin of this special movement of this skin area. After all, the fact that hormones selectively cause growth of feathers at one skin locus rather than another should suggest to us that the different areas of the skin are physiologically not equivalent, even before they have begun to look different. We should not assume without analysis that the skin, muscles, neurones, feather papillae, etc., at this area are anatomically and physiologically quite the same as at other areas, and quite the same as in other species, and that there just happens to be a center in the brain of this bird which apportions the impulses to the correct muscles to make this bird perform its proper movement. I think Dr. SCHNEIRLA has made this kind of point very clearly in connection with his studies of the army Ant, and that he would reject, equally with Dr. LORENZ, the oversimplified relationship suggested by LORENZ between the feather and the movement which displays it.

Dr. LORENZ mentions HEINROTH's work as an example of the study of ontogeny. We all have great respect for HEINROTH's valuable studies and for the enormous amount of information provided by them. They are ontogenetic in a sense. HEINROTH has described in great detail, for a great number of bird species, the order of development of elements of behavior, and the characteristics of the developing behavior patterns and of their functional relationships. I mean no disrespect for these contributions of HEINROTH when I say that they are not a substitute for the analysis of the physiological conditions which are changing during the emergence of the behavior elements, and which constitute the development from one stage to the next, which accounts for the behavioral changes. The kind of ontogenetic study which Dr. SCHNEIRLA wishes to suggest, I think, is not a descriptive study of the order of development of activities, but rather some understanding of the physiological background of the order of development. Now, this understanding of the physiological background must, I think, imply something more than the assumption that every time a new act appears in ontogeny this is because a central mechanism specific for the act has matured, with no further analysis of what the maturation consists of, what the physiological processes involved are, and so on. I know that this is very difficult, and is a task for the future, as Dr. LORENZ implies. But I don't think it settles the problem to say that the study of ontogeny has been or is being taken care of, because it has not been taken care of.

Dr. LORENZ refers to genetical evidence. Such evidence is extremely important, and should be collected. We'll be much better off having as much evidence as possible about the genetics of behavior patterns. However, it must be noted that genetic evidence does not by itself show *what* is being influenced by heredity. Mendelian segregation does not indicate very much about the origin of a behavior pattern. For example, if we cross two strains of Mice having characteristically different temperature preferences, we will get segregation in Mendelian ratios, showing that hereditary factors are influencing the behavior. The crucial question however, is: *What* is being influenced by genetic factors? In this particular case, **Herter** and **Sgonina** have shown that what is being inherited is not a central mechanism which makes the animal prefer a certain temperature, but rather histological characteristics of the skin. We see here that the description of the behavior, on the one hand, and the carrying out of breeding experiments, on the other hand, do not show much about the nature of the inheritance, or about the causes of the behavior, *unless* they are combined with an epigenetic analysis. And I think that the existence of a relatively schematic conception that each of a certain category of behavior patterns emanates from centers which are specific for the acts, is not conducive to such epigenetic analysis.

With reference to KUO's work. Dr. LORENZ says I desperately support KUO's work. Well, I must agree with that to a certain extent. Although I don't think Kuo's work covers all the possible explanations of where such behavior patterns come from, it is nevertheless the only explanation offered of where the pattern comes from. When you tell me the behavior matures, you are not answering the question I ask when I ask where it comes from. I'd like to know what is the nature of the processes going on in the egg, which makes the bird behave the way it does when it emerges. Now, KUO may be wrong. I think he probably is wrong in identifying the processes he observed as «conditioning». However, he has shown the existence of conditions in the chicken egg which affect nerve growth in a way which is not the same as learning or conditioning in the adult nervous system, but is certainly not the autogenous maturation of an independent center, either.

One gets the impression that the concepts developed by the ethological school do not encourage students to think in terms of inner *epigenetic* processes of which the behavior is the external expression. For example, when, in discussing DESMOND MORRIS' excellent paper here yesterday, I suggested a physiological approach to certain problems, his reply was: «Yes, this should be done, but it takes a different kind of person than I.» But, if this should be done, why should not those students who are interested in the *behavior* be exposed to physiological, epigenetic formulations of problems, rather than to schematic neurologizing?

Now, I don't want to minimize the extraordinary success that the ethologists have had in posing such problems and in developing an overall picture of the organization of many different forms of behavior. I must say that I am in the very peculiar position of criticizing Dr. LORENZ for some of his approaches to problems which I might not have known about, had it not been for him. I think anyone but LORENZ must find himself in the same position, and this is a clue to how much we owe to him, even if we disagree with him. If this was not made sufficiently clear in my critique, I am very glad to correct it now.

K. LORENZ. — I think what Dr. LEHRMAN has just said brings us very near to a mutual understanding of what each of us means when he talks of «Ontogeny». Of course, I entirely agree that we must study the individual development of behaviour much more thoroughly and with a very similar technique as the one used in experimental embryology. Our excuse for not having done more in this direction as yet is that we had to begin in a purely descriptive way before proceeding to physiological analysis. I agree that there may be some cases in which the transmittance of behaviour patterns may lie rather more in the periphery than in the central nervous system. I may remind you of the examples of the different races of the domestic Pigeons in which the rhythm and the sequence of the cooing movements is very probably determined by the volume of the bird's crop. Mrs. BAERENDS VAN BOON has shown that many colour patterns of Cichlids are lying in a peripheral coordination of chromatophore cells and only loosely dependent on the central nervous system. But I am more doubtful about what you said concerning the possibility that the «innateness» of the Bearded Tit's displaying its «beard» may lie in properties of the muscles moving the feathers. In such cases the enormous difference in sizes existing between feathers of the juvenile plumage and the nuptial plumage seem to me to make this explanation rather improbable. And, finally, if we see a motor pattern as complicated as, for example, a Weaver Bird's weaving, I should strongly urge that the coordination of movement lies in the central nervous system alone and is highly independent of afference in general and proprioception in particular. How else could it be that the movements of carrying a blade of grass to the perch, treading on it, reaching for it with the bill under the perch, drawing it through and treading on it again etc etc are performed in exactly the same way whether the bird has got a blade of grass or not.

As to the genetic evidence of what is inherited I agree that our directly genetical material is very scanty. I can only say that we have not been blind to these problems. I think we are, each of us, guilty of thinking the opponent in our discussion much less sophisticated than he really is.

I now come to your final point that students, exposed to what you call «Nativistic Theories» will inhale antifinalistic and antiinductive attitude. The answer is that they don't. A statement which can be proved by very many cases in which the experimental works of young ethologists have forced us to abandon our earlier positions. I must concede to you, however, that, what is not true of our own students, is occasionally true of other scientists not in direct contact with ethological research, particularly of psychoanalysts and psychiatrists. We have forever to fight against their tendency to regard our very hypothetical and very provisional concepts and explanations for gospel truth.

P. P. GRASSÉ — Il me semble que les thèses soutenues d'un côte par M.M. SCHNEIRLA et LEHRMAN et d'un autre par M. M. LORENZ et TINBERGEN sont en réalité moins contradictoires qu'on ne pourrait le croire.

Les aspects du comportement considérés par les deux écoles coïncident rarement et quand ils sont les mêmes, ils sont examinés par les uns et les autres sous des angles bien différents. Une étude exhaustive et non tendancieuse montrerait, nous en sommes convaincu, que les deux thèses sont plus complémentaires l'une de l'autre qu'opposées.

Une autre cause de divergence tient au fait que les animaux étudiés par les uns et les autres appartiennent à des Classes zoologiques très distinctes.

Qu'il me soit permis de dire ici que les entomologistes français, dont les initiateurs furent REAUMUR et H. FABRE, ont découvert à peu près tous les principes mis en œuvre par 1'École objectiviste. Mais ils ont eu le tort de ne pas les fondre en un corps de doctrine. Mon essai de 1942 sur l'essaimage des Termites et la parade nuptiale est resté totalement ignoré des Objectivistes qui s'intéressent surtout aux Oiseaux, aux Mammiffères et, à titre épisodique, aux Insectes.

M. KLEIN. — Nous avons dans notre laboratoire une souche de Souris présentant une mutation se manifestant par une dégénérescence de la rétine et une souche de Lapins (venant de l'élevage de Nachtsheim) dans laquelle tous les individus ont une cataracte. Autant que l'observateur peut en juger, le comportement de ces animaux ne diffère pas du comportement sexuel normal de l'espèce.

O. KOEHLER. - Wenn es heute noch erlaubt ist, von Genetik in dem Sinne zu reden, wie man naturwissenschaftliche Begriffe verstand, bevor sie politisiert wurden, so lehne ich die von Dr. LEHRMAN zitierte Formulierung ab: «Vererbung reicht bis zur Zygote; alles folgende ist Entwicklung». Gewiss entwickelt sich die Zygote samt all ihren Merkmalen. Aber sie entwickelt sich, wie die *Phaenogenetik* lehrt, in *Zusammenarbeit* von *Genen und Aussenfaktoren*. Korrektur des LORENZ-Beispiels rote Blütenfarbe; unter den verschiedenen Rassen von *Primula sinensis* haben manche ein rein erbliches Rot, eine blüht rot im Zimmer, weiss im Warmhaus. Wärme phaenologiert den rezessiven Erbfaktor für Unterdrückung der Anthocyanproduktion.

Die Verhaltensweisen des Schlüpfens werden nur einmal im Leben durchgeführt, können also nicht erlernt sein. Ein Säugetier, das nicht atmen kann erstickt, bevor es zu atmen «lernte». Der Vogel *kann* fliegen. Müsste er es lernen, so stürzte er beim ersten Versuch zu Tode. Lachen, Weinen, Schlucken, Niesen, Schnüffeln, Husten, Rufen und Sprechen sind lauter Abwandlungen des Atmens. Für jede ist getrennt zu untersuchen, wie viel davon angeboren, wie viel erlernt ist. LEHRMAN hat *nicht* erklärt, warum *alle* Artgenossen jede LORENZ'sche Erbkoordination übereinstimmend zeigen. Er weicht auf komplizierte Handlungen aus, nimmt LORENZ' Tatsachen nicht zur Kenntnis. Dabei bleibt seine Kritik völlig unfruchtbar und erweist sich als rein nomenklatorisch. Aber seine Nomenklatur, die den Begriff des Lernens ungebührlich erweitert, ist nicht annehmbar.

H. PIÉRON. — Au moment de clore cette longue discussion, où les points de vue se sont précisés et très utilement rapprochés, je tiens à redire, après le

Professeur GRASSÉ, que, dans ces questions d'instinct, il y a lieu de ne pas se limiter à quelques groupes d'animaux: 1'école éthologique française s'est particulièrement adressée aux Hyménoptères, et, de fait, c'est bien chez des Guêpes solitaires qu'on trouve les exemples d'instincts les plus purs. Des femelles préparant, au moyen de comportements complexes, le développement de larves qu'elles ne connaîtront pas, la génération nouvelle présentera les mêmes comportements spécifiques sans avoir jamais eu le moindre contact avec la génération précédente.