Konrad Lorenz 1950

The comparative method in studying innate behavior patterns

Symposia of the Society for Experimental Biology 4 (Physiological Mechanisms in Animal Behavior): 221-254.

The comparative method in studying innate behavior patterns

I. INTRODUCTION

Like many other branches of biological research, comparative ethology owes its existence to a discovery. The discovery of a *new particulate* process, the function of which is comparatively independent from the function of the organism as a 'whole', always opens a new line of analytical approach. The nature of the process then determines the method most favourable for its experimental investigation, and this method, in its turn, determines the direction in which analytical research continues to proceed. There are many cases in which the development of a new and independent branch of biological science has thus been determined by the character of one particularly favourable object, modern genetics being the most obvious example.

The distinct and particulate physiological process whose discovery may be identified with the origin of comparative ethology as an independent branch of science is represented by a certain type of innate, genetically determined behaviour patterns. Charles Otis Whitman, who was the first to discover them, called them simply 'Instincts'; Oskar Heinroth, who, ten years later, independently rediscovered them, spoke of 'arteigene Triebhandlungen'; I myself have called them 'Instinkthandlungen', 'Erbkoordinationen' and 'Instinktbewegungen' successively, thus further mixing up terminology. I shall, in the conference on terminology, included in the programme of this Symposium, propose the term *endogenous movements* for this type of innate behaviour pattern. Endogenous movements were not only discovered and recognized as a very distinct phenomenon by C. O. Whitman as early as 1898, but also systematically studied and evaluated as taxonomic characters. Nevertheless, their extreme importance as independent elements of behaviour was not generally realized until much later. It was only about 1930 that the discovery of endogenous activities began to act as a centre of crystallization, about which concerted efforts to analyse innate behaviour patterns began to become organized. From then on, however, a quickly growing number of investigators began to apply the methods dictated by the nature of the favourable object which had been discovered so much earlier by Whitman and Heinroth. Thus comparative ethology developed, and therefore it is distinguished by a particular set of

methods from all other schools also occupying themselves with the innate behaviour of animals and men. To convey some idea of this particular set of methods is the task I have set myself in this paper.

I shall set about this task from two sides. Before trying to explain what comparative ethology is trying to do, I propose to state, at least as clearly, what it is trying *not* to do. I deem it most necessary to show what particular errors of method, committed by the vitalistic and by the mechanistic schools of behaviour study, we are meticulously trying to avoid, also to make it quite clear why these errors have prevented some fundamental facts about innate behaviour from being discovered half a century sooner than they actually were. After thus defining our own methods *per exclusionem,* I shall proceed to describe them in some detail.

This plan involves some serious criticism of both vitalistic and mechanistic schools, on 'purposive psychology' and some branches of 'Gestalt' psychology, as well as on behaviourism and Pavlov's school of reflexology. I confidently assert that this criticism is irrefutable from the methodological point of view. But I want to make it absolutely clear at once that comparative ethology has no right whatsoever to claim credit for not having repeated the methodical errors of which we accuse vitalists and mechanists. A preconceived idea is a very terrible danger indeed to all inductive research, the very essence of which is unprejudiced observation. The narrow path of inductive natural science is hemmed in on both sides by methodological pitfalls, and is, therefore, by far easiest to walk along blindfolded. And this is exactly what Whitman and Heinroth did. Happily ignorant of the great battle waged by vitalists and mechanists on the field of animal behaviour, happily free from even a working hypotheses, two 'simple zoologists' were just observing the pigeons and ducks they loved, and thus kept to the only way which leads to the accumulation of a sound, unbiased basis of induction, without which no natural science can arise. Small tribute is due to them for not tumbling into the methodological traps, into which vitalists and mechanists succeeded in shouldering each other, as I shall at once proceed to explain. No very great tribute either is due to them for applying the phyletic method to the study of innate behaviour. Being comparative morphologists, it was only natural for them to do so. But by doing it, they discovered a fact which could not be discovered from any but the phyletic point of view; they discovered an independent, particulate function of the central nervous system which, as an element of animal and human behaviour, is, at the very least, equally important as the reflex or the conditioned reaction.

II. CONSEQUENCES OF THE DISPUTE BETWEEN VITALISTIC AND MECHANISTIC SCHOOLS OF BEHAVIOUR STUDY

(1) *Antagonistic exaggerations*

Without any doubt the dispute between vitalism and mechanism has created and exaggerated a number of erroneous preconceptions which subsequently developed into a serious obstacle to analytical research. It would be a difficult task for the historian to decide which side originally sent the pendulum swinging and was responsible for the whole dispute. One must not forget, however, that vitalism is much older than mechanism, that the concept of entelechy comes from Aristotle, and that Johannes Müller and Claude Bernard were quite decidedly vitalists, though they also undoubtedly were the pioneers of analytical physiology. Furthermore, the quarrel has had particularly disastrous results for the analytical investigation of such life processes as embryonic development, regeneration and instinctive behaviour, which, because of their 'wholeness', their 'directedness' and their apparent spontaneity, have, since the very beginning of the dispute, constituted the stronghold of vitalism. Last, but not least, the theoretical and philosophical position of vitalism is much more fundamentally wrong than the few much less portentous methodical errors, of which we accuse the mechanistic schools. For all these reasons I think that we are justified in regarding the vitalistic errors as primary and the reciprocal errors of the mechanists' reactions justified in themselves and only erring through exaggeration.

Vitalists base all their arguments on the purely dogmatic assertion that all life processes are governed by an essentially non-explainable, preternatural 'factor', termed vital force, entelechy, whole-producing factor, and so on. The legitimate answer to this is obviously that no man can know to what extent causal analysis is going to succeed in explaining the processes of life, and that, if a man prefers to meditate upon the supernatural instead of trying to explain things in a natural way, a lamasery is a much more suitable place to do so than a research institute. Instead of which, mechanists replied that all life processes could be explained on the foundation of the laws of classical mechanics. If they relinquished this position later, they only did so because modern physics did.

If vitalists asserted that the existence of organic systems was due to a whole-producing factor (Müller's *ganzmachende Kraft),* and therefore not explainable by way of synthesis, mechanists answered that organic systems could be explained very simply as a sum of very few sorts of elements. They even grew quite dogmatic, in some cases, as to what these elements were.

If vitalists asserted that life was the result of a directing force, mechanists altogether neglected the fact that life processes do, in some cases, continue to run in a certain direction. If vitalists regarded the spontaneity of some life processes as a wonder and as the direct effect of their preternatural factor, mechanists replied by denying the very existence of spontaneous processes. If all the vitalistic factors, vital forces, directing forces, entelechy, instinct and however they were called, were, if we come down to fundamentals, nothing else than the old, preternatural, immortal *soul* in a new guise, mechanists tried to build up a psychology without a soul, and went so far as to neglect the existence of subjective phenomena altogether, even where introspection can tell us some most important facts about our own ways of acting and reacting.

The very nature of these antagonistic exaggerations, into which vitalism and mechanism were forcing each other, makes it intelligible that of all fields of analytical research the investigation of *behaviour* suffered most. Its well-defined character as a 'whole' or system, its directedness and purpose and, in some cases, its evident spontaneity, brought animal behaviour into the very focus of the great dispute. Especially innate behaviour suffered from this, mainly because 'instinct' was one of the cardinal points of dissension. To make clear the methodical point of view held by comparative ethology, I think it necessary to explain in some detail the reciprocal errors which both the vitalistic and the mechanistic schools of behaviour study committed regarding the items mentioned above.

(2) *Reciprocal errors in the treatment of systems*

The conception of the 'whole' was to vitalists the very essence of what never could be explained, being the direct consequence of a preternatural factor. Particular stress was laid on the thesis that a whole could never be explained by synthesis of particulate elements. To this fatal resignation of analysis on the vitalistic side mechanists replied by trying to synthetize all the systems of behaviour on the basis of too few elements. This 'atomism' is an error very characteristic of mechanistic schools. This optimistic attempt was, of course, doomed to failure, but not before it had brought valuable results. Even very crude simplisms have done less damage to the progress of science than resignation.

One of the most deplorable consequences which resulted from the 'atomistic' attempts at explaining behaviour was the counter-recoil of 'Gestalt' psychology. It is an everlasting merit of Gestalt psychologists to have been the first consciously to introduce the method of a truly correlative analysis of organic systems. They were the first to prove the inherent fallacy of the atomistic method of artificially isolating a single chain of causation

where in reality there was an immeasurably complex system of interaction. Gestalt psychology should have undertaken to correct the atomistic errors of behaviourism and of reflexology and to introduce the method of a correlative analysis into the study of behaviour. But it did not. Instead of correcting the errors mentioned, it merely committed the reciprocal errors. That is to say, the conception of 'Gestalt' has assumed, with a good number of Gestalt psychologists, a character dangerously akin to that of a vitalistic factor. To very many authors 'Gestalt' is something that neither stands in need of, nor is susceptible to, a natural, physiological explanation. Also, 'Gestalt' has been very badly overrated as an explanatory principle. The characters of 'Gestalt' were uncritically attributed to all 'wholes' and therewith to all organic systems in general. I want to show that this is just as much of an error as it is to regard organism as 'sums' or 'mosaics' consisting of only a few elements.

There is not a single organic system which is really a 'Gestalt', nor one that is a mosaic. Every real organic system is built up on *both* principles, mutual interaction of correlated parts playing a role as well as particulate elements influencing the whole in one-way causation. It is extremely important to know, in every single instance, with what kind of relation analysis has to deal as its method has to conform to the actuality of its object. It is as much a methodological error to treat a one-way causality as if it were an 'amboceptoric' interaction, as to mistake mutual interaction for linear one-way causation.

It is a pre-eminent characteristic of that phenomenon of perception, to which alone the term 'Gestalt' should be applied, that it is largely independent of the elementary parts out of which it is built up. A melody, for instance, retains its particular 'Gestalt' quality, whether it is played on a violin or on a piano, whether it is reproduced in one key or the other. Of course, no real objective system is in the same way independent from its component elements; even the examples chosen by Wolfgang Köhler in his paper on 'Physikalische Gestalten', such as the electrical charge on the spherical conductor, the soap-bubble, etc., decidedly are not. It seems absurdly commonplace to state that a spherical conductor cannot be charged with soap solution and that one cannot blow bubbles from electricity. But this very error has been just as crudely committed again and again by sociologists and group psychologists who were misled by a total contempt of the particulate element. This contempt of the particulate element is legitimate exclusively in the study of 'Gestalt' as a phenomenon of *perception*. In the study of all other kinds of 'wholes' it is disastrous! Every Gestalt is a whole, but not every whole is a 'Gestalt'.

Otto Koehler has defined the organismic whole as a self-regulating

system of universal causal interaction of all its parts.[1] This conception of the whole has nothing metaphysical about it, and the most convinced mechanist must concede that very many organic systems are, at least partially, just this kind of a whole. The system of endocrine glands is a very good example. So far from being a 'Gestalt', a living organism is not even completely a whole in this much wider sense. No organism is a system of really universal interaction of its parts, because every organism contains a number of discriminate parts which, while certainly influencing the form and the function of the whole by a linear one-way causation, are not in turn influenced to an appreciable extent by the whole. Skeleton elements, at least in their definite state of development, are good examples of this kind of independent constituents. Even in the embryo, where interaction generally is much more universal than in the grown organism, there are instances of constituent parts behaving with an amazing independence of the whole, the cells of the two-cell stage of the ascidian embryo being the classical example. Spemann's useful distinction between 'mosaic' embryos and 'regulative' embryos can be, *mutatis mutandis,* applied to any other organic structure or function. The application of an analogous distinction to behaviour seems to me particularly advantageous. The behaviour of the sea-urchin, for instance, is quite literally a mosaic of the independent functions of its organs and can be as literally 'synthetized' by tying a broken-up sea-urchin shell together again with a piece of string. Uexküll, in his drastic manner, has said: 'When a dog runs, the dog is moving his legs, when a sea-urchin runs, the legs are moving the sea-urchin' — which beautifully expresses the difference between the mosaic system and the system of universal interaction.

I do not think that there are any other organic systems, in which independent, mosaic-like constituents and regulative systems of mutual interaction alternate and interlock in so utterly incalculable a manner as they do in the behaviour systems of higher animals. It is, therefore, of superlative importance to ascertain, as early as possible, to which type of system a given object of investigation belongs. It is an extremely pertinent question, whether the dog moves his legs, or the legs the dog, quite especially in group and social psychology. We may summarize the reciprocal methodological errors of vitalists and mechanists by saying that the former dogmatically assume that it is exclusively the whole which is influencing its parts, while mechanists as dogmatically confine their attention to one-way causalities, leading from the part to the whole. Vitalists overrate the 'whole' and totally neglect the particulate element, mechanists neglect

---

[1] Maybe it is necessary to state that Gestalt psychologists strictly reject this definition as a definition of the Gestalt, asserting definitely that a Gestalt is *more* than the sum of all interrelations possible between its elements

regulative interaction and overrate those particulate independent elements which they happened to succeed in isolating. Of these errors the mechanistic one is obviously far less detrimental to research than the 'Gestalt' psychological one. Linear causal influence, acting exclusively from an independent part towards the system as a whole, *does* exist, at least in some cases, and the atomistic investigator is not guilty of any methodological error, as long as he really is examining a comparatively independent constituent part. It is just because they may legitimately be isolated theoretically and experimentally that the discovery of independent constituents always is such a tremendous step forward in analytical research. On the other hand, linear causal influence leading from the whole to the part, as assumed by those overrating the 'Gestalt' principle, simply does not exist, any part influenced from the side of the whole always reacts upon it.

The causal interaction which constitutes wholeness in an organic system is, of course, a very real thing. It is therefore evidently absurd to expect 'wholeness', comparable to that of Gestalt perception, in the behaviour of animals lacking the complicated nervous system which serves as an apparatus of integration and renders possible so universal a form of interaction as occurs in the perceptual functions of higher animals and man. When Alverdes repudiates von Uexküll's conception of the 'reflex republic' of the sea-urchin, on the grounds that it is 'incompatible with the fiction of wholeness' ('der Fiktion der Ganzheitlichkeit widerspreche'), then the misunderstanding is centred in the belief that 'wholeness' is a 'fiction'. Where wholeness in our sense of universal interaction of constituent parts *does* exist, there it is anything but a fiction, and there we have to conform to its reality by applying the slow and cautious method of correlative analysis on a broad front. Where it does *not,* there we may bore in with linear analysis and with experiments isolating constituent parts. But *whether* it exists, and to what extent, is not a question that can be settled out of hand by metaphysical speculation or by the dogmatic misapplication of a slogan, but one that must be decided for every single particular case by patient inductive research.

(3) *Reciprocal errors in the treatment of directedness of behaviour*

The undeniable facts that animal behaviour in most cases develops a definite survival value and that, in some cases, it is directed towards a certain purpose, have, in consequence of the vitalistic-mechanistic dispute, received a treatment very similar to that accorded to the whole.

Survival value and purposivity of innate behaviour did not, to vitalistic thinkers, appear to offer any problems. 'Instinct' and 'purpose' were, by them, spelled with very big capitals and were regarded as direct effects of

the non-explainable directive factor of life. Thus *two* problems were hushed up by one pseudo-explanation and therefore appeared as one. Whether an animal is strenuously striving to attain some end or goal, changing its behaviour time and again adaptively to reach it, or whether a stereotyped behaviour pattern automatically develops some survival value, the 'directive factor' is, in the opinion of purposive psychologists, one and the same: the 'infallible' instinct is telling the organism what it has to do. Therefore it is only consistent to identify the survival value of any kind of innate behaviour patterns with the end or goal, at which the organism as a subject is aiming.

It was Wallace Craig who cleared up this confusion and who, once for all, exploded the myth of the 'infallibility' of instinct. He did so by showing, with a wealth of observational evidence, that the animal as a subject is certainly not aiming at the survival value of its activities, but merely at the *discharge* of certain actions, termed *consummatory action* by Craig. The recognition of this indubitable fact is one of the utter commonplaces which are so amazingly hard to discover. Introspective self-observation makes it superlatively obvious that the purpose of what Craig termed *appetitive* behaviour is the discharge of instinctive action and not its survival value. I cannot stop myself eating, though it is my purpose to lose weight. However obvious and even commonplace Craig's discovery may *seem* on close inspection, it nevertheless undoubtedly was one of the most decisive steps forward towards a real understanding of behaviour. As Goethe says: 'Das ist das Schwerste von Allem, was dich am leichtesten dünket, mit den Augen zu sehn, was vor den Augen dir liegt.

The greatest damage done to the analytical investigation of behaviour by the teachings of vitalists was, however, not caused by the confusion of purpose and survival value of behaviour, but by confounding finality with causality. It is a fateful mistake to believe that the teleological 'understanding' of behaviour (or, for that matter, of any process of life) makes it superfluous to gain insight into its causation. If Bierens de Haan says 'Wir betrachten den Instinkt, aber wir erklären ihn nicht' ('We contemplate instinct, but we do not try to explain it'), our answer to this thesis is very clear. It is, of course, perfectly legitimate to meditate upon the obvious finality of any organic structure or function. It is even possible to reach, by this contemplation, a very valuable 'understanding' of it — in the teleological sense of the word. But this sort of understanding does not invest us with the power to *change* the natural sequence of events. Mankind owes its power over nature to its insight into causality. As regards wholes or systems, they have a disconcerting way of getting out of order and thereby supply us with a strong motive for wanting insight into their causal texture.

My teleological understanding of my car is not worth a brass farthing if a drop of water has got into the jet of the carburettor, and Medicine, the queen of all applied natural sciences, is forever in exactly the same position. No whole-producing factor helps the man in whose appendix a cherry stone has got stuck. What I strongly resent is the ever-recurring vitalistic aspersion that our emphatic quest for causal understanding implies materialistic blindness to the existence of the great goals of humanity. Without full recognition — teleological recognition! — of these goals, our quest for causality would lack its purpose. Without insight into causality the active pursuance of these goals would be impossible. We have particularly urgent reasons to want insight into the causal context of 'instinct'. With atomic bombs in its hands and with the endogenous aggressive drives of an irascible ape in its central nervous system, modern humanity is a whole or system which has got very thoroughly out of balance. No teleological meditation will help us, we shall have to *do* something about it, and this implies the necessity of causal insight.

If vitalists persistently ignored the question *why* behaviour develops survival value, or why it is purposive, one should expect mechanists to stress the urgent necessity of putting just these questions. Instead of doing this, the mechanistic schools treated the very *fact* of survival value and purpose exactly as if it were just another vitalistic superstition like entelechy, instinct and the like, that is to say, they flatly ignored it. It is perhaps too much to say that the question 'What for?' was strictly barred from the contemplations of behaviourists and reflexologists, but certainly no sufficient consideration was given to it. This effectively obstructed the mechanists' way of approaching the problems of innate behaviour from a selectionistic point of view, which, though certainly not 'vitalistic', is only possible if the survival value of a behaviour pattern is drawn into consideration.

In saying above that no mechanist has ever raised the question after a causal explanation of directedness and purposivity of behaviour, I have neglected one memorable instance. No less a man than I. P. Pavlov has not only raised this question, but actually tried to give an answer to it. In a paper published in 1916 he writes: 'Analysis of the activities of animals and men has led me to the conclusion that, amongst other reflexes one particular reflex, the reflex of the goal (рефлекс целм) must be conceived, a striving for the attainment of one definite object sending out stimuli' (translated from the Russian). Later on, he adds that this reflex is standing in a close relation to the unconditioned reflexes of taking food and of copulation. It is quite obvious that here purposive behaviour, in the special form of appetitive behaviour, has obtruded itself to Pavlov's notice, also that, observing it chiefly in dogs and humans, he believed that

food appetite and sexual appetite were the only ones in existence. It is a subject for deep meditation that the great mechanist did not see how closely akin this new 'reflex', created with the sole intent of explaining something hitherto unexplainable, is to any vitalistic factor introduced for the very same purpose.

(4) *Reciprocal errors in the treatment of spontaneity*

In a strictly analogous way, as the vitalistic-mechanistic dispute prevented a sensible analytical treatment of the whole, and of survival value and purpose of behaviour, it also obstructed the way to a causal explanation of spontaneity. Exactly as in the cases already discussed, the vitalists saw the phenomenon in itself, but regarded it as a 'wonder' and refused to ask for its natural explanation. William McDougall has certainly gained very great merit by stressing the importance of spontaneity of behaviour as an argument against the chain-reflex theory of the mechanistic schools. His sentence that 'it is evidently inadmissible to speak of a *re*-action to a stimulus not yet received' is something we ought to keep well in mind when formulating our modern terminology of behaviour. Also, his slogan, 'The healthy animal is up and doing', which he threw into the teeth of the chain-reflex theory, is worth remembering. But he and other purposive psychologists did not confine themselves to using the fact of spontaneity as an argument against the chain-reflex theory, but regarded it also as an argument against the general assumption that behaviour is causally explicable. At least none of them ever made the least attempt to offer a physiological explanation of spontaneity.

Instead of unrelentingly demanding this explanation, behaviourists as well as reflexologists evaded the problem by the simple means of ignoring the fact. In my opinion it is the most serious accusation against the working hypotheses of mechanists that they conducted only such experiments as were beforehand destined to confirm the theory. This is about the worst fault a working hypothesis can have. With exceedingly few exceptions, the experiments of mechanists confined themselves to letting some sort of stimulation impinge upon the organism and then to record its answering reaction to this stimulation. This kind of experiment could not but create and confirm the opinion that the function of the central nervous system was restricted to receiving and reflecting external stimuli. No mechanist ever thought it worthwhile to observe what healthy animals do when left to themselves. So the central nervous system, poor thing, never got the opportunity to show that it could do more than answer to stimulation.

Again there is one exceptional case, in which a reflexologist did take notice of spontaneity, and again it is I. P. Pavlov himself who did so. In

describing his experiences with a certain small and very lively dog who would on no account keep still when tied to the framework, to which reflexologists attach their dogs, Pavlov actually has introduced a new reflex to meet the case, the 'reflex of freedom'. The most confirmed vitalist could not have done better by introducing an instinct of freedom, and, curiously enough, he would have been far nearer the truth than the great mechanist. It is very far from my mind to make fun of Pavlov. On the contrary, I regard this jarring *contradictio in adjecto* the 'reflex of freedom', as a reminder of the limitations of the human mind!

(5) *Reciprocal errors in the treatment of innate behaviour*

The conception of 'instinct' is one of the doubtful legacies left to us by the scholastic philosophy of the middle ages. From the first, this conception was introduced to offer what appeared to be an explanation for such types of animal behaviour as were not explicable on the familiar terms of insight and intellect and yet had a definite survival value to the animal. Medieval science was very prodigal with just this kind of 'explanation'. The *horror vacui*, the 'phlogiston' and many other conceptions are further examples. John Dewey, in his book *Human Nature and Conduct,* has given so irrefutable a critique of this type of explanation that it is really superfluous to add even one word. If we accept a 'homing instinct' as an explanation for the fact that a pigeon flies back to its loft, then, next time a child asks me what makes the train go, I shall answer that this is caused by a special factor, called the locomotive force. The justification in both cases is absolutely the same. If we concede it as a scientifically legitimate sort of proceeding, to bridge any arbitrarily chosen gap in our present understanding of nature by assuming an obliging little wonder, then all scientific research becomes a pure farce.

The obvious answer to the vitalistic assumption of the 'wonders of instinct' would have been to explode these wonders one by one, by giving a sensible physiological explanation for each of them, just as hosts of similar vitalistic 'wonders' have, since the days of Johannes Müller and Claude Bernard, been shattered by the progress of analytical research. It is a *real* wonder that no mechanist ever seriously tried to do this! Maybe innate behaviour, with its evident character of a system, its obvious survival value and its undeniable spontaneity, did not seem attractive to the mechanistic methods of research; maybe it was only the great stress vitalists laid on 'instinct' that made it distasteful to behaviourists and reflexologists. Anyhow, none of the mechanists ever systematically investigated innate behaviour. The few reflexologists who deign to mention innate behaviour patterns at all, confine themselves to the rather obvious statement that they

consist of chains of unconditioned reflexes, while some behaviourists, chief among them J. B. Watson, go so far as to deny the existence of any more highly differentiated forms of innate behaviour, conceding only that of simple 'motor mechanisms'.

It is hardly an exaggeration to say that the large and immeasurably fertile field which innate behaviour offers to analytical research was left unploughed because it lay, as no man's land, between the two fronts of the antagonistic opinions of vitalists and mechanists. Small wonder, indeed, if it became 'the sporting ground of fruitless philosophical speculation', as Max Hartmann said on a memorable occasion.

(6) *Lack of observational basis*

A short account of a philosophical quarrel, such as the one just given, of necessity, does an injustice to both sides. In fact, every abridged rendering of a philosophical system is an impudent caricature, tending to make the philosopher look a fool. It is, on principle, impossible to summarize philosophical opinion in the same way as we are wont to do with the results of our research. This must be borne in mind, lest my representation of the reciprocal errors of vitalism and mechanism seem an insolent libel of men whose immense merit I would be the last to depreciate. I am quite aware of the immense over-simplification of all that has been said above and of the many exceptions that have been left unmentioned. I only wanted to make quite clear the *general* influence which the great vitalistic-mechanistic dispute has had upon the investigation of *innate* behaviour. I may have over-estimated and exaggerated this influence, and on this point I am open to discussion and very ready to make amends where I have erred.

There is one point, however, in our methodological criticism on the vitalistic and mechanistic schools of behaviour study on which I do not think that serious discussion is possible. It means striking at the very roots of the teachings of a scientific school if one accuses it of insufficient knowledge of facts, of insufficiency of basis of induction. Yet I do not see how this reproach can be spared to either of the great schools of behaviour study. It is an inviolable law of inductive natural science that it has to *begin* with pure observation, totally devoid of any preconceived theory and even working hypothesis. This law has been broken by one and all of the great schools of behaviour study, and this one fundamental, methodical fault, is at the bottom of all the errors of which we accuse vitalists and mechanists. To put it crudely in two examples. If William McDougall had known all H. Elliot Howard knew about 'reactions incomplete through lack of intensity', he would never have confounded survival value and purpose.

If J. B. Watson had only once reared a young bird in isolation, he would never have asserted that all complicated behaviour patterns were conditioned. It was a really crushing blow to cherished ideals when, as a young student, I first realized that the great authorities on 'instinct', such as Lloyd Morgan and W. McDougall, *did not know* the relevant facts about innate behaviour with which I, ignorant boy though I was, was mentally struggling even then; reactions not attaining their goal because of lack of intensity, vacuum activities and the innumerable ways in which innate behaviour patterns were miscarrying, were evidently unknown to the great theorists.

I know of only two students of animal behaviour who really *knew* the animals about which they wrote and who were, at the time of their writings, considered 'scientists' and not just 'bird lovers'. One of them is H. S. Jennings, who may, in a loose sense, be considered as a behaviourist; the other is Jakob von Uexküll, who certainly was a vitalist. In spite of the world-wide discrepancy of their philosophical positions they have one fundamental point of departure in common: both of them hold that the observation *of all there is to be observed* in the behaviour of a species must go *before* the quest for explanation of the single items of behaviour. This means that both of them treat the behaviour of a species as it must unconditionally be treated: as an organic system. To Jennings we owe the conception of the *system of actions* of a species, and though J. v. Uexküll gave a vitalistic name *(Bauplan)* to the same reality, he also approached it with the same method as Jennings, with the method of a truly correlative analysis, proceeding on a broad observational front.

If there is one behaviorist or reflexologist of Pavlov's school, or one purposive psychologist, who also approached the problems of behaviour by the obligatory method of correlative analysis, that is, who began by observing all there is to be observed in a species, making an inventory of its system of actions before forming a working hypothesis, then I am very sincere in asking his forgiveness; I am not a very well-read man and have failed to hear of his existence. But all other professional students of animal behaviour have been guilty of the one unpardonable offence against the most fundamental law of inductive natural science: they have one and all formed a hypothesis *first* and proceeded to look for examples to confirm it *afterwards*. The protean multiformity of organic nature and quite particularly of the behaviour of higher animals is such that a circumspect search for examples can never fail to detect a wealth of evidence for literally *any* theory, however arbitrarily you chose to invent one. *The facts* in themselves may be quite correct, but *choice* of facts in itself is ever a falsification of the inductional basis. And this statistical falsification of the very foundation

of natural science can only be prevented in one way: unprejudiced observation of all there is to be observed must go temporarily *before* the building up of hypothesis.

III. METHODS PECULIAR TO COMPARATIVE ETHOLOGY

(1) *Observational basis of induction*

It is a fact worthy of very serious contemplation that very nearly all the relevant details of innate behaviour, the ignorance of which so seriously impaired the theories of the two great schools of behaviour study, mechanism and vitalism, have long been known to and fully appreciated by *bird lovers*. H. Eliot Howard, Edmund Selous and many other men who would have been considered mere 'amateurs' by the 'scientific' schools, have been conversant with these facts, without, however, knowing how badly these facts were needed by psychology. Also the professional zoologists whom we consider as the pioneers of comparative ethology, such as C. O. Whitman, O. Heinroth, Julian Huxley and Jan Verwey, at first regarded their observational work more as a hobby or at best as a very secondary occupation. Indeed, sitting in a blind observing birds, or just staring into an aviary with pigeons, or on a pond with a collection of ducks, or into an aquarium, does not, at first sight, appear to be as 'scientific' as the tremendous experiments of mechanists or the deep philosophical speculations of vitalists. Yet it is very far from being accidental that just this kind of observation yielded facts which remained unknown to the great schools.

The development of any inductive natural science proceeds through three indispensable stages: the purely observational recording and describing of fact, the orderly arrangement of these facts in a system, and finally the quest for the natural laws prevailing in the system. These three steps have been termed the idiographic, the systematic and the nomothetic stage by Windelband. For rather obvious reasons, which I need not expound here, the relative importance of the strictly observational basis of any natural science is in direct proportion to the degree in which its object bears the character of a whole or system: the greater the number of constituent parts of a system, the more complicated their interaction, the more necessary it evidently becomes to get an *inventory* of these parts, before beginning the analysis of their correlations. Now the system of actions of any animal is at least as much of a 'whole' and possesses at least as many particulate constituent parts as its body. Therefore the only legitimate manner of proceeding in the study of the behaviour of any species of living organisms is to begin, quite exactly as H. S. Jennings has done, with what I would call a morphology of behaviour, by a thorough observation and description of *all* the behaviour patterns at the disposal of the species.

Now this, in higher animals, is a tall order. If the morphologist must spend months in getting an approximate survey of the anatomy of a species, the ethologist must spend years to do the same regarding its system of actions. And that is exactly where the 'fancy' of the 'amateur' comes in. I confidently assert that no man, even if he were endowed with a superhuman patience, could physically bring himself to stare at fishes, birds or mammals as persistently as is necessary in order to take stock of the behaviour patterns of a species, unless his eyes were bound to the object of his observation in that spellbound gaze which is not motivated by any conscious effort to gain knowledge, but by that mysterious charm that the beauty of living creatures works on some of us!

(2) *The keeping of animals as a scientific method*

In many natural sciences, such as botany, zoology, mineralogy and others, scientific activity has begun with collecting, and I do not doubt that this collecting was, in most cases, at first motivated much more by 'fancy* for attractive objects than by cognitive purpose. No comparative ethologist of my acquaintance has ever denied that his scientific career began in the same manner. Heinroth was ten when he started collecting and keeping ducks and geese; I myself was still younger when I did the same. Whitman is said to have been addicted to pigeon keeping at about the same age. Though having done this undoubtedly is not a merit, it nevertheless was the methodologically correct thing to do, and I think I am justified in ranging the keeping of animals in captivity first among the methods peculiar to comparative ethology.

By 'keeping' an animal I do not mean the mere attempt to keep it alive in captivity for as long as possible, but the endeavour to make a given species unfold its whole system of actions under constant, controllable conditions. Keeping, therefore, always implies the attempt to *breed* the species in question.

It is far from me to disparage the advantages of field observation and the merits of field observers. But for the purposes of correlative analysis it is, as I have already stressed, of the first importance to get an inventory of the particulate behaviour patterns of a species and to get some notion to what extent these constituents of behaviour patterns are woven into a regulative 'whole'. I have already emphasized (p. 226) the necessity of ascertaining, at an early stage of analysis, how far a system of actions is a regulative whole and how far it is a mosaic of relatively independent elements. This question is extremely difficult to decide in field work, because in the natural surroundings of a species its system of action is apt to *seem* much more adaptive and its several activities much more purposive than they really are. Thus

adaptedness is easily confounded with adaptability. *It is only by miscarrying that any behaviour pattern can show its nature of a particulate element*. Now, of course, it is possible to notice miscarrying behaviour patterns in field observation, as H. Eliot Howard has sufficiently proved. But it is quite impossible *not* to see it in observing animals kept in captivity.

It is hardly possible to exaggerate the importance of miscarrying behaviour patterns as a source of our knowledge. W. Craig's great discovery that it is the discharge of consummatory actions and not the survival value which is the goal of appetitive behaviour was exclusively due to the observation of behaviour patterns being executed without attaining their 'normal' survival value. The existence of innate releasing mechanisms would never have been discovered and their function would not have been possible to analyse if it had not been for the observation of cases, in which they were activated 'erroneously' by stimulus situations, in which the released activity was thoroughly miscarrying. The whole set of phenomena connected with the process of accumulation of action-specific energy (such as lowering of threshold, explosion activity, etc.) also could only be discovered by observing innate behaviour patterns miscarrying when discharged at an inadequate object.

It is not only the miscarrying of reactions caused by the absence of normal environmental stimulation which makes the observation of animals kept in captivity so valuable. The physiology of the central nervous system has gained much of its knowledge about particulate functions by studying cases in which some functions had dropped out, because of pathological processes, or had been experimentally destroyed. Very much the same manner of proceeding has led comparative ethology to analogous results. Very slight disturbances of the general 'condition' of captive animals are apt to cause surprisingly far-reaching disintegrations of their systems of actions. Endogenous activities lose much of their normal intensity or drop out altogether; innate releasing mechanisms lose much of their selectiveness. The general disintegration of the species' system of actions caused by these two main processes is essentially *reversible*. If one starts keeping a *new* species, with whose needs one is not yet familiar, one automatically gets an opportunity to observe this particular form of disintegrated behaviour, very often a jumble of unconnected behaviour patterns whose normal survival value is often very difficult even to guess. Yet this jumble of disconnected behaviour patterns is extremely valuable for the purpose of taking stock of the particulate, genetically fixed 'mosaic stones' of behaviour. When, later on, one learns how to keep the species in question and when, with the improvement of technique, the animals are got back into the pink of condition, then the jumble of disintegrated parts is slowly reassembled

into a functioning system which fully delivers its normal survival value. I hardly know a more *instructive* object of observation than just this type of disintegration and reassembling of the system of actions in animals kept in captivity. It is, in fact, an actualized example of analysis and resynthesis of behaviour!

If disintegration is a valuable source of our knowledge about behaviour and, indeed, the most valuable fulcrum for its analysis, it must also forever be remembered as a possible source of error. I want to give one warning example of this. The red-backed shrike, *Lanius collurio* L., has got a very beautifully differentiated endogenous movement for impaling insects on thorns. This activity has a taxis component generally directing it to branches or twigs, but apparently none that directs it to a thorn. The reaction to the thorn was indubitably acquired by the trial-and-error method by the shrikes I observed as early as 1932, and in a paper then published I enlarged upon this particular case of innate behaviour patterns interlocking with trial and error and conditioning. Now G. Kramer has recently reared red-backed shrikes with a view to studying their migration activities and incidentally observed the development of their reaction to the thorn. What he saw at first was in perfect accord with what I had written in 1932; the shrikes showed the movement first and got conditioned to the thorn by trial and error. Kramer is a past master in rearing birds, and you may rest assured that these shrikes were in the best of condition. And yet, when he tried still further to improve his feeding technique and started breeding silkworms for the young shrikes, the birds thus reared needed no conditioning to the thorn, but most amazingly proved to have an innate directive mechanism reacting to the specific optical sign stimuli emanating from a sharp end or thorn. This particular source of error must be kept in mind.

As a method of analysis of animal behaviour, *keeping* truly deserves the adjective 'correlative', because it very strictly compels the investigator to consider the behaviour patterns of a species in correlation to the environmental conditions to which they are adapted. Again, it is the observation of miscarrying behaviour patterns, from which the keeper must be able to deduce what particular conditions of the artificial environment of the animal he must *change,* to make those behaviour patterns attain their normal survival value. Just as he would deduce from the morphological characters of a mole's forepaws that this species needs earth to dig in, so he must, from slight 'hints' of miscarrying behaviour patterns, be able to deduce the corresponding environmental exigencies of the species. Perhaps the most important cognitive value of this proceeding lies therein, that it forcefully compels the observer to treat the several behaviour patterns of a species exactly as he would treat organs. The observer is very convincingly

taught that behaviour patterns are not something which animals may do or not do, or do in different ways, according to the requirements of the occasion, but something which animals of a given species 'have got', exactly in the same manner as they 'have got' claws or teeth of a definite morphological structure.

From the recognition of this fact it is only a very short step to the systematic *comparison* of the innate behaviour patterns characteristic of allied species. It is, indeed, only in keeping animals that this comparison obtrudes itself to the observer's notice. The discovery of *phyletic homology* between innate behaviour patterns was unavoidable, once a scientist conversant with the methods of comparative morphology got the opportunity to observe closely a number of species belonging to the same systematic group. It is there that C. Q. Whitman's 'fancy' for pigeons and O. Heinroth's partiality to Anatides have played a very decisive part. A man knowing the single system of actions of every species as they knew it could not fail to notice that certain innate behaviour patterns were just as characteristic of a species, a genus or a family, as any morphological character. As early as 1898, C. O. Whitman wrote the sentence that marks the birth of comparative ethology. 'Instincts and organs are to be studied from the common viewpoint of phyletic descent.'

(3) '*Comparative anatomy' of behaviour*

With the discovery of phyletic homology of behaviour patterns the study of behaviour may be said to have grown out of the purely idiographic stage of its development and to have reached the second systematic stage. This discovery was of the greatest importance in several respects. Not only could innate behaviour patterns be used as very valuable and certainly very welcome new taxonomic characters in ascertaining the phyletic relations between allied forms, but the special form of certain innate behaviour patterns became accessible to a causal explanation based on the understanding of their phyletic origin. Both of these facts, though certainly important enough in themselves, attain an even greater secondary importance by proving the great independence of the behaviour patterns in question, as *particulate elements* of behaviour. Thus not only the well-tried method of comparative morphology became applicable to the study of behaviour, but it also became possible to *isolate* a very distinct physiological process as an independent constituent of behaviour and to study it separately, in a legitimate departure from the otherwise obligatory method of correlative analysis on a broad front. Therefore, physiological analysis followed closely on the heels of the comparative and systematic study of the elementary process in question.

Zoological systematics and comparative morphology are, by many,

considered tedious and rather mummified branches of research. It is too easy to forget that we owe them the most revolutionary discovery of the last hundred years, the discovery of evolution. Though I emphatically deny the charge that comparative morphology is a spent science which has already borne all its fruits, I should concede that it certainly has borne the most important of them. Now there is some danger that the same might be thought, very prematurely, of comparative ethology. In the study of behaviour the phyletic viewpoint has yielded, as a very valuable result, the possibility of isolating and studying in linear, experimental analysis an important, particulate central nervous function, the endogenous activity. In consequence of this, a second, nearly as independent *perceptual* function, the so-called innate releasing mechanism, has become experimentally accessible. Each of these two functions, as a constituent of behaviour, doubtless plays as important a part as the reflex and the conditioned response, and there is a very great temptation to repeat the error of which we have reproached behaviourists and reflexologists, by believing that we have got hold of 'all' the necessary 'elements' to explain 'everything', and to plunge into linear, experimental analysis without giving any further thought to the necessity of further collecting purely observational facts. Of course, the fulfilling of this duty will not keep us from eagerly following up the leads to linear, experimental analysis which we have discovered. But it is well that we should keep in mind the extreme youth of our branch of science and that we should cherish no illusions about the breadth of the observational basis of induction that has hitherto been attained. A precipitate transition from systematics to nomothesis would be particularly disastrous to our branch of research, and the longer and the more we lay stress on the *descriptive* side of comparative ethology, the better it will be in the long run.

Since the days of Charles Darwin the term 'comparative' has assumed a very definite meaning. It indicates a certain rather complicated method of procedure which, by studying the similarities and dissimilarities of homologous characters of allied forms, simultaneously obtains indications as to the phyletic relationships of these forms of life and as to the historical origin of the homologous characters in question. I need not enlarge on the details of this method which is a commonplace to biologists and physiologists. We all know perfectly well what we mean by 'comparative' anatomy, morphology, physiology and so on. But it is all the more misleading if psychologists, who evidently are not familiar with what we mean when we speak of the comparative method, apply the same term in a very loose sense to all behaviour studies concerned with different forms of life. I must confess that I strongly resent it, not only from the terminological viewpoint,

but also in the interests of the very hard-working and honest craft of really comparative investigators, when an American journal masquerades under the title of 'comparative' psychology, although, to the best of my knowledge, no really comparative paper ever has been published in it.

Phyletic comparison is slow and painful work, even in morphology, where the comparable, homologous characters are immediately and permanently accessible to the anatomist's knife. It is obvious how the difficulties are increased in the study of innate behaviour patterns which are not there continuously, just to be looked at and described, but for which one must wait in patient observation. It is therefore easy to understand that only very few systematic groups of animals have hitherto been thus studied with any appreciable degree of thoroughness. Historically the first and perhaps still the most thoroughly studied group is the order of pigeons which was investigated by Whitman. Second are the order of Anatidae, as studied by Heinroth, and one family of this order, the Anatinae, more especially studied by Heinroth and by myself. If, as a third group, I add the cichlid fishes, investigated by A. Seitz, G. P. Baerends & Baerends van Roon and A. Steiner, whose paper on dwarf cichlids is, however, not yet published, our list is complete. There are some very good papers on lizards which can, to a certain extent, be evaluated comparatively, though wide gaps still remain between the known species, and there is a comparative investigation on herons by O. Koenig nearly finished. The only paper aiming at giving even a superficial survey of the comparative ethology of a group of mammals, is the paper by O. Antonius on Equidae. Concerning invertebrates, O. Plath has used the behaviour patterns of nest building and provisioning of humble-bees as taxonomic characters, and analogous work was done by A. Petrunkewitch with spiders. There are, of course, hosts of unconnected facts known that may eventually, when gaps are bridged, become accessible to comparative evaluation.

The immense field of observation which is still waiting to be systematically exploited needs whole armies of investigators. These armies are, however, already in existence, at least two of them: the bird-lovers and the fish-fanciers. It is a superlative merit of a book like that of the Rev. E. A. Armstrong that it calls the amateurs' attention to the important details which we need to know. There can never be too many such really scientific and yet generally intelligible books on behaviour. I have already explained why the bird or fish 'lover' is in some respects the ideal observer. The task is, to enlist him to help us in concerted effort.

The methodologically first task is, without any doubt, the *intensive* study of all of the innate behaviour patterns of a restricted group of forms. Besides this, it is a legitimate way of proceeding, *extensively* to study throughout the

animal kingdom one given homology of behaviour pattern. O. Heinroth (1930), in a paper as interesting as it is short, has given us a survey of the extension and distribution of some exceedingly widely spread and evidently exceedingly old behaviour patterns of vertebrates, such as yawning and scratching the head with the hind leg. Curiously enough, I do not know of another paper proceeding in this way, though this way of pursuing a behaviour pattern as a homologous character throughout a large group is interesting work and gives quick results in comparison with other comparative investigations. At present I am collecting notes on the scratching movements of mammals, particularly of rodents. In this group, and also in primates, the areas scratched with the hind leg and with the forepaw respectively are a taxonomic character whose distribution is most interesting.

Only in two groups (in ducks and cichlid fishes) have our intensive studies of the single species and our extensive studies of the several behaviour patterns progressed far enough to make possible what in comparative morphology is quite a commonplace thing, that is, to represent both lines of investigation in a tabular index. In one of my papers (1947) I have given such an index concerning a number of behaviour patterns of sixteen species of ducks belonging to different families (Anatinae, Cairininae and Casarcinae). This method of letting, metaphorically speaking, two lines of investigation cross each other at right angles, is fundamental to every kind of phyletic investigation of homologous characters. Only this kind of broad survey can give us the possibility of forming a firm opinion about the relative age and phyletic conservativity of any taxonomic character.

In some cases which are particularly favourable to this kind of investigation, it has been possible to form a quite well-founded opinion concerning the lines along which the evolution of certain behaviour patterns has taken place. Always keeping in mind that there are *no* 'primitive' forms of life, and that therefore any linear taxonomic arrangement of living animals or plants is necessarily sheer nonsense, it is nevertheless possible and legitimate to attribute the quality of relative primitivity to *single characters*. It is a dangerously loose and misleading expression to call any recent form of life, however many primitive characters it may possess, a 'primitive' animal. In regard to all the characters of his mouth and teeth, man is much more primitive than the *Platypus*. What alone may be arranged in a linear sequence are the different forms of actualization which one and the same homologous character shows in related forms of life. The ramifying 'line of differentiation' thus obtained does, very probably, correspond to the actual stages of evolutional development of the character in question. A number of indubitable sequences of differentiation could be established among innate behaviour patterns.

In all cases where it has been found possible to do this, the innate behaviour pattern in question was a 'releasing ceremony'. This is far from being accidental. There are two papers being read here on the subject of social releasers, so I must be very short. A social releaser is a device — either a property of colour and/or shape, or a special sequence of movements, or, for that matter, of sounds, or a scent — specially differentiated to the function of eliciting a response in a fellow-member of the species. To every releaser, as an organ for sending out sign stimuli, there corresponds a perceptual correlate, an 'organ' to receive sign stimuli and to activate the answering reaction. This we call an innate releasing mechanism *(auslösendes Schema)*. The function of social releasers and of answering innate releasing mechanisms is very much like that of a human signal code, or of that of human word language. Exactly as the several forms of the single word symbols of our language do not have any direct connexion with their meaning, but are only fixed by the *convention* of one particular sign code, so also is the particular form of any social releaser determined by an intraspecific 'convention' between the sender and the receiver of sign stimuli. The important consequence of this is that we may exclude from our consideration the possibility of convergent adaptation when comparing similarity and dissimilarity of releasers. It is immeasurably improbable that the similarity of the words *mother, mutter, mater, μήτηρ* and мать, in English, German, Latin, Greek and Russian, should be due to anything else than to their common derivation from a mutual Indo-European 'ancestral form'. If, therefore, the comparative philologist is fully justified in neglecting any other possibility, then the very same holds true for any resemblance between releasing 'ceremonies' of phyletically allied species. This is why we know more about the origin and the evolution of releasing ceremonies than we do about any other innate behaviour patterns. This is also why, on the basis of releasing activities used as taxonomic characters, it is, in quite a number of cases, possible to ascertain phyletic interrelations of species with a certitude and a wealth of detail, hardly ever attainable on the basis of purely morphological characters.

We know of two phyletically distinct ways, by which non-social, mechanically effective endogenous activities may develop into social releasers: in one case the so-called 'intention movement' *(Intentionsbewegung*, Heinroth), in the other the so-called 'displacement activities'. Both types of movement are, in their primary form, mere by-products of action-specific excitation and certainly devoid of any survival value. The intention movement is nothing but a slight hint of a certain innate behaviour pattern, as will occur whenever action-specific excitation only reaches a very low level of intensity. Displacement activities are the result of a very different physiological

process. If action-specific excitation is at a comparatively high level of intensity and finds its path to its normal outlet suddenly blocked — for instance, by activation of an antagonistic drive or by sudden disappearance of the adequate object — it 'sparks over', as Makkink very expressively describes it, into a nervous path not normally its own and finds its expression in behaviour patterns belonging to a quite different action-specific excitation. Makkink, Tinbergen, Koortlant and E. A. Armstrong have studied displacement activities very extensively.

Intention movements as well as displacement activities are, to an observer well conversant with the system of actions of a species, very reliable indicators for the present 'mood' of an animal, that is, in objectivistic terminology, for its present internal state of specific readiness for certain activities. Now in very many animals an analogous 'understanding' of the intention movements and the displacement activities of a fellow-member of the species has evidently been developed on the basis of innate releasing mechanisms. (It seems well worth mentioning that as yet we do not know of a single instance in which a similar 'understanding' is brought about by conditioning!) In other words, the characteristic movements in question developed a totally new function as social releasers. From that point onwards both types of releasing movements underwent an exceedingly characteristic process of differentiation. The primarily important, mechanically effective constituent parts of the movement are lessened in strength and amplitude, while all *optically* effective features of the movement are exaggerated and emphasized in a very peculiar and striking way. We know to-day of a very great number of examples of this particular process of evolution; there are all possible gradations between movements, as yet hardly different from their original form and behaviour patterns, whose differentiation along the lines described above has gone so far as to transform them into grotesque 'ceremonies' or 'dances' whose actual homology to the primary intention or displacement activity can only be ascertained through a thorough study of intermediate forms — if such happen to exist. Releasing ceremonies derived by this over-accentuation or 'mimical exaggeration' from intention movements were called 'symbolic movements' *(Symbolbewegungen)* by Heinroth. In the case of displacement activities a terminological difference has not yet been made between primary displacement and fixed, ritualized, mimically over-accentuated ceremonies.

In a very great number of known cases, the differentiation of a homologous releasing behaviour pattern has, in allied species, taken place along divergent lines. Very often different morphological devices have been evolved to accentuate the optical effect of a ceremony, thus emphasizing different parts of one homologous behaviour pattern in different species.

In surface-feeding ducks there are a good many instances of this. The evolutive process described makes it easily intelligible why in many instances the behaviour pattern should be — as it evidently is — phyletically very much older and much more conservative than the morphological devices, colour and/or structure, that help to accentuate it. Another notable fact is that the sequence of movements, constituting a releasing ceremony, is, in very many cases, much more conservative than its 'meaning', than the innate releasing mechanism activated by this particular set of sign stimuli in a fellow-member of the species. The extensive comparative study of one distinct releasing behaviour pattern often leads to amazingly similar results, as the comparative study of a root word in the historical development of language. Just as the meaning of one word symbol may split up into different and even opposite meanings of its derivatives (for instance, in the English and German words *knight* and *Knecht,* which have both been derived from a common root describing an armed follower of a war lord but have assumed the opposite meanings of a lord in English and of a serf in German), so does, to cite only one instance, the behaviour pattern originally expressing inferiority in cichlid fishes assume the exactly opposite meaning of a threatening gesture in the 'dwarf cichlids' of the genera *Nannacara* and *Apistogramma*. What is more, we know the phyletic development by which it has done so.

A good example of a line of differentiation of mimetically over-accentuated intentive movements is offered by the releasing behaviour patterns which, in cichlid fishes, elicit and direct the young fishes' reaction of following after their parents. There are two elements in the normal movements of a fish starting to swim which are particularly effective in an optical way and suitable for mimetic over-accentuation. One is the sideway swing of head and body, the second is the movement of the median fins which, in cichlids as in most other acanthopterygians, are furled when the fish starts to swim and re-erected whenever it stops. Both these elements have undergone an independent and divergent differentiation and also a 'splitting up' of their 'meaning' in the course of the evolution of cichlids. In the most widely spread and doubtlessly most primitive form of the releasing behaviour pattern in question, the swinging of the head and the furling and erecting of median fins are still coupled in the same obligatory way as in the original movement which has not yet got a releasing function. In this primitive form of the releasing and directing behaviour pattern, it differs from a normal swimming start only in that, after all the grand preparation, the fish does not get farther than 4 or 5 cm. and then stops again. Also in this primitive form, as we find it in *Aequidens, Hemichromis, Geophagus* and most species of the genus *Cichlasoma,* the *directive* function of the sideways swing of

the head is very clear. The swarm of young 'obediently' turns to the left or to the right accordingly, which is especially striking, when the young are swimming 10 or more cm. in front of the guiding parent. Even in some of these species the movement of the median fins is becoming independent of the body movements, and a quick lowering and raising of fins can be observed, especially when the parent fishes are a bit alarmed. There is an indubitable correlation between these independent movements of the median fins and their colouring: the dorsal fin is richly beset with 'jewels' in species, in which the movement is developed. In *Hemichromis bimaculatus,* in which the dorsal fin is particularly richly adorned, the up-and-down movement has taken the form of an exceedingly quick twitching that makes the jewels on the fin flicker like a heliograph. Also this movement, in its higher intensities, has assumed a specialized meaning; it is used quite particularly when the young are called together and tucked up for the night in the nest-hole.

In the genus *Apistogramma* and *Nannacara,* on the other hand, the sideways swinging of the head has taken an independent path of differentiation. Without any concomitant movement of the median fins, the females of these species (which alone lead the brood) twitch their head sideways in a lightning jerk. The body and tail are not moved, and the homology with the original form of the movement is only apparent when the fish really starts to swim. The brooding females of these species wander about very little, but 'browse' their flock of youngsters for long intervals in one spot, all the time executing their sideways flicking of the head with the regularity and about the same frequency as a mother hen utters her clucking call note. In old *Nannacara* females the flicking movements can be elicited by putting the fish into a dense swarm of *Daphnia*. Though the fish will eat single *Daphnias*, it will refuse to eat them if they are too close together, in which case it proceeds to 'brood' them. In all species of *Apistogramma* the broody female has a bright black and yellow patterning of the head and throat which goes to accentuate the optical effect of the flicking movement. Steiner's experiments to investigate the releasing and directing function of these colour patterns on the young were interrupted by the war.

In *Herichthys cyanoguttatus* (formerly *Neetroplus carpintis)* a movement doubtlessly homologous to the 'call' of the dwarf cichlid females has assumed the function of a *warning* signal to the young. *Herichthys* resembles the dwarf cichlids in a number of ethological traits. The female has a particular brooding colour, being jet black on the throat and along the underside of its body, and undertakes most of the brooding of eggs and young, while the male takes only short spells of these functions and is chiefly concerned with defending the territory. When the fishes are alarmed

by strong stimuli, as very big fish in their tank or the experimenter's hand approaching them, the female begins a furious sideways twitching movement of head and body. The fish remains absolutely stationary all the time, and the young, as if drawn by a strong magnet, converge from all sides and lie down on the bottom just under their mother, at the same time 'becoming heavy' through contraction of their swimming bladder, just as they do whenever one of the parents catches them in his mouth. The releasing and directing value of the female's movement is easy to prove; any black object, e.g. a fountain pen, twitched sideways between the fingers, will attract the young *Herichthys* in exactly the same way, and if the object is blacker and twitched more furiously than the mother's body, it will even draw the swarm away from the mother, notwithstanding the male's furious attacks upon the substituted object! The warning movement of the *Herichthys* female is, in a way, farther differentiated from the original swimming-away-movement than is the head flicking of the female *Sannacara* and *Apistogramma,* because no intermediates between it and the original behaviour pattern could be observed, while frequently enough occurring in the latter species.

This kind of 'comparative philology' of releasing behaviour patterns is not only a fascinating study in itself, but it may, once we know more about its object, develop a very practical value. I would stress the fact that the human expression of emotion is largely built up on exactly the same kind of intention movements as Charles Darwin knew long ago. In man, in whom innate behaviour patterns are, to a great degree, rudimentary, the study of these innate expressions of emotion may become a most valuable clue to the human 'instincts'!

(4) *Approach to physiology*

(a) The accumulation of action-specific energy

C. O. Whitman and O. Heinroth were phylogenists and not physiologists. Their chief interest in innate behaviour patterns was of a systematic and taxonomic nature. If they had, as we have reasons to believe, some shrewd suspicions of the physiological singularity of the innate behaviour patterns which they so accurately described, they never said so in so many words and they certainly did not separate them conceptually from other innate behaviour patterns which are of a reflex nature, as taxes, innate releasing mechanisms and others. But while systematically describing and arranging what they called 'instincts' and 'arteigene Triebhandlungen' respectively, they did, maybe quite unconsciously, discriminate a very distinct type of innate behaviour pattern from all others. On the grounds of what we know to-day, it is quite obvious why the endogenous behaviour patterns are much

more useful as taxonomic characters than reflex ones. Maybe it was only this that made the pioneers select endogenous activities for their object. But *by* selecting them and grouping them together as something distinct, they brought to light certain striking characteristics which seemed to be clamouring for a causal, physiological explanation. And this is exactly how, in a healthy inductive science, nomothesis will automatically grow out of systematics.

What particularly seemed to demand an explanation was a very unexpected correlation which evidently existed between the *spontaneity* and the *invariability* of the innate behaviour patterns in question. According to the vitalists' opinion, spontaneous activity must automatically be considered as purposive, and must, therefore, show adaptive variability in the pursuit of its end or goal. According to the mechanists' opinion, any innate and individually invariable behaviour pattern must be considered to be a chain of unconditioned reflexes and must, therefore, be totally devoid of spontaneity. In defiance of both these dogmas, just those highly differentiated innate sequences of movements that not only were absolutely invariable individually, but even in phylogeny were rather conservative and slowly changeable characters, proved to possess a very distinct and striking kind of spontaneity.

At the level of superficial observation the innate behaviour patterns in question appeared reflex-like in that they were set off by a sort of 'trigger-action' in a very specific stimulus situation. But on closer inspection it became apparent that these activities are, at bottom, to a very high degree independent from external stimulation. Captive animals, deprived of the normal object or releasing situation of an innate behaviour pattern, will persist in discharging the same sequences of movements at a very inadequate substitute object or situation. The longer the normal stimulation is withheld, the less necessary it becomes, in order to set off the reaction, to supply *all* of the stimuli pertaining to it. The longer the reaction does not go off, the finer the trigger that releases it seems to become set. In other words, the threshold of the stimulation necessary to release this type of innate reaction, is not a constant, but is undergoing a continuous process of lowering, going on throughout the time during which the reaction is not released. This gradual lowering of threshold does, in a good many cases, actually reach the theoretically possible limit of zero, that is, the activity in question will finally go off *in vacuo,* with an effect somewhat suggestive of the explosion of a boiler whose safety valve fails to function. This occurrence has been termed 'Leerlaufreaktion' in German, vacuum reaction and explosion reaction. I would move the general acceptance of Armstrong's term 'energy accumulation activity' for reasons discussed later.

The consequences of the 'damming up' of a certain innate activity are, however, not confined to the threshold of the mechanism (whatever that mechanism may be) which releases the activity. It is not only a facilitation of the releasing process, not only an increase of passive excitability that takes place, but, quite on the contrary, an active and peculiar excitation. Any one of these particular innate behaviour patterns, however small and unimportant it may seem in itself, develops into an active source of excitation which influences the whole of the organism whenever it finds its outlet blocked. In this case, the undischarged activity becomes a *motive* in the literal and original sense of the word, derivated from *movere*, 'to move'. In the simplest and most primitive case the organism shows undirected, 'random' locomotion, *kineses* as we term it. In more highly differentiated types these kineses are interlaced with taxes orienting the organism's locomotion in space, or even with conditioned responses and all the most complicated and least analysed forms of animal and human behaviour, which, for lack of a better term, we are wont to describe as 'intelligent'. Though the activities thus elicited comprise the whole range of behaviour, from its simplest to its most complex form, they have one decisive character in common: they are all *purposive* in the sense which E. C. Tolman has given to this term, that is to say, they all tend to bring about, by *variable* movements, an *invariable* end or goal, and they go on until this goal is reached or the animal as a whole is exhausted. The invariable end or goal is represented by the releasing stimulus situation and, therewith, the discharge of the specific behaviour pattern that had been dammed up. The purposive behaviour striving for this discharge was called *appetitive* behaviour by Wallace Craig, the behaviour pattern finally discharged was termed *consummatory action*.

I want to emphasize what a great wealth of observational evidence is underlying the facts condensed into the two preceding paragraphs. It took the life's work of at least three excellent observers to gather that evidence: Whitman, Heinroth and Craig. All these facts are strongly suggestive of a very definite assumption, and it is eminently characteristic of these three men that every one of them has conscientiously recorded those facts while none of them put this assumption into words. This is all the more significant of the value they set on observation free of any hypothesis, as they must have found it quite hard to avoid descriptive terms like damming up, discharging, etc., which already imply the assumption *that some sort of energy, specific to one definite activity, is stored up while this activity remains quiescent, and is consumed in its discharge*.

This hypothesis is, roughly speaking, identical with the assumption that the behaviour patterns in question are caused by processes of endogenous

generation of motor stimuli, such as have been studied by von Holst, P. Weiss and others. The parallels between both types of processes go so far that, in my opinion, there cannot be any serious doubt as to their fundamental identity. The difference between what von Holst calls an automatic rhythm and what we call endogenous activity lies exclusively in the level of integration, as Prof. Tinbergen will explain to you presently.

(b) The innate releasing mechanism

The conception of a wound-up spring implies the existence of a trigger mechanism, holding it back until the right moment and setting it off when this moment arrives. W. Thorpe says of endogenous activities that 'they are set off by a kind of trigger action'. J. A. Portielje has, at a very early date, fully recognized this double nature of endogenous activity which always is an 'Aktion-und-Reaktion-in-Einem' an action and a reaction in one, as he expresses it. While it is obviously inadmissible to speak of a re-action to a stimulus not yet received, for instance, when the organism is striving by trial and error to attain a certain releasing stimulus situation (appetitive behaviour in W. Craig's terminology), the organism's answer to this situation, once it is attained, just as obviously *is a* re-action in the truest sense of the word. Indeed, this reaction has all the earmarks of what I. P. Pavlov would call an unconditioned reflex. With the recognition of the peculiarity and independence of endogenous activity as a distinct physiological process, there evidently arises, as a physiological problem by itself, the question about the 'trigger' mechanism releasing the accumulated action-specific energy. The statement that this mechanism is an unconditioned reflex, though indubitably correct, does not help us any further, because the essential part of the problem does not lie in the reflex process as such, but exclusively in its perceptual side. The intriguing problem lies in the *selectivity* of the reaction. The observational facts are suggestive of a mechanism akin to a filter, letting through only certain particular stimuli while strictly excluding others, or of a complicated lock which can only be unlocked by a very specific key. The adaptation of the perceptual organization to certain characteristic key stimuli is very evident.

Through the work of a considerable number of recent investigations some very peculiar facts have become known about the perceptual organization of these innate releasing mechanisms. What acts as a 'stimulus' is, in the great majority of cases, not a simple physical influence of *absolute* quality and quantity, but a *relational* property. These *innate* reactions to relational properties differ from reactions to acquired Gestalt perceptions only by their extreme simplicity. In acquired reactions, the Gestalt that elicitates the response consists of an indivisible unit of literally hundreds of

interdependent relational properties. In innate releasing mechanism we do not yet know a single case in which the innate and immediate reaction is elicited by a relational property comprising the relation between more than *two* elements. The innate releasing and directing mechanisms of the gaping activity of young thrushes *(Turdus)* are a good example. The nestlings will gape at *(a)* the nearer of two objects, *(b)* the higher of two objects and *(c)* the smaller of two objects, the optimum relation of the smaller to the bigger being 30%. All three of these relational properties are characteristic of the normal object of the reaction, the parent's head. Each of them, considered by itself, is a true, if extremely simple, 'Gestalt', showing all of Ehrenfels' 'Gestalt' criteria, most important of all, transposability. Each of these relational properties represents a key-stimulus setting of the *same* innate releasing mechanism, but each of them does so quite independently from the other. Unlike the immeasurable number of relational properties inextricably woven into the whole of a 'Gestalt' perception, *these single relational key stimuli act merely as a sum of non-interdependent elements*. This process of summation of key stimuli, belonging to one and the same innate releasing mechanism, has been termed 'Reiz-Summen-Phänomen' by A. Seitz, who was the first to study it intensively. N. Tinbergen translated this into English by 'law of heterogeneous summation'. What I have said about the innate releasing mechanism suffices for the understanding of the subsequent section on dual quantification, especially as the subject will probably be expounded in detail in the papers that are to be read on social releasers.

A few words must be added about the term. The mechanisms in question were first discovered in their function of setting off endogenous activities; they can, indeed, most advantageously be studied in this particular function, for reasons explained in the next section. But evidently the very same type of perceptual organization as the one that receives the key stimuli setting off endogenous activities also plays a part just as important in a great many quite different functions. The perceptual side of taxes may be organized in exactly the same manner, appetitive behaviour may be activated by evidently identical processes and so may specific inhibitions. Especially important is the function of innate releasing mechanisms in the hierarchical system of moods, as explained in N. Tinbergen's paper. In his investigation of the gaping reactions of young thrushes, Tinbergen distinguished between releasing and directing mechanisms, according to whether they activate discharge of endogenous activity or a taxis. I think that this terminological differentiation is not advisable. Of course, it is not very elegant to talk of an innate mechanism 'releasing' a taxis, or, still worse, a social inhibition. But somehow we ought to express in our terminology the fundamentally

important fact that it indubitably is *the same* innate organization of perception that is filtering and selecting the key stimuli activating these very different responses.

(5) *The method of dual quantification*

A very considerable percentage of all animal activities consists of the typical successive links of appetitive behaviour, attainment of a desired stimulus situation, to which an innate releasing mechanism responds and sets off the discharge of accumulated endogenous action. In the vast majority of cases where we find an organism responding specifically and without previous experience to certain stimulus situations, closer investigation will reveal one or other of the innumerable variations to this theme, always leading up in one way or the other to the final discharge of consummatory actions. What we can objectively observe is exclusively this discharge. But this discharge is dependent upon two absolutely heterogeneous causal factors: (1) the level attained by the accumulated action-specific energy at the moment and (2) the effectiveness of external stimulation. None of these two factors is directly accessible to our observation. Absolutely identical reactions can result, in one case, from an extremely low level of endogenous accumulation and strong stimulation, and, in the other, from a high level of accumulated action-specific energy and a very weak external stimulation, or even, in the case of explosion activity, from internal factors alone, external stimulation not taking any part in the activity at all. This has to be taken into very serious consideration in the experimental study of perceptual organization. If, after the elimination of one or more single stimuli, the activity can still be elicited in its normal form, this does not in any way justify the conclusion that these stimuli are ineffective in activating the releasing mechanism pertaining to the activity in question. If Stone's (1923) rats discharged certain innate behaviour patterns apparently normally, although they were deprived of important sensory organs, this is in no way astonishing. A mother rat who, in spite of the removal of her olfactory bulbs, continues to foster her young, is in no other position than an old virgin Scotch terrier bitch who, with a sufficient lowering of threshold, proceeds to discharge homologous reactions with a cushion for a substitute object.

What is constant is not the effect actually produced by a certain key stimulus at a given moment, but the relation between this effect and the organism's momentary internal state of accumulation of action-specific energy. The constancy of this correlation only becomes apparent when both the internal and the external factors are quantitatively investigated *simultaneously*. The method of doing this truly deserves the name of a *correlative*

analysis. In a dabbling and uncertain way I sensed the possibility of this method as early as 1926, when I was experimenting with my first free-flying tame jackdaw. The observations I then made are still very vivid in my memory, and though it has taken me years to see their real purport, they are a good and simple illustration of what I am trying to explain. The following reaction of a hand-raised and fully fledged young jackdaw *(Coloeus monedula)* is elicited by a small number of single stimuli which, though apparently simple, nevertheless imply the necessity of assuming an innate perceptual organization responding to *relational* properties. The experimenter who wants to elicit the reaction which the young birds give to the stimuli emanating from its parents guiding it, must do at least *one* of three definite things. He must either more or less quickly move *away from* the bird, or *upwards* from its position, or he must utter a good imitation of the call-note of the species. (A fourth very effective stimulus, pertaining to the same releasing mechanism, is the sudden unfolding of a pair of black wings, but this is not so easy for the human experimenter to imitate. Its existence is, however, immaterial for our present concern.) When I walked abroad with that young jackdaw, the bird would, at first, follow me very willingly. It would fly up in pursuit even when I walked away from it quite slowly. (Though it was always possible to get away from the bird, without having it following after me, by the method of letting the stimulus 'creep in', walking away with extreme slowness.) After a time it became necessary for me to walk away *abruptly,* over-accentuating my movements very much in the same way as a parent cichlid does with his swimming-away movements. After a few more performances I had to *add* another stimulus, that is, I had either to call, or to crouch low to the ground beside the sitting bird and jump up in starting. At last, I had to do *all* of these things simultaneously and with the utmost intensity, crouching close to the jackdaw, jumping up suddenly, running away as quickly as I could and yelling jackdaw-calls all the time, in order to make the bird take to wing at all. In this simple experience two important facts are obtrusively apparent: *(a)* the activity is *exhaustible* independently from the general state of exhaustion of the organism as a whole, *(b)* the stimuli which release it are *interchangeable* and the general releasing effect of a situation is dependent on the *sum* of the single releasing stimuli contained in it. Furthermore, another fact mentioned earlier is again illustrated: internal and external motivation may add up to exactly identical results if the weakness of one is compensated by strength of the other.

Whenever we put stimulation in front of an organism and register its answer to this stimulation, we have to deal with an equation containing *two* unknown factors. The quantification of each of these factors is, on

principle, impossible without simultaneously ascertaining the quantitative effect of the other. What is visible to us is *(a)* the stimulus situation we are putting before the animal, and *(b)* the discharge of a specific activity thereby released. The varying internal state of specific excitability is only accessible to us through the means of these two indicators. If we are looking for an object favourable to an exact solution of this equation containing two unknowns, we must obviously search for an activity, the discharge of which has a number of clearly distinguishable grades of intensity, and the releasing mechanism of which consists of an appreciable number of distinct stimuli, so that by the addition of these stimuli we may obtain a gradation of different releasing values.

A very extensive observational basis is needed to obtain a certain knowledge of all the different forms of movement activated by *one* quality of action-specific excitation. The internal state of heightened action-specific excitability may betray itself by small intention movements, and from the merest hint of these up to the activity of full intensity there are all possible gradations. For endogenous activity as a whole, the very contrary of an 'all-or-nothing law' holds true. (Not, however, for the single neural elements of endogenous activities which certainly do obey the all-or-nothing law, as von Holst has clearly shown. The differences of form and of amplitude which endogenous activities show at different levels of action-specific excitation are due to the fact that the single neural elements, pertaining to the same quality of specific excitation, have slightly different thresholds, so that different numbers and, in some cases, different kinds of elements are activated at different levels of reactional intensity.) To an observer who is familiar with the systems of actions of the species in question, these finely graded intention movements can tell very exactly what to expect from the animal at the next moment. But, because the slight intensive movements grade imperceptibly into the full activity, it is difficult to gain an objective criterion for absolute quantification.

Luckily for our analytical purposes, this is not true for such intention movements as have, by the evolutionary process described (p. 242), developed a new function as social releasers. The intensity scales of these consist, in the majority of cases, in a series of behaviour patterns which do not grade into each other, but each of which has not only a very definite and distinctive form of movement, but also a quite distinct threshold that must be reached by action-specific excitation in order to activate it. To describe only one of the many examples obtruding themselves: the welling-up of the excitation specific of fighting activity in the cichlid fish *Astatotilapia strigigena*, activates a sequence of not less than five behaviour patterns in the succession of their respective thresholds: (1) taking on display colouring; (2) standing

parallel to the adversary with median fins maximally spread; (3) distending of gill membrane; (4) sideways beating of the spread caudal fin; (5) ramming the adversary. In *Betta splendens,* an osphromenid fish, there are two more steps distinguishable in the same ladder. Of course, each one of these single activities may be executed with greater or lesser intensity, thus giving opportunity for further differentiation; but even without this, a graduation of five steps, not to be confounded with each other, is a tremendous help for quantitative study.

For the purposes of dual quantification it is necessary that not only the intensities of the activity released, but also the releasing effect of external stimulation should be accessible to an exact graduation. This is obviously best in cases in which the innate releasing mechanism is activated by a comparatively great number of independent stimuli, in other words, in the most complex and most highly differentiated releasing mechanisms. These, indubitably, are the ones that correspond to social releasers. In this respect, the fighting reactions of certain fishes again prove to be an admirable object, being released by a number of visual stimuli which not only are easy to reproduce in a dummy, but also very different from each other as to their respective releasing values.

Before describing in detail how we proceed in our simultaneous quantitative study of endogenous generation of action-specific energy and of the respective effectiveness of single releasing stimuli, I want to emphasize what a tremendous amount of purely observational work has to be done, to furnish us with the *measure* with which we quantify these factors. The observer has to get thoroughly familiar with *all* the innate behaviour patterns of the species with which he is going to experiment, in order to know what movements are correlated to what independent quality of action-specific excitation. He must possess an exact knowledge of the sequence, in which the single behaviour patterns correspond to different levels of intensity of this specific excitation. The task of correlating single behaviour patterns to specific qualities of excitation is not made easier by the frequent occurrence of displacement activities which also must be drawn into consideration and which, in higher animals, tend to complicate matters immensely.   Also, the experimenter must already have attained a rough working knowledge of the stimuli pertaining to certain releasing mechanisms.   If these conditions are thoroughly fulfilled, the ethologist is, in a good many cases, in a position to prove the correctness of his hypotheses in the most exact manner known to natural science, that is, by correctly *predicting* what will happen in the situation he creates experimentally. My friend Seitz, who is, what every comparative ethologist ought to be, a past master of the motion-picture camera, had a really uncanny way of predicting

what his cichlids were just going to do. When demonstrating some experiment on fighting or courtship activities of his fishes, he always quite unconsciously dropped into the same manner of speaking as when demonstrating a film that he knew by heart, forever anticipating by a few seconds in his explanations what the fishes were doing, calling the attention of the onlookers to the minutest detail of behaviour which he *knew* would occur in the next moment.

The practical way of proceeding in experiments of dual quantification is obvious, after what has already been said. Presenting the animal with a given stimulus situation and recording the intensity of its reaction presents us, as I have explained, with an equation containing two unknowns: we do not know how much of the intensity recorded is due to internal accumulation of action-specific energy and how much is due to external stimulation. The obvious thing to do, is to let *maximal* stimulation impinge upon the organism immediately after the first experiment, in order to see how much specific energy is 'left'. This already gives us a definite notion about the *relative* effectiveness of the stimulation supplied in the first experiment. What we are doing is best illustrated in a hydro-mechanic model which, in spite of its extreme crudeness and simplicity is able to symbolize a surprising wealth of facts really encountered in the reactions of animals. In Fig. 1 the tap T supplying a constant flow of liquid represents the endogenous production of action-specific energy; the liquid accumulated in the reservoir R represents the amount of this energy which is at the disposal of the organism at a given moment, the elevation attained by its upper level corresponds, at an inverse ratio, to the momentary threshold of the reaction. The cone-valve V represents the releasing mechanism, the inhibitory function of the higher centres being symbolized by the spring S. The scale-pan SP which is connected with the valve-shaft by a string acting over a pulley represents the perceptual sector of the releasing mechanism, the weight applied corresponds to the impinging stimulation. This arrangement is a good symbol of how the internal accumulation of action-specific energy, and the external stimulation are both acting in the same direction, both tending to open the valve. It can also easily and obviously represent the occurrence of explosion activity. The activity itself is represented by the spout discharged from the jet J. The intensity of the reaction is symbolized by the distance to which the jet springs, in other words, by the speed of the outflow. This automatically corresponds to the proven fact that the consumption of action-specific energy in the time unit is in direct proportion to the intensity of the reaction. The intensity of the reaction can be read on the scale G. To this apparatus we can easily attach a gadget exactly symbolizing the way in which a sequence of different movement patterns

belonging to one scale of action-specific excitation is activated. A row of little funnels attached below the gradation will meet the case where, with the attaining of a higher level of excitation, the activities corresponding to lower levels are discontinued (as, for instance, in the taking-to-wing ceremony of the greylag goose). It is, however, much more usual that the
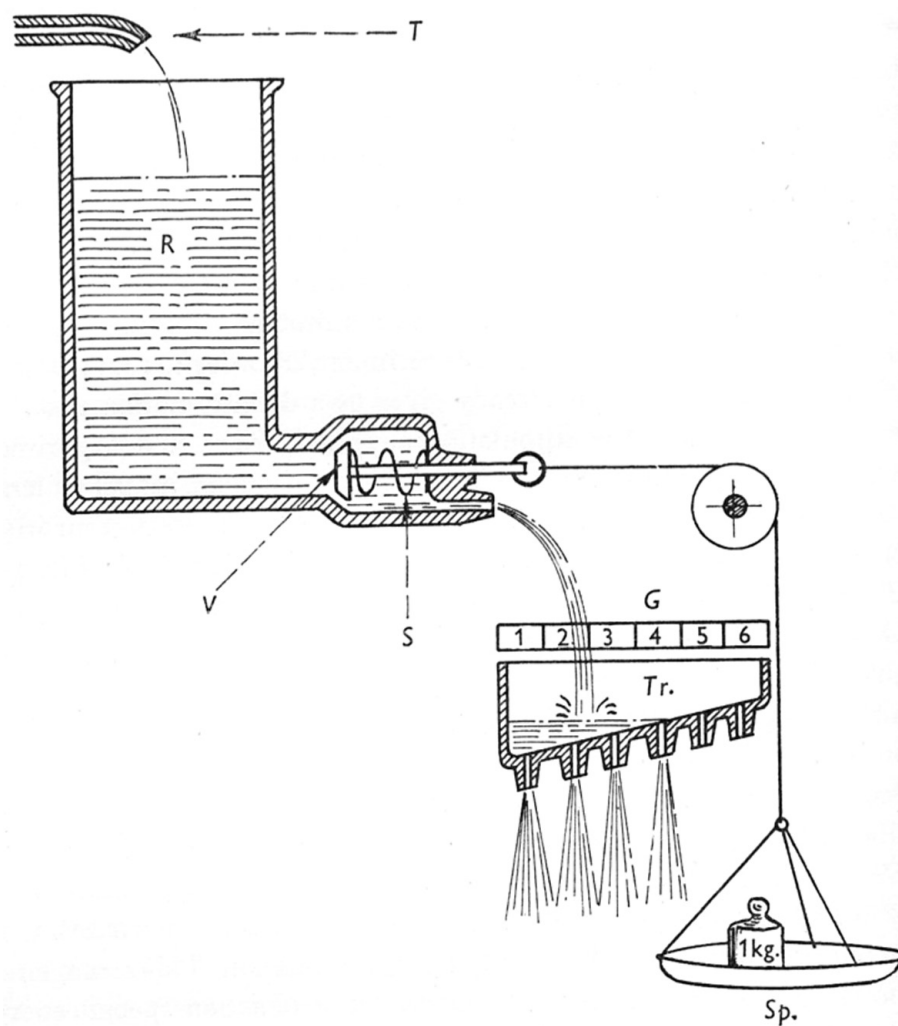

Fig. 1

movements activated at the lowest levels of action-specific excitation are continued unceasingly all the while those corresponding to higher levels are discharged. We can symbolize this by fixing below the scale G an oblong trough Tr which has an oblique bottom perforated by a number of holes. The outflow from these holes then represents the intensity scale of a sequence of different activities, such as fin-spreading, gill-membrane expanding, etc. For reasons subsequently to be expounded, we have arranged the scale tray representing the receiving section of the innate

releasing mechanism in such a manner as to let some of the ultimate flowing out of liquid impinge on it in a diffuse way.

This contraption is, of course, still a very crude simplification of the real processes it is symbolizing, but experience has taught us that even the crudest simplisms often prove a valuable stimulus to investigation. As an instrument for the quantification of external and internal stimulation this model has already proved to be of some value. Let me explain its use. Suppose we present an organism with a stimulus of unknown effectiveness. All we can immediately record is, as already explained, the intensity of the reaction. In the terms of our model, we do not know what weight we have applied to the pan. In order to ascertain it, we must try to get some notion of the pressure pushing on the valve from the inside. The simplest way to do this is to open the valve altogether and record the distance which the spout delivered by the jet will now attain. In other words, we shall present our animal with the *normal* object of the reaction which may be roughly (though not theoretically) identified with its optimal object, and record the intensity of which the reaction is capable at the moment. Out of both data the relative effect of the first stimulus can be roughly calculated, as well as the pressure acting from within. In other words, we have now got two equations with two unknowns.

There can be a very great number of variations to the intrinsically identical method of calculation described above. Which of them is the most favourable largely depends on the object and on the particular questions which are in the experimenter's mind at the moment. If, as it is most advisable at the very start of any investigation, we are interested in taking stock of all the stimuli that activate the innate releasing mechanism, it is a very good way of proceeding, to 'pump out' the reservoir of action-specific energy gradually. We begin by presenting a comparatively simple dummy which is reacted to only with little intensity and only for a short time. When the reaction to this dummy noticeably begins to flag, we 'improve' upon the dummy by introducing additional stimuli. In the terms of our hydromechanical model, we are lowering the internal pressure to such an extent, that the releasing weight x ceases to open the valve, while the weight x plus 1 still will do so. We get the threshold of the reaction exactly *between* the releasing values of the two successive dummies. We may continue with this procedure until we arrive at dummies whose releasing value cannot be increased any more. In many cases, the objects thus attained by far surpass the releasing effect of the natural object of the reaction in question, a fact which in itself is a serious blow to the vitalistic belief in the infallibility of 'instinct'. And not only has the experimentation of human scientists succeeded in discovering such 'supernormal' objects, but the evolutionary adaptation of certain

social parasites to the releasing mechanisms of their hosts has evidently done the very same thing. The cuckoo, for instance, is obviously presenting a superlatively strong stimulation to the innate mechanisms releasing the feeding activities of many small passerines, far excelling the one emanating from young of the respective species. Heinroth, in his drastic way, once said that cuckoo feeding may become a real *vice* indulged in by most of the occupants of an aviary. Though meant as a joke, this utterance contains a very serious truth, because some human vices are evidently nothing more than a continued search for supernormal stimulation. What is true for the cuckoo very probably is also true of many social parasites of termites and ants. All these organisms are a challenge to the ambitious ethological experimenter.

If a releasing mechanism contains the perceptual correlates to a comparatively large number of key stimuli, it is possible to construe an immense number of combinations and permutations of these stimuli. By this we obtain the further possibility of comparing the stimulating effect of objects whose releasing value is approximately the same, but is brought about by a summation of entirely different constituent key stimuli. By patiently constructing a great number of dummies of approximately equal releasing value, but different elementary stimuli, A. Seitz (1942) was able to show rather conclusively that the releasing value of the single constituent stimulus is absolutely constant in all possible combinations. This is what he termed 'Reiz-Summen-Phänomen' in German, and what Tinbergen translated into English by 'Law of heterogeneous summation'. Wolfgang Schmidt (to be published) investigated the human reaction to the visual stimuli of laughing with exactly the same method and obtained strictly analogous results. The effect of heterogenous summation could be demonstrated even more clearly in this case, because in experimenting with humans it is possible to compare directly the releasing values of two dummies, by applying the choice method. In experimenting with animals, especially with the lower forms, this method has a very serious drawback: it frequently occurs that the stimuli, activating an innate releasing mechanism, are *not identical with those that direct it in space,* and therefore very misleading results can be obtained by letting an organism 'choose' between two dummies. As Tinbergen has shown conclusively in the greyling butterfly, *Satyrus semele,* it is quite possible that one object elicits the discharge of endogenous activity, while the second is sending out directing stimulation guiding the organism's reaction to itself.

There are endogenous activities which have a rather quick generation of action-specific energy, but, speaking in the terms of our hydromechanical metaphor, a narrow reservoir in which to hold it. The gaping activity of

young passerines, for instance, 'fills up' from total exhaustion to explosion activity within half an hour or an hour and, in smaller species, is exhausted after a discharge lasting only a fraction of a minute. In rearing such birds by hand, it is, in very many species, quite impossible to feed all of the nestlings during one gaping 'burst'. If there are six nestlings, nos. 4, 5 and 6 will cease to gape, before one has finished feeding nos. 1, 2 and 3. This also very clearly shows how the activity is not motivated by a directive 'food instinct' or 'hunger'. In such quickly exhaustible activities the enormous inconstancy of the level of action-specific energy is a very serious obstacle to the comparison of releasing values of different stimuli. Even the obvious method of presenting the stimulus suspected to be 'stronger' immediately after the reaction to the weaker stimulus has ceased, does not give reliable results. It is very possible that a stimulus which is really quite appreciably stronger than the preceding one, fails to elicitate any reaction when thus presented. Here we have to take into consideration an effect which has been very aptly termed *inertia* of reaction by A. Seitz. When we suddenly deprive an animal of the object of its reaction, the activity never breaks off abruptly but nearly always continues a considerable time *in vacuo*. Doubtless it is a consequence of the same phenomenon that the 'momentum' gained by any activity will carry it on for an appreciable time after the moment when its releasing threshold, rising continually throughout the duration of the discharge, has reached the value corresponding to the external stimulation impinging at the moment. This is also the reason why an organism that is left continually in the presence of a releasing object does not continually react to it with a constant intensity, as otherwise would be expected. The inertia of a reaction carries the threshold high above the value corresponding to the ever-present stimulating object. After the reaction has ceased, the gradual lowering of the threshold during its period of quiescence acts exactly as a correspondingly slow increase of stimulation would act upon a constant threshold, that is, it results in the well-known phenomenon of 'creeping in' of stimulation. Because of this, the new burst of activity does not occur until the threshold is very appreciably *below* the value corresponding to that of the constant stimulation. The result of this is the usual form of discharge, in rhythmically recurring 'bursts' of activity. The heightening of threshold, caused by inertia of reaction, may be so considerable that it can supersede a quite substantial difference between the stimulating effects of two dummies. If we let the animal react to one combination of stimuli until activity ceases and then *fail* to elicit any response by the presentation of another set of stimuli, we are not yet in possession of conclusive proof that the second combination is not quite considerably stronger than the first. For obvious reasons this

fact is all the more important, the more quickly the activity in question is exhaustible.

It is probable that the *initial* inertia of endogenous activities and their propensity to *continue* longer than corresponds to present stimulation, are two entirely different phenomena, requiring different physiological explanations. The way in which quiescent activities respond to stimulation is more suggestive of initial *friction*. They 'behave' exactly as if the valve releasing their discharge was a bit sticky. Furthermore, there arises the question whether there is not a distinct relationship between creeping in of stimulation and what we call habituation. Contrary to these phenomena of an initial resistance to stimulation, the continuance of activity after cessation of adequate stimulation is easily explainable on the assumption that the activity is *self-stimulating*. A strong argument for this assumption lies in the fact that this type of inertia of an activity is evidently in exact direct proportion to the intensity the discharge has attained. If in our hydrostatical model we arrange the scale-pan receiving the weights representing stimulation in such a way as to let part of the outflow of the activity impinge upon it in a somewhat diffuse way (Fig. 1), we are able to reproduce a very exact replica of the avalanche-like way in which the endogenous activities tend to grow after being released. Also we can account for the fact that the valve stays open much longer than corresponds to the added values of internal pressure and weights on the scale-pan. A very considerable part of all endogenous activities is in this way self-exhausting and self-stimulating at the same time, a fact which has been stressed by Julian Huxley long ago.

(6) *Analysis of taxis and kinesis constituents of 'instinct'*

As long as the whole of innate behaviour was considered a chain reflex, there was no reason to make any particular distinction between the single constituent reflexes which are building it up. The discovery of endogenous generation of action-specific energy has considerably changed this position. I have already shown in what way the recognition of the very peculiar physiological character of these functions forces us to conceive of endogenous activity and of the perceptual organization releasing it as of two very distinct physiological processes which, though they are strictly interdependent constituents of one mutual function, each demand a different method of analytical approach. In very much the same manner as the discovery of endogenous activity has influenced our conception of the releasing mechanism, it also necessitates some corrections of our notions about the mechanisms *directing* activity in space. Correlative analysis is like the solving of a crossword puzzle, in that the correction of one word which had been put in erroneously makes it necessary to revise our notions

about all the parts interlocking with it. I need not say anything here about the interdependence of endogenously automatic activities and taxes as constituents of innate behaviour; a much better authority on the subject will do so.

I would, however, say a few words in answer to an evidently widely spread misconception about our conceptional distinction of physiologically independent constituent functions. It is in the very nature of analysis that it leads to a progressive narrowing in of formerly wider and more general conceptions. What formerly was very simply conceived of as 'an instinct' is shown by the advance of analysis to be a very complex mechanism of very distinct and very different constituents, such as endogenous automatisms, releasing mechanisms, taxes, kineses and, maybe, quite a number of further as yet unrecognized particulate functions. For this we have been reproached by many psychologists, all of them more or less under the influence of vitalistic and finalistic preconceptions. We were accused of pulling to pieces what really was a whole, and it has been said of us what Goethe said of a certain type of analytical science: 'Sie haben die Teile in der Hand, fehlt, leider, nur das geistige Band.' I would emphatically deny this charge. When we distinguish independent and particulate constituent functions of innate behaviour, we are just as much justified in doing this as the physiological anatomist is justified in distinguishing between the bones, joints, muscles and nerves of, let us say, a human arm or leg. The conceptional distinction of constituent parts and of their particular qualities does not in any way preclude the fullest cognizance of the general mutual interdependence and interaction of these parts. It does not, in any way, prevent us from seeing the organism as a whole or system. This will seem a very commonplace thing to say to physiologists, as, indeed, it really *is*. But it is a deeply regrettable fact that it seems to be exceedingly necessary to say it again and again to some psychologists.

(7) *The hierarchy of moods*

Doubtless a quite considerable percentage of all the activities of animals and men are compounded of the three successive links described in the classical diagram given by Wallace Craig and further differentiated by Tinbergen and myself: (1) accumulation of action-specific energy giving rise to appetitive behaviour; (2) appetitive behaviour striving for and attaining the stimulus situation activating the innate releasing mechanism; (3) setting off of the releasing mechanism and discharge of endogenous activity in a consummatory action. Doubtless this tripartite organization of behaviour does occur. Pessimists assert that yesterday's truth is to-day's error. In biological research work it is certainly more correct to say that the

truth of yesterday is, not the error, but the *special case* of to-day. In biological research, an all-too-cautious abstaining from forming a hypothesis would get us nowhere, and we must have the courage to formulate preliminary hypotheses, though we are well aware that these preliminary formulations are much too simplistic and correspond, at the best, to a particularly simple special case. In fact, the discovery of a natural law has been, in many instances, identical with the discovery of a special case, in which it was actualized in a particularly simple manner. We are therefore neither surprised, nor pained, that the original, tripartite diagram of the organization of innate behaviour has proved a typical example of this kind of simplification. That is to say, it meets a good many cases, but is much too simple for most cases.

It was a most decisive step forward in our understanding of innate behaviour when Baerends (1941) pointed out that appetitive behaviour by no means always leads immediately to the discharge of consummatory action. In the vast majority of cases, the appetitive behaviour with which an activity begins is of a much more *generalized* nature. The releasing situation attained by this first step of appetite and the innate releasing mechanism activated in this situation, do not lead to the discharge of the final consummatory act, but, as the next step, to another form of appetitive behaviour of a distinct and *more specialized* form, striving for another, also more specialized, releasing situation. A very general 'mood', in the sense of a readiness to certain activities, as, for instance, the 'reproductive mood' of a male stickleback, which comprises the several readinesses to a very considerable but finite number of consummatory acts, is, step by step, narrowed down to the discharge of one of these. There is, in other words, a hierarchical order of wider and narrower readinesses or moods. The action-specific appetite and the discharge of the consummatory action are the *lowest* rung in this ladder of superimposed commanding instances or 'centres'. Baerends has extensively studied the 'Hierarchy of moods' in the digger wasp, *Ammophila campestris,* and Tinbergen in the stickleback. As the latter is going to read a paper on the subject himself, I need not say more here.

From the methodological viewpoint, which is the subject of this paper, it must be emphasized that the conception of a hierarchy of 'instincts', at which we have arrived, is something entirely different from what W. McDougall and other purposive psychologists conceive of as chain appetites, first and second order drives and the like. These conceptions have been arrived at from the opposite direction of approach. We have not gone out from finalistically considering what the animal *ought* to do, in order to sustain itself and its species, but from what it actually *does*. We have not

started from the hypostatization of a 'reproductive instinct', deduced from the fact that sticklebacks reproduce their kind, but from the observation and inventory of the lowest rung of the hierarchical ladder of integration, with the consummatory actions, and worked our way inductively *up* that ladder instead of deductively down. The conceptions of the successive levels of integration are therefore determined *causally* and not ideologically. Therefore Tinbergen's and Baerend's conception of hierarchically superimposed 'centres', though determined exclusively from a functional point of view, may prove a most valuable hint to the experimenting physiologist as to the number of localizations for which he has to look.

(8) *The psychological aspect of comparative ethology*

There is an amazingly widely spread prejudice that a given process of behaviour can only have *either* a physiological *or* a psychological explanation. In F. Hempelmann's otherwise admirable text-book this fundamental error keeps recurring every few pages. Of course there simply is no psychological process which does not have its physiological correlate and which does not demand a physiological explanation as well as a psychological one. The serious consequence of the erroneous 'either-or' lies therein *that it implies the superfluity of physiological explanations in all cases where a psychological explanation can be found*. On the other hand, there are a lot of processes comprised in animal behaviour which do not have a psychological explanation. In other words: every psychological process has its physiological side, but not every physiological process is correlated to psychological phenomena.

Though comparative ethology is resolutely and exclusively concerned with an *objectivistic* study of behaviour, as long as it is concerned with animals, we do not, by any means, shut our eyes to one important fact: just those particular physiological processes that are the main object of our investigations, undoubtedly belong to the kind which *does have a correlated psychological side to it*. This is true of all the three most important elementary processes of innate behaviour, of endogenous-automatic activities as well as of innate releasing mechanisms and of taxes.

There cannot be the least doubt that the discharge of accumulated action-specific energy is accompanied by very intense and very specific subjective phenomena. I fully agree with W. McDougall in his fundamental assertion that man has just as many 'instincts' as he has qualitatively distinguishable emotions. Jan Verwey, an indubitably objectivistic student of animal behaviour, is evidently of the same opinion when, in his famous paper on the grey heron (1930), he writes: 'Where reflexes and instincts can be distinguished from each other at all, there the reflex is functioning mechanically, while instinctive activities are accompanied by subjective phenomena'

(translated from the German). Heinroth used to answer to anybody's assertion that animals were reflex machines by saying jocularly: 'Quite on the contrary, animals are exceedingly emotional people, possessing very little intellect'. The same opinion is evidently underlying Heinroth's conception and treatment of 'moods' *(Stimmungen)*. Our firm conviction that there exists a subjective, emotional side to 'moods', as well as to the discharge of action-specific energy, does not in any way imply our making illegitimate assertions about the nature and quality of an animal's subjective experiences. These are, and ever will be, inaccessible to our knowledge. I would lay great stress upon the fact that Heinroth's conceptions of 'moods' can one and all be strictly defined from a purely objectivistic point of view, as specific internal states of readiness to discharge a certain complex of behaviour patterns. Even Heinroth's terms are not derived from human subjective phenomena, but from the objective activity itself, as, for instance, 'Flugstimmung', 'Fortpflanzungs-Stimmung' (flying mood, reproductive mood) and others. We still hold that a real 'psychology' of animals is on principle impossible. But in its application to *man*, the fact that the discharge of certain endogenous activities is correlated to certain distinct emotional phenomena may become of tremendous importance.

The psychological aspect of innate releasing mechanisms presents some parallels to that of endogenous activities. We know for a certainty that the attainment of the releasing stimulus situation represents the end or goal to which appetitive behaviour is directed. We can give an exact and purely objective definition of this kind of directedness or purpose (p. 248). In all human behaviour, which also objectively fits this definition, we furthermore know for certain that the organism, as an experiencing subject, is striving for certain pleasurable subjective phenomena accompanying as well the perception of the releasing stimulus situation as the discharge of the accumulated endogenous activity. I do not think that any observer really familiar with appetitive behaviour in higher animals will ever doubt the fact that the animal as a subject also experiences intense sensual pleasure as the subjective correlate of attaining the releasing stimulus situation. W. Craig gives a convincing description of the behaviour of a young male dove on attaining the specific situation eliciting the nest-calling activity: When 'a ready-made nest is put into his cage, the inexperienced dove does not recognize it as a nest, but sooner or later he tries it, as he has tried all other places for nest-calling, and in such trial the nest evidently gives him a strong and satisfying stimulation (the appetitive stimulus) which no other situation has given him. In the nest his attitude becomes extreme; he abandons himself to an orgy of nest-calling (complete consummatory action), turning now this way and now that in the hollow, palpating the

straw with his feet, wings, breast, neck and beak, and *rioting in a wealth of new, luxurious stimuli'* (italics mine). Again, we cannot say anything about the specific quality of the animal's subjective experiences. But again the laws we have found in animal behaviour find an enormously important application to the special phenomena of human psychology. We do not go far wrong if we suspect the existence of an innate releasing mechanism, wherever we can introspectively ascertain a specific quality of sensual pleasure. To give a good example of this, and quite a proper one at that: it is a distinct and indubitably sensuous pleasure to fondle a nice plump, appetizing human baby. The stimulation emanating from such a baby even elicits one of the very few motorically innate behaviour patterns of our species, a quite distinct movement of taking the infant on one arm, holding it with the other. In fondling the baby, we behave to its 'sweet' stimulation very much like Craig's pigeon does to the nest. By introspection I can ascertain that the pleasure I feel in fondling and petting the baby is certainly qualitatively different from any other kind of sensual pleasure, especially, whatever psycho-analysts may assert to the contrary, from that of a sexual nature. Indeed, I can assert that my pleasurable sensations in fondling a sweet human child are of the same quality as those I experience in fondling a chew-puppy, or a baby lion. There is not even an appreciable difference of intensity between these reactions; indeed, it is questionable whether a young lion is not, in some respects, what we call a supernormal object to my reaction. But I would seriously warn any psychoanalyst against telling me that I am reacting sexually to that lion! In this case, the existence of a true innate releasing mechanism in man has been clearly proven, the relational properties which the object must possess have been analysed, and the fact that their common effect is obeying the law of heterogeneous summation is quite evident. Also, the objective and subjective reactions activated by the mechanism are clearly distinguishable. A normal man — let alone a woman — will find it exceedingly difficult to leave to its fate even a puppy, after he or she has enjoyed fondling and petting it. A very distinct 'mood', a readiness to take care of the object in a specific manner, is brought about with the predictability of an unconditioned response. Quite especially a strong inhibition to hurt or kill the 'sweet' baby is activated by the innate releasing mechanism in question. When, much against my emotional inclination, I once forced myself for rational reasons to kill a number of young hooded rats who still were in a 'sweet' stage of development, I acquired a very slight, but indubitable neurosis; that is to say, I repeatedly *dreamt* of the occurrence in an emotionally super-accentuated way. This particular innate releasing mechanism of our species is, for obvious reasons, an exceptionally favourable object for the method of approach just described.

But there is no doubt that in many more cases introspection, circumspectly applied, can lead to similarly important discoveries.

Perhaps an even greater theoretical interest is due to the psychological aspect of *taxes*. It can be shown irrefutably that it is not possible to draw a sharp distinction between taxes and *insight* either from the objectivistic or from the psychological point of view. Considered from the objectivistic viewpoint, taxes, as constituents of appetitive behaviour, are represented in all possible gradations of complexity, ranging from simple and clearly analysable directing reflexes to those complex processes of spontaneous solution of spatial problems that we are wont to call 'insight'. The former merge gradually and imperceptibly into the latter, without giving us an opportunity to draw a distinction between both. Neither is it possible to arrive at a clear conceptual distinction between taxis and insight from the psychological, introspective side of the matter. The subjective experience of insight which Karl Bühler so very expressively has termed the 'Aha-Erlebnis', always characteristically takes place in the exact moment when disorientedness gives way to orientation. But in this also there is no essential difference between the simplest and the most complicated processes of 'orientation'. The specific experience of the 'Aha' crops up in the moment when we attain an 'illumination' concerning some very complicated problem, but it also does in the case of a simple and indubitable tropotaxis. When, for instance, our tropotactic orientation to gravity has been removed, let us say by narcosis, or, as I have experienced it twice, in a vasomotoric collapse, then the reorientation sets in again with what I should metaphorically call an audible click, and this click is accompanied by a superlatively strong and qualitatively distinct 'Aha-experience'!

In my opinion, every physiological process which can, in the manner just described, be approached simultaneously from the objective and from the subjective side is of a paramount theoretical and practical importance. The cardinal problem of psychology, the question of the interdependence of body and mind, cannot be inductively approached in any other way than by studying those not too common cases, in which the intrinsic unit of one of these highest life processes *can* be studied from the objective, physiological side as well, as from the subjective, psychological one. To refrain from introspection in such cases would mean renouncing a superlatively valuable source of knowledge for purely dogmatic reasons which would be about the worst thing a natural scientist could do. On the other hand, it is high time that social and group psychology began to occupy itself with the physiological side of behaviour and more especially with the innate processes of which I spoke above. It is high time that the collective human intellect got some control on the necessary outlets for certain endogenously generated

drives, for instance 'aggression', and some knowledge of human innate releasing mechanisms, especially those activating aggression. Hitherto it is only demagogues who seem to have a certain working knowledge of these matters and who, by devising surprisingly simple 'dummies', are able to elicit fighting responses in human beings with about the same predictability as Tinbergen does in sticklebacks.

REFERENCES

Allen, Arthur A. (1934). Sex rhythm in the ruffed grouse *(Bonasa umbellus* L.) and other birds. *Auk,* 51, 180-99.

Antonius, O. (1937-38). Ueber Herdenbildung und Paarungseigentümlichkeiten der Einhufer. *Z. Tierpsychol*. 1, 259; 2, 115.

Armstrong, E. A. (1942). *Bird Display*. Cambridge University Press.

Baerends, G. P. (1941). Fortpflanzungsverhalten und Orientierung der Grabwespe *Ammophila campestris*. *Tijdschr. Ent*. 84, 68-275.

Baerends, G. P. (1950). An introduction to the ethology of cichlid fishes. *Behaviour* (in the Press).

Bierens de Haan, J. A. (1940). *Die tierischen Instinkte und ihr Umbau durch Erfahrung*. Leiden: Brill.

Bühler, Karl (1922). *Handbuch der Psychologie,* I. Teil. Jena.

Craig, W. (1918). Appetites and aversions as constituents of instincts. *Biol. Bull. Woods Hole,* no. 2, pp. 91-107.

Darwin, C. (1874). Der Ausdruck der Gemütsbewegungen (German translation, Stuttgart).

Dewey, John (1918). *Human Nature and Conduct*. New York: Henry Holt and Co.

Eliot, Howard H. (1929). *An Introduction to the Study of Bird Behaviour*. Cambridge University Press.

Heinroth, O. (1910). Beiträge zur Biologie, insbesonders Psychologie und Ethologie der Anatiden. *Verh. V. Int. Ornithol. Kongr.*

Heinroth, O. (1930). Ueber bestimmte Bewegungsweisen von Wirbeltieren. *S.B. Ges. naturf. Fr. Berl.* pp. 333-42.

Heinroth, O. & M. (1924-8). *Die Vögel Mitteleuropas*. Berlin.

Holst, E. v. (1935). Alles oder Nichts, Block, Alternans, Bigemini und verwandte Erscheinungen als Eigenschaften des Rückenmarkes. *Pflüg. Arch. ges. Physiol.* 236**,** Hefte 4, 5 and 6.

Holst, E. v. (1936). Versuche zur relativen Koordination. *Pflüg. Arch.ges. Physiol*. 237**,** Heft 1.

Holst, E. v. (1936). Vom Dualismus der motorischen und der automatisch-rhythmischen Funktion im Rückenmark und vom Wesen des automatischen Rhythmus. *Pflüg. Arch. ges. Physiol*. 237**,** Heft 3.

Huxley, J. S. (1914). The courtship habits of the great crested grebe *(Podiceps cristatus)*; with an addition on the theory of sexual selection. *Proc. Zool. Soc. Lond*.

Jennings, H. S. Das Verhalten der niederen Organismen (German translation by Mangold 1910). Leipzig.

Koehler, Otto (1933). Die Ganzheitsbetrachtung in der modernen Biologie. *Verh. Königsberger Gelehrten Gesellschaft*.

Köhler, Wolfgang (1933). *Die physikalische Gestalten in Ruhe und stationärem Zustand*. Braunschweig.

Koortlant, A. (1938). De uitdrukkingsbewegingen en geluiden von *Phalacrocorax sinensis* Shaw & Nodder. *Ardea*.

McDougall, W. (1933). *An Outline of Psychology,* 6th ed. London.

Makkink, G. F. (1936). An attempt at an ethogramm of the European avocet *(Recurvirostra avocetta* L.) with ethological and psychological remarks. *Ardea,* 25, 1-60.

Matthaei, R. (1929). *Das Gestaltproblem*. München.

Morgan, C. Lloyd (1909). *Instinkt und Erfahrung* (German translation by M. Semon). Leipzig and Berlin.

Petrunkewitch, A. (1926). The value of instinct as a taxonomic character in spiders. *Biol*. *Bull*. *Woods Hole*, 50, 427-32.

Plath, O. (1938). *Bumble Bees and Their Ways*. Boston.

Portielje, A. F. J. (1938). *Dieren zien en leeren kennen*. Amsterdam.

Seitz, A. (1940). Die Paarbildung bei einigen Zichliden. I. Die Paarbildung bei *Astatotilapia strigigena* Peffer. *Z. Tierpsychol*. 4, Heft 1, pp. 40-84.

Seitz, A. (1942). Die Paarbildung bei einigen Zichliden. II. Die Paarbildung bei *Hemichromis bimaculatus* Gill. *Z. Tierpsychol*. 5, 74-101.

Seitz, A. (1950). Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae). *Z. Tierpsychol*. (in the Press).

Selous, E. (1905). Observations tending to throw light on the question of sexual selection in birds, including a day-to-day diary on the breeding habits of the ruff *(Machetes pugnax). Zoologist,* fourth series, 10, no. 114.

Stone, C. P. (1922). The congenital sexual behaviour of the male albino rat. *J. Comp*. *Psychol*. 2, 95-153.

Stone, C. P. (1923). Further study of sensory functions in the activation of sexual behaviour in the young male albino rat. *J. Comp*. *Psychol*. 3, 469-73.

Thorpe, W. H. (1948). The modern concept of instinct. *Bull*. *Anim*. *Behav.*

Tinbergen, N. (1940). Die Uebersprungbewegung. *Z. Tierpsychol*. 4, 1-40.

Tinbergen, N. (1942). An objectivistic study on the innate behaviour of animals. *Bib*. *Biotheoretica,* 1, 39-98.

Tinbergen, N. & Kuenen, D. J. (1939). Ueber die auslösenden und richtungsgebenden Reizsituationen der Sperrbewegungen von jungen Drosseln *(Turdus m*. *merula* L. und *T*. *e*. *ericetorum* Turton). *Z. Tierpsychol*. 3, 37-60.

Tinbergen, N., Meeuse, B. J. D., Boerema, L. K. & Variosseau, W. W. (1942). Die Balz des Samtfalters, *Eumenis (Satyrus) semele* (L.). *Z. Tierpsychol*. 5, 182-226.

Tolman, E. C. (1932). *Purposive Behaviour in Animals and Men*. (Century Psychol. Series.) New York and London.

Uexkull, J. v. (1921). *Umwelt und Innenwelt der Tiere*. Berlin.

Verwey, J. (1930). Die Paarungsbiologie des Fischreihers. *Zool*. *Jb*., Abt. allgem. Zool., 48.

Watson, J. B. (1913). Psychology, as the behaviorist views it. *Psychol*. *Rev*. 20, 158.

Weiss, P. (1937). Further experimental investigations on the phenomenon of homologous response in transplanted amphibian limbs. *J. Comp*. *Neurol*. 66, 181-209, 481-535, 537-48; 67, 269-315.

Whitman, C. O. (1899). *Animal Behaviour*. Biol. Lectures of the Marine Biological Laboratory, Woods Hole, Mass.