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THE FUNCTIONAL ORGANIZATION OF BEHAVIOUR*

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The aim of causal analysis in ethology is to understand, through the application of methods and explanatory principles customary in the sciences, the mechanisms underlying behaviour. In the symposium organized by the Society for Experimental Biology in Cambridge in July 1949 (a meeting which gave the start to the series of ethological conferences held since every second year) Niko Tinbergen started his stimulating lecture on the hierarchical organization of behaviour with the remark that the variability and plasticity of behaviour (even of the behaviour which at that time was called instinctive) seemed a major obstacle to mechanistically oriented explanations and was still a central plank of the vitalists' platform.

Lorenz had tried to solve the problem offered by the variability of 'instinctive behaviour' by restricting the concept to the relatively simple stereotyped, and species-specific units which he called 'instinctive activities', or 'Erbkoordinationen' in German, and for which in English the names 'fixed motor pattern' or 'modal action pattern' (Barlow 1968) are now commonly used. From his lecture in the above-mentioned symposium (Lorenz 1950) it is clear that by postulating this concept Lorenz hoped to dislodge the study of 'innate' behaviour from the vitalistic versus mechanistic dispute. In a way it was a kind of compromise: the mechanists he satisfied with the rigidity of the motor coordinations and the reflex-like character of its 'innate releasing mechanism'. The vitalists could still cling to the spontaneous fluctuations in the tendency for these activities to occur, although the 'reaction specific energy' Lorenz postulated to account for these fluctuations was certainly open to various mechanistic explanations.

In his main theoretical statement on this 'instinctive activity' concept Lorenz (1937a, b) denied the existence of superimposed mechanisms controlling the elements in groups, as had been asserted by McDougall (1923) in his theory of the hierarchy of instincts. In this Lorenzian view the occurrence of a particular activity was only dependent on the external stimulation and on the threshold for the release of that activity. Plasticity in behaviour should then be attributed to variation in one or both of these factors.

Particularly amongst students of insect behaviour, plasticity versus rigidity was an ever returning issue for discussion. In insects, examples of rigid concatenations of stereotyped activities, executed fully independently of their effects, could be found beside examples of a more flexible use of these activities, well adapted to variations in the external situation. Extreme examples of rigidity and of plasticity could even be found within the behaviour repertoire of one single species. I shall take some examples from my earlier work on the digger wasp *Ammophila pubescens* (Baerends 1941a, b). (At the time that study was carried out this wasp was known as *Ammophila campestris* Jur. According to Richards (1946) the correct name is *Ammophila pubescens* Curtis.)

This wasp digs in a sand surface a 3-cm deep nest for each of its larvae, at distances of 50 to 100 cm from one another. The provisioning of each nest takes place in three phases (Fig. 1). In the first phase only one caterpillar is stored and an egg is laid upon it. In the second phase the hatched larva is provided with another one or two caterpillars. In the third phase the wasp adds five to seven caterpillars, after which she closes the nest finally. In between two phases in one nest, phases in one or two other nests are executed. Each phase begins with an inspection visit. It was experimentally proved that the foraging behaviour of the wasp during a phase is initiated by this visit and adjusted to stimuli (size of larva, amount of food consumed) perceived at that time. Only inspection visits (i.e. visits without a caterpillar) had this effect. Changes made in the nest content during provisioning visits (in which the wasp also enters the nest chamber completely) have no such effects. This means that during the inspection visits a motivational state is activated in the wasp which in some way corresponds to a task to be achieved, often in more than 1 day, and in which numerous activities are incorporated in a generally well adapted way. By contrast, a phase is usually concluded without reference to the ultimate purpose of all these activities. Even if, during the last provisioning visit, the entire

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*The Niko Tinbergen Lecture, 1975.

nest contents were experimentally removed, final closure still took place.

When activated by the inspection visit the wasp hunts for caterpillars and transports them towards the nest, each time opening the nest, drawing in the caterpillar and then again closing the nest entrance. The motivational state persists although the wasp from time to time interrupts its provisioning behaviour to feed itself or, during the night and when the weather is insufficiently favourable for these duties, to sleep outside the nest in the company of other wasps. Within the sequence of provisioning behaviour different subordinate states can be distinguished on the basis of differences in responsiveness towards the same external stimulus situation. For instance, when a caterpillar is placed by the experimenter over the open entrance of a nest at which the wasp is at work, she may either take it up and carry it away from the nest, *or* catch it, sting it and draw it into the nest, *or* she may also use it as a plug to close the nest entrance. Which activity occurs depends on the motivational state of the wasp at the moment, on whether it is occupied with digging, with hunting, or with closing the nest. Therefore, we must assume that during her work at the nest, different groups of activities become alternatively available to her. The inspection visit can be regarded as appetitive behaviour leading towards the release of one of the three main motivational states of nest care. Within each of these states appetitive behaviour of a 'lower' order in the hierarchy, e.g. for locating prey (hunting), for getting the prey to the nest, and for finding and testing clods to close the nest entrance, can be distinguished. Therefore, appetitive behaviour not only leads to consummatory acts or consummatory situations (Craig 1918; Lorenz 1937a, b; Holzapfel 1940) but may also lead to the activation of motivational states. The occurrence of appetitive behaviour prior to the release of 'instinctive activities' was one of the arguments given by Lorenz for a 'spontaneity' or 'inner urge' in the mechanism underlying such activities. Whether valid or not, the same reasoning could be applied to appetitive behaviour of a higher order. However, the recognition of different levels of appetitive behaviour led also to the alternative postulation that the causes for the occurrence of appetitive behaviour are not in the mechanism of the activity whose release they promote, but in a superimposed mechanism.

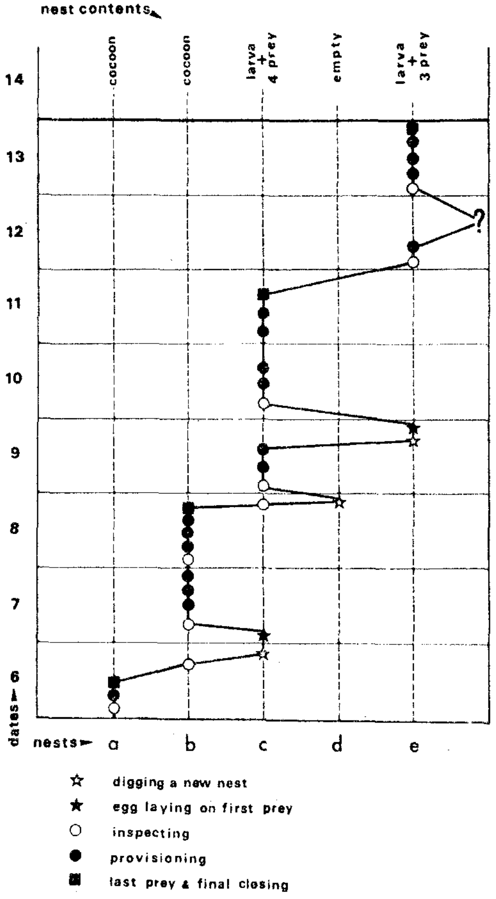

Fig. 1. Record of the provisioning behaviour of one individual digger wasp, *Ammophila adriaansei* in different nests (a to e) on consecutive days in August 1940. The heavy line connects the visits the wasp successively made; on August 12 the wasp visited a nest (?) outside the area kept under constant observation. When the nests were dug out on August 14, nest d proved to be unfinished; it probably had been started too late on August 8 to be remembered on the next day.

The relations between the different levels of organization in the reproductive behaviour of *Ammophila pubescens* have been represented in Fig. 2.

Summarizing, the experiments showed:

(1) that particular activities can only be released when the animal is in the appropriate motivational state;

(2) that motivational states of different levels exist; states of the same level inhibit one another, states of higher level control subordinate ones;

(3) that states of all levels become active through specific external and internal stimu-

lation, and probably also spontaneously; once aroused, they tend to persist for some time;

(4) that special appetitive behaviour often leads to the activation of a motivational state.

In the late thirties these phenomena were also found in other animals. Kortlandt (1940) described the occurrence of motivational states in the behaviour of the cormorant and considered interaction between such states as a cause for the appearance of displacement activities ('sparking-over' hypothesis). Tinbergen had recognized the importance of the concept of motivational states in the organization of the reproductive behaviour of the three-spined stickleback. He found that this behaviour only appears after the fish have been exposed for some time to increased daylength, and that the territorial behaviour of the males only takes place when they have found an area with green plants. Moreover, after territorial behaviour has started, the male stickleback passes successively through three phases: a first one mainly consisting of nesting behaviour in which the male shows little susceptibility to stimuli from a ripe female; a second one in which females intruding into the territory are enticed to spawn in the nest, and a third one in which the brood is taken care off, while females are chased away.

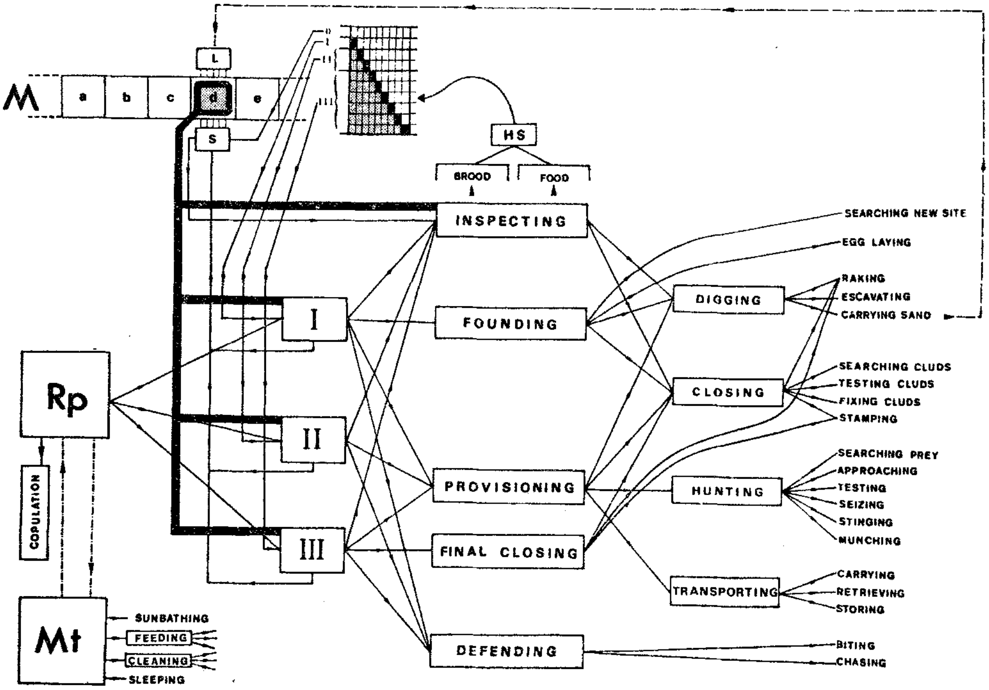

Fig. 2. Diagram of the hierarchical organization of provisioning behaviour in *Ammophila adriaansei*. The fixed action patterns used for the various aspects of provisioning behaviour (right column) are controlled by four sub-systems which are themselves under the control of sub-systems of higher order (central column). Of these sub-systems 'founding' is exclusively controlled by the system for phase I, 'final closing' by that of phase III; the other systems can be activated in each of the three phases. The phases themselves are controlled by a superimposed 'reproductive system' (Rp), which itself competes with a 'maintenance system' (Mt). Each phase begins with nest inspection; if during that visit a larva is found, its size and the amount of food still available determine via a heterogeneous summation unit (HS) which phase will occur, i.e. the amount of caterpillars to be brought in; the black blocks in the inserted grid represent the caterpillars stored during the three phases. If no larva is present (as well as when a phase is completed) a scanning mechanism (S) searches the memory (M) and focusses the attention of the wasp on the oldest yet uncompleted nest, which will then be inspected. If no such nest is available a new one is founded (phase I). In the memory (M), a to e represent the nests already existing; the situation of a new nest is learned (unit L) during digging. During a phase attention is focussed on one nest only (heavy bars). (Modified from Baerends 1941.)

Van Iersel (1953) measured the activity levels of the sexual and the parental system by quantifying the courtship zig-zag dance and the parental fanning behaviour, respectively, and showed that the transfer from the sexual to the parental phase is brought about by at least two factors: fertilization causing a decline of the sexual phase and carbon dioxide production of the eggs stimulating the parental phase (Figs 3 and 4).

After Niko Tinbergen had realized the theoretical importance of these findings, he used it as a basis for re-formulating in an objective way the idea of a hierarchy of instincts (Tinbergen 1942, 1950), which had earlier been expressed by, for instance, Freud (1915), Lloyd Morgan (1920) and McDougall (1923). And above all he showed how the principle of hierarchical organization of the interrelations between behavioural mechanisms could be used to explain the causation of interruptions of behaviour sequences by the occurrence of apparently irrelevant activities, as well as the evolution of a great many communicative activities in animals and man (Tinbergen 1952). It was especially this type of spectacular behaviour which turned birdwatchers into early ethologists. They began by enjoying these often fascinating ceremonies, then wondered about their biological significance, but now also began to understand how many of these communicative activities are derived in the course of evolution from behaviour elements with a direct instrumental function, and what factors could have led to their special form.

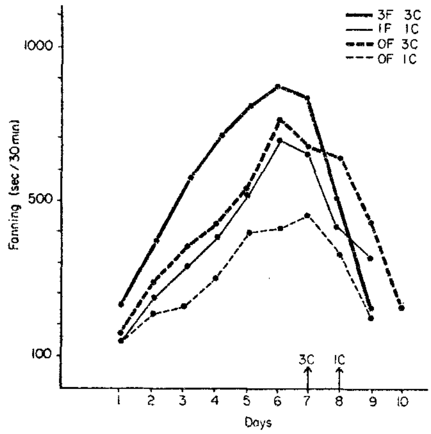

Fig. 3. The activation of the parental system on successive days of the parental cycle, measured as the number of seconds spent fanning during 30-min daily test periods. The number of times the male got an opportunity to fertilize (F) and the number of clutches (C) present in the nest were manipulated in the experiment, as indicated by the different types of lines. Day 1 is the day after fertilization, the arrow marks the average hatching day of the young (from Van Iersel 1953).

Tinbergen (1950) concluded that this hierarchical system of 'instincts' had to correspond to a hierarchical system of nervous 'centres', an opinion which was initially endorsed by Hinde (1953) on the basis of his work on the behaviour of the great tit. Hinde added to it the important remark that 'the behavioural organization of the whole animal must be pictured as a set of *closely interwoven* hierarchical systems' (p. 221). Later, however, he has repeatedly warned against a sloppy 'physiologizing' of ethological findings. His statement that 'satisfactory physiological confirmation of the higher levels of such a hierarchy of mechanisms is so far lacking' (Hinde 1970, p. 609) should be kept seriously in mind.

In 1950 Tinbergen found it too early to give a definition of what he, in the context of a hierarchical organization, had called 'an instinct'. He felt that such a definition should give: (a) the neurophysiological foundation, (b) the goal at which the instinct is directed, and (c) its dependence on internal and external factors. Moreover he was of the opinion that the innate

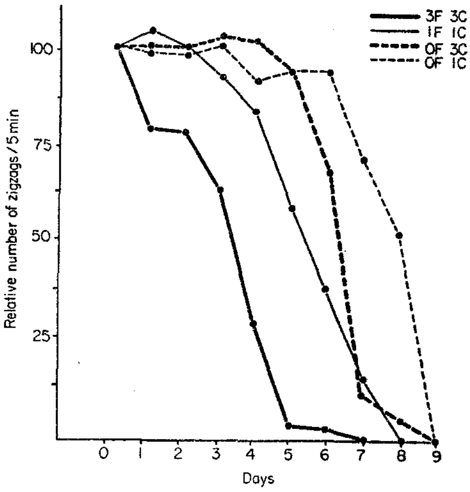

Fig. 4. The activation of the sexual system on successive days of the parental cycle, measured as number of zigzags per 5 min and expressed as per cent of the value on the day of fertilization. Symbols as in Fig. 3.

and self-differentiating character should be stressed. In the present paper I prefer to use the word 'system' because it probably has fewer ontogenetic, morphological or physiological implications than 'instinct', 'centre' or even 'mechanism'. I hope to get gradually closer to a definition of what should be meant by the term 'system'.

However, the fascinating possibilities offered by the concept of hierarchical organization have often led to the too easy assumption of the existence of systems underlying internal motivational states in an animal species. The painstaking work of properly consolidating the concept of behavioural systems and of developing methods to identify them with causal analysis (as the objective methods required) did not keep pace with the application of these ideas for understanding causes and evolution of communication behaviour. Too often the existence of such systems was taken for granted by implications of functions or survival value, as had been the main method of the earlier authors mentioned. The uncautious postulation of systems raised criticism (e.g. Lehrman 1953; Hinde 1956, 1959a; Brown & Hunsperger 1963), particularly among students with a more physiological interest in behaviour. Their critical attitude was probably strengthened by some equally uncautious speculations and generalizations about the underlying physiological mechanisms of the motivational systems, made in an attempt to bridge the gap between ethology and physiology and perhaps also to make the young discipline look more dignified. Because the critics had more knowledge of physiology they sometimes drew more far-reaching conclusions from the naïve statements than the ethologists probably ever meant. I personally feel that, as a consequence the critical discussion contained a considerable amount of fighting over straw men which threatened to throw the 'behavioural systems' baby away with the bath water. The main points of criticism were:

(1) that it is unjustified to expect behaviour systems to have, in a causal sense, a unitary and uniform character;

(2) that for the assumption of spontaneous activation of such systems (which was often considered to be one of their characteristics, e.g. Lorenz 1966) no conclusive evidence was available;

(3) that a one-way traffic of information, which the term hierarchy was assumed to suggest, is unlikely.

Before proceeding to the way in which I think we should look at the hierarchy hypothesis today I would like to comment on the validity of these criticisms.

Whether it is true or not that in the early postulation of systems these were meant to have a unitary and uniform character, at present we are fully aware that this is not the case. Although studies on the causal mechanism of systems or parts of them are still scarce, they show a great amount of variation in machinery. Spontaneity, i.e. changes in the output of a system without a corresponding change in input (Hinde 1970) has to be accepted in a number of cases, but should not be blindly assumed as essential for a system (Hinde 1956, 1959a).

The emphasis on one-way traffic actually originates from Lorenz's attempts to fight earlier vitalistically oriented statements of purposive psychology. He generalized from a single case, in which an instinctive activity (egg-retrieving) appeared to be only released and not directed by the external situation (Lorenz & Tinbergen 1938), to all other instinctive activities. Bastock, Morris & Moynihan (1953) were the first to question the general validity of this generalization, in a paper suggesting that the increase of re-settling, nest-building and preening in black-headed gulls after eggs had been taken away from their clutches, was caused by a discrepancy between the feedback stimulation received and that expected during incubation. We had made similar observations on herring gulls and, by using glass eggs as dummies deficient in visual but satisfactory in tactile aspects, we confirmed their hypothesis. Since then, an extensive study of the incubation behaviour of the herring gull (Baerends et al. 1970) has forced us to assume that the maintenance of incubation is controlled by a mechanism in which negative feedback plays a crucial role. Interruptions of incubation behaviour could be induced by experimentally causing (by removal or addition of eggs, increase or decrease of egg temperature) discrepancies between the feedback stimulation from the clutch and the optimal or expected values. As a result of such discrepancies incubation was suspended and behaviour occurred which was controlled by three different systems or sub-systems; appetitive behaviour tending to restore the situation on the nest (re-settling), nest-building behaviour and trimming behaviour. The latter behaviour patterns were always too incomplete and erratic to contribute effectively to nest construction or cleaning. To explain why these three types of patterns occur and what causes their relative frequency, it was found necessary to assume interactions between different behaviour systems, according to the model given in Fig. 5 (Baerends 1970). One of these, the incubation system, could be considered as a closed-loop control system, the negative feedback resulting from contact with the clutch. It has at its disposal a sub-system (settling) enabling the gull to restore a feedback stimulation which has become deficient.

Since behavioural systems distinguished on the basis of common causation are usually found to subserve a particular biological function, it is an attractive idea that such systems might always be characterized as circuits closed by a negative feedback loop. One might even consider a hierarchical system as a construction of negative feedback loops of a lower order of integration, enveloped by more complicated but similarly structured closed-loop control systems of higher order, several of which are again enclosed in some superimposed closed-loops. Kortlandt (1955, 1959) has advocated this idea, calling it 'concentric needs'. Miller, Galanter & Pribram (1960) came up, probably independently, with a similar proposition. Kortlandt pointed out that McDougall, in his theory of a hierarchy of instincts, when considering these instincts as purposive or goal-directed behaviour, had actually hinted at what we nowadays call a cybernetic system. He consequently concluded that the ethologists had been wrong in calling McDougall's hierarchy of instincts a functional and not a causal concept.

In only a few cases to date do we possess sufficient evidence to decide whether in a motivational system a feedback loop has to be postulated or not. The 'hunger' system is probably the best analysed example. Negative feedback loops had to be incorporated in the models for these systems as developed by Ruiter, Wiepkema and Veening (1974); Geertsema and Reddingius (1974); Wiepkema (1977) has also postulated a negative feedback loop in a model for aggressive behaviour. Kortlandt postulates negative feedback loops in 'concentric systems' of nest-building behaviour in cormorants. But in the nest-building behaviour of the herring gulls intensive control through feedback seems unlikely, while the research so far carried out on preening behaviour in gulls (Van Rhijn, in preparation), terns and mice (Van Iersel & Bol 1958; Fentress 1972) argues for, at the most, a very restricted negative feedback control.

It is interesting to mention here that to account for the maintenance of the state of a system, and for the 'warming up' phenomenon, positive feedback loops also have been assumed, in particular by Wiepkema in models for the 'hunger state' (Wiepkema 1971) as well as for aggressive behaviour (Wiepkema 1977).

However, as Hinde (e.g. Hinde 1958, 1970; Hinde & Stevenson-Hinde 1970) has repeatedly pointed out, the mechanism which brings a certain behaviour to an end may differ from case to case. I do not think we can maintain the idea, however attractive it might be, that systems can always be characterized as circuits closed by a negative feedback. However, the frequent occurrence of feedback loops certainly implies that we should not think of a hierarchy in terms of a uni-directional information flow. It might be more appropriate to speak of an organization of interconnected networks.

It has now become pertinent to ask whether it is really possible and useful to think in terms of systems of behavioural elements whose causal mechanisms have characteristics in common, when so much variety exists that no unitary causal definition of such systems can be given. Although such systems cannot be expected to have a uniform structure, and probably each system on its own makes use of the various kinds of building units available, my answer to this question is affirmative. For within the organization of behaviour, systems act as relatively independent units when the occurrence of behaviour in its full complexity is concerned.

Certainly the heterogeneous character of systems makes it difficult to recognize them in practice. Several methods are in use; they should be improved and increased in number. Moreover, it is advisable to use more than one method in combination. For a first approach statistical analysis of the distribution of elements in behaviour sequences will help to obtain a quantitative survey of the temporal or sequential relations between different behaviour elements. Methods like, for instance, cluster analysis (Van Hooff 1973; Everitt 1974) and factor analysis (Wiepkema 1961; Harman 1967; Balthazart 1971) are useful here. More recently the application of formal logical analysis, like syntactic structure analysis (Chomsky 1957; Marshall 1965) has given promising results. It should however, be borne in mind that such methods do not give more than surveys of types

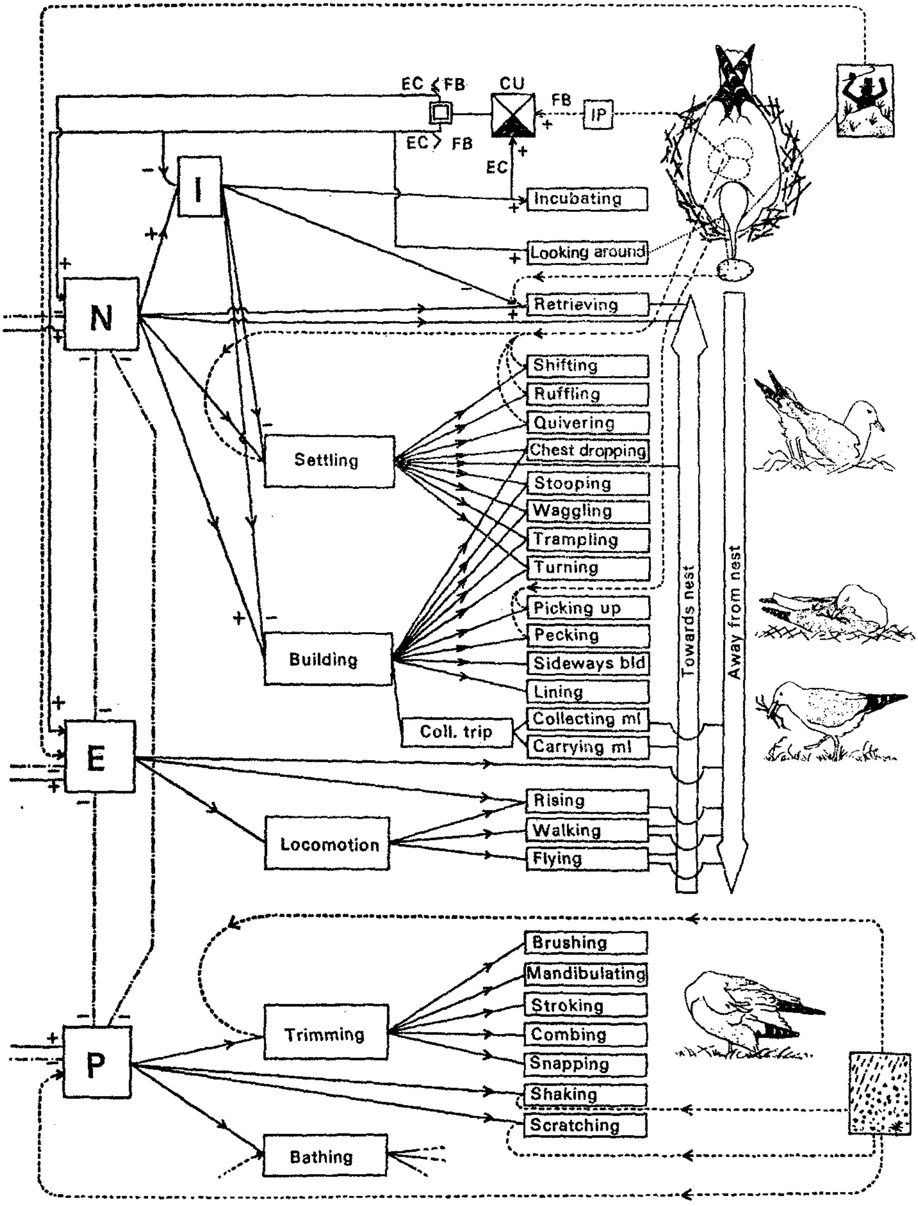

Fig. 5. Model for the explanation of the occurrence of interruptive behaviour during the incubation of a herring gull (after Baerends 1970). The fixed action patterns are in the right column and superimposed control systems of first and second order are represented left of them (N = incubation system, E = escape system, P = preening system). The large vertical arrows represent orientation components with regard to the nest. Incubating is the consummatory act. Feedback stimulation from the clutch, after being processed in IP, flows to a unit (CU) where it is compared with expectancy, an efference copy or corollary on the input for incubation. This input is fed through a unit (I), necessary to explain the inhibition of settling and building when feedback matches expectancy. The effect of feedback discrepancy on N (and I), E and P can be read from the arrows. The main systems mutually suppress one another; P is thought to occur as interruptive behaviour through disinhibition of N and E. P can be activated directly by external stimuli like dust, rain or parasites, E can also be stimulated by other disturbances than deficient feedback from the clutch.

of interrelations between elements. For instance, the factors found in factor analysis should not be identified with behavioural systems without further research They could just as well be the influence of external factors leading directly to the release of a number of different activities. The exact nature of the factors responsible for clustering has to be investigated with experiments designed to manipulate an entire system or sub-system. Another possibility is the monitoring of systems, i.e. a constant or regular measuring of their activity level (Baerends et al. 1970). If this is done by means of the frequency or duration of activities characteristic for a system, it will in general be necessary to use more than one activity, since, as again Hinde (1958, 1970) has pointed out, the correlation between different activities within a system, or even between different parameters of the same activity, is often relatively low. This fact in itself is not surprising, because different activities or parts of it usually have different functions and are thus differently adapted to the external situation. It shows again the complex and non-unitary character of the system. It is an important practical problem, but it is not a reason to reject the hypothesis of behavioural systems.

In animals which, like fishes, are able to change their colour pattern this feature may be used to monitor the activation level of systems (Baerends, Brouwer & Waterbolk 1955; Baldaccini 1973). However, this method too is not without complications, because the colours of these animals usually subserve not only the communication of motivation or motivational balance, but a cryptic function too.

Why is it, despite these doubts and difficulties, worthwhile to stick to the system concept? This is, in my opinion, because of the perspective offered by thinking in terms of systems for the study of complex behaviour. I will expand on five aspects of this.

1. Temporal and Individual Difference in Responsiveness

Differences in responsiveness of one individual at different times can be understood on the basis of variations in the balance between different motivational systems. For instance, in 817 tests an incubating herring gull was confronted with a pair of egg models of different size on the rim of its nest. It retrieved in 659 of these tests the largest one first, even if this model exceeded the normal egg size, but in a minority of 158 tests the smaller egg was consistently preferred (Baerends & Kruijt 1973). Such 'minority' choices were characterized by a relatively long latency of the bird in coming back to the nest, by a higher probability of interruptive behaviour, and by a relative high frequency of preening compared with building in that interruptive behaviour. All these effects could be interpreted as due to a shift of the motivational balance: as a relative increase in the tendency to escape, compared with the tendency to incubate.

In experiments on instrumental conditioning of males of the three-spined stickleback in which he used biting of a rod as an operant and either fighting or courting as a reward, Sevenster (1973) found that the readiness to learn this task depended on the type of reward. When rod-biting was rewarded with an opponent for fighting, learning took place much more quickly than when a gravid female was used to reinforce rod-biting.

Rowland (1975a, b) has successfully applied the idea of interaction between systems (i.e. between the tendencies to attack, to escape and to behave sexually) to interpret the temporal and individual variations in the occurrence of various types of dummy-elicited behaviour in the jewel-cichlid fish (*Hemichromis bimaculatus*). For instance, unpaired males predominantly responded to a red model (the nuptial coloration of the species) with the courtship activity quivering, as long as they stayed in their territory unpaired. However, after pairing with a female the reactions of the male shifted to predominantly biting (an aggressive activity negatively correlated with quivering). When red models of five different sizes were presented to the approximately 10-cm long males, the biting frequency showed an increase with dummy-size in two males, but a decrease in one male. In two other males an increase of biting at the smaller models of the size-series was followed by a decrease when larger models were presented. Decrease of biting went hand in hand with an increase of the activities fluttering and fin-rest, each of which is negatively correlated with biting as well as with quivering. The data clearly show that the individuals varied characteristically in the 'average' balance between the thresholds, or levels of activation, of different motivational systems. This holds despite the fact that the external situation can temporarily shift this balance considerably. In the usual procedure of pooling data from different animals, such differences will no longer be discernible; the resulting blurred picture may completely mask phenomena of great interest. Consequently, much is to be said for drawing conclusions from the behaviour of a single animal, and this is possible when its motivational balance is monitored. The development of appropriate methods for such a procedure will be essential for human ethology, where individuals must be understood no less than the average for the species.

2. Interactions Between Systems: Internal Conflicts

I have already mentioned that the occurrence of behaviour interrupting a sequence in a way which to the observer seems irrational, irrelevant or inappropriate, or at least unexpected, has been an important incentive for postulating the hierarchy hypothesis and for sticking to it. It has led to the acknowledgment of the behavioural phenomena of ambivalence, redirection and displacement (Tinbergen 1952) and it has given insight into the evolution of signal activities and probably also of other types of behaviour (Baerends 1975). The notion of conflicts between systems also has implications for abnormal behaviour, particularly of the neurotic type. Such behaviour often reminds us of behaviour caused by ambivalence redirection or displacement. Gulls staying for longer periods on clutches which could not produce the expected feedback stimulation often appeared neurotic to the observer. Consequently it seems to me of heuristic value to raise the question whether it would be possible to understand cases of neurosis in man as the result of discrepancies between the feedbacks expected and received and the ensuing conflicts between systems. A model given in Fig. 6, in fact a generalization of the model of the functional organization of incubation behaviour (Fig. 5) was tentatively suggested for this purpose (Baerends 1976). A multitude of symptoms is called neurotic, and clinical observations indicate that various causes can lead to them. The model can explain how, all through deficiency of feedback, different failures in the causal mechanism (e.g. in the appetitive behaviour, in the consummatory response, in the feedback from the consummatory situation, in the comparison with expectation or in the value of the expectation itself) may lead to a number of different effects (stimulation of appetitive behaviour, inhibition of the activated system, activation of systems for escape and for attack, conflicts between these systems, displacement phenomena). When applying this model to human behaviour it is particularly important to recognize that the expected value with which the feedback is compared may result from learning processes and that these may be incorporated in a, relatively more or less open (Mayr 1974), genetical program.

A considerable amount of evidence indicates that the average threshold of a system (and consequently also the probability of conflicts between this system and other systems) may differ consistently between individuals during periods varying from a few hours to the entire life span. This difference may be genetically caused, but can also be the result of (possibly genetically programmed) acquisition of experience during ontogeny. The relatively large variety of activities so far shown to be involved in such differences indicates that they concern systems of rather high order.

3. The ontogeny of Complex Motor Patterns

Kruijt (1964) has shown in the jungle fowl that the influence of the systems controlling flight, aggression and sex appear at different times in the course of the development of the individual. First, the chicks show fleeing only in response to various kinds of relatively strong stimulation. After about two weeks it can be demonstrated that the direction of fleeing is no longer random, but that the chicks actively go for one another, so that clashes result. Out of this early behaviour fighting gradually develops, and, correspondingly, indications of conflict between the tendencies to attack and to flee are increasingly shown. When after the fourth week sexual elements begin to appear, this new component seems to exert a stabilizing influence on the tendency to attack and the tendency to flee, as a result of which the behaviour of the chicks becomes more harmonious. Deprivation experiments (Kruijt 1971) showed that for normal development the presence of conspecifics is necessary. Cocks isolated during the early months of life showed irreversibly abnormal social and sexual behaviour when brought back into the flock; the degree of abnormality depended on the duration and age of isolation. Apart from difficulties in orientation with respect to the opponent or partner, their behaviour was disturbed in particular by irregular bursts of strong attack or fleeing behaviour. Although the cock is able to perform the motor activity of copulation, it is not able to adjust itself motivationally in such a way that it can apply this motor pattern to a suitable female. The abnormal social, sexual and parental behaviour in some of Harlow's (Harlow, Harlow & Hansen 1963; Harlow 1969) experimental rhesus monkeys can probably also be partially explained as a result of a failure to keep the tendency to attack and to flee in balance, due to deficits of experience during ontogeny.

4. The 'Planning' of Behaviour

A functional organization of hierarchically organized behavioural systems is a method

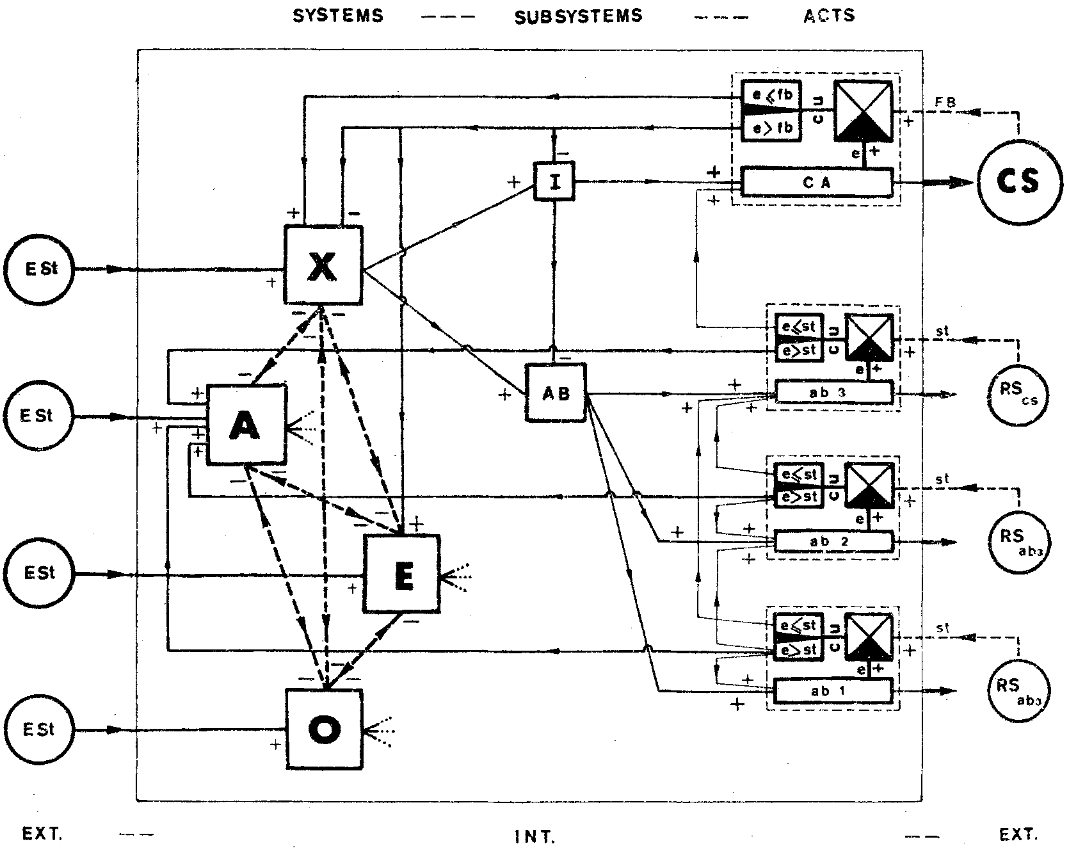

Fig. 6. Model, generalized from Fig. 5, for the occurrence of neurotic behaviour. When system X is activated appetitive behaviour (AB) occurs first. This behaviour is postulated to encompass three different activities (ab_1, ab_2, ab_3) of which only ab_3 leads to the releasing situation (RS_{cs}) triggering the consummatory act (CA) of system X. The appetitive activity ab_3 is triggered when the releasing situation $RS_{ab}3$ appears and this can be brought about by ab_1, as well as by ab_2. Therefore, ab_1 and ab_2 are alternative possibilities for the release of ab_3, which itself is obligatory for the occurrence of CA. The result of each appetitive behaviour (RS) is checked in a comparison unit (CU) specific for each act. If the expectancy (e) against which the received stimulus (St) is checked is found to be deficient the act can be repeated or the alternative act can be tried. Failure of an appetitive act is in addition postulated to stimulate the system for attack (A). (The relations between the various appetitive acts, the sub-system AB and system X are undoubtedly much more complicated and likely to vary from case to case; however, any attempt to account for this would make the model unnecessarily complicated for the present purpose.)

The appetitive behaviour is inhibited by sub-system (I) as long as the consummatory situation resulting from CA is satisfactory. A comparison unit checks the feedback input from CS with a specific expectancy. A feedback discrepancy acts negatively on I and X and stimulates the system for escape (E). (O) stands for any other system which can become overtly active through disinhibition if mutual inhibition of two or more different systems occurs. The level of the system A, E, X and O is thought to be influenced by internal and external (E St) stimulation. (After Baerends 1976.)

through which behaviour can have adaptive plasticity without loss of control. One might say that the activation of high level systems determines a strategy, which is usually maintained the longer, the higher the order of the system. Which sub-system is activated during this period and which activity is released depends on the tactics possible within the system (Miller, Galanter & Pribram 1960; Pattee 1973; Powers 1973; Dawkins 1976). Chomsky (1957) has recognized such a hierarchical principle as the basic framework upon which the use of language depends. He argues that the same system applies for all languages and can also account for the amount of creativity in their usage. This illustrates how variation and plasticity is possible on the basis of a functional organization: an architectural scheme which is ultimately controlled by the genes, which are the basis of the species-specific behavioural organization and the causes of interspecies differences.

The planning possibilities can be influenced by changes in the course of evolution. A change in one part of the functional organization may lead, through the interaction of systems, to a variety of behaviour differences. In this way it is conceivable that relatively small genetic changes may cause considerable behavioural differences. This is likely to be of great importance in the speciation of animals. For example, if ecological factors select for a relative low threshold for fleeing, the resulting shift of motivational balance is also likely to affect communication behaviour, and this will promote ethological isolation of the new form (e.g. Hinde 1959b; Baerends & Blokzijl 1963). Differences in the behaviour of the sexes can similarly be manipulated by shifts in the motivational balance primarily adapted to ecological factors.

I have already stated that the knowledge of behavioural organizations so far obtained from causal analysis is still unsatisfactory. This makes it all the more striking that in so many studies of the phylogeny of communication behaviour in animals of different taxonomic groups, it has been found helpful to assume systems for, for instance, aggressive, escape, sexual and parental behaviour. It is possible that systems have developed convergently in widely different groups because it is more economical and efficient when functionally related activities depend on the same causal factors (Dawkins 1976). It may also be for this reason that striking correspondences occur between the control of preening in gulls (Van Rhijn, in preparation) and grooming in mice (Fentress 1972). But I am of the opinion that we should also entertain the possibility that several behaviour systems may be phylogenetically old, older than species, families or even phyla. For morphological structures like the skull, the muscles and the heart in vertebrates and even the neurons in animals from vertebrates to jellyfishes, as well as for the physiological mechanisms which make them work, a long phylogenetic history is generally accepted among biologists. With regard to behaviour, however, the idea that parts of the functional organization of the behaviour of an animal might be tens of millions of years old is hardly ever entertained.

As part of a programme to develop animal models of depression Bouhuys (1976) has made a detailed study of the behaviour of rats with lesions in the serotonergic raphe system of the brain, in comparison with sham-operated controls, in situations favouring separately exploratory, agonistic and sexual behaviour. The main significant difference found was an increase in locomotion activity in the raphe-lesioned rats. Analysis of the frequency, duration and sequence of activities performed showed that this increase could not be attributed to a change in the amount of locomotion subserving sexual or agonistic behaviour, but was probably due to locomotion not related to social behaviour. The data suggest to me that the operation had changed the capacity of the animals to enter a motivational system, i.e. to 'plan' its behaviour.

5. Paving the Way for Physiological Research

Finally, for an understanding of the machinery of behaviour as far down as the physiological and even molecular levels, I consider the analysis of the functional organization of behaviour as important as the study by physiological methods of the nervous and endocrine mechanisms. Through system analysis of complex behaviour we shall gain insight into the software underlying the programs which the physiological machinery can achieve. The hierarchy-hypothesis and its derivatives should be seen as steps on this way, always open to improvement. The 'systems' and 'sub-systems' postulated after analysis of complex behaviour sequences can best be defined as control-systems of different orders fulfilling special tasks or sub-tasks in the context of the hierarchical organization. What aspects of behaviour (motoric and sensoric) they control and in which way, and what kind of physiological mechanisms are involved, is likely to be different for each system. These are the kind of problems for the solution of which ethologists and physiologists should meet and work together.

With this fragmentary presentation of the history of the hierarchy-hypothesis and of its possible usages for understanding the behaviour of species and of individuals, I have tried to stress the importance of one of Niko Tinbergen's main contributions to ethology. The best way we can give further tribute to this stimulating pioneer work is to develop and modify it further, with an always critical, but positive attitude.

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