

Konrad Lorenz 1955

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Morphology and behavior patterns in closely allied species

Some years ago Max-Planck (1) wrote a paper called *The Naive and Scientific Picture of the World*, the gist of which was that there was no difference between the two. He started from observations on babies, saying that babies, relying on the functioning of their Gestalt perception, started labeling perceptions. Gestalt perception has the interesting way of doing something intrinsically similar to abstraction by picking up out of a background of irrelevant, accidental data, certain relevant stimuli and putting them together into a whole relevant meaning.

When a child starts talking, he gives a name to everything. The scientific man, calling species by names, does the same. It is not predictable what levels of integration will be chosen as "natural" units. I know the case of a child who made his parents quite desperate because he seemed so stupid. He said "bow-wow" not only to dogs, as was expected of him, but also to cats and rabbits, to horses and so forth. Subsequent trials with different animals showed that "bow-wow" meant *mammal* to him, and it meant quite precisely *mammal*; it did not matter whether it was large or small, but the class was clearly distinguished from all other animals. That is what Gestalt perception does.

Of course, Gestalt perception depends largely on what material is offered to it; there are certain Gestalts which are difficult to see and which will not stand out from the background unless they are presented in a very particular manner. This, incidentally, concerns one of the differences between the methods of approach in American experimental psychology and in ethology. The pioneers of ethology, Charles Whitman (2) and Oskar Heinroth (3), were zoologists who did not know much about psychology. Whitman knew some, but Heinroth definitely did not know or even care about psychology. Indeed, Heinroth

had a deplorably low opinion of psychology and philosophy in general, which had a regrettable influence on the terms he coined, as he did not care in the least whether they coincided or overlapped with psychological terms.

However, what these two men did was to look at the behavior of one species after another. What happens in such a case is roughly this: If you look at one species alone, or only at species that are distantly related to each other, you see certain regularities in their behavior, but you have little or no indication to make you suspect that these behavior patterns have a common phylogeny. If, however, you observe many closely related species simultaneously, their common behavior traits will suddenly become apparent to you amidst all the nonessential, accidental data, in the way Gestalt perceptions do. So you see, there *is* really no other way of seeing unlearned species-predictable motor patterns, than by looking thoroughly at many closely allied species simultaneously. That is why people who have never done so, hardly believe in the existence of such motor patterns.

What I am going to discuss now, will be mainly a kind of morphology of these behavior patterns which, for lack of a better term, I propose to go on calling instinctive movements. I called them "inherited coordinations" earlier in my life, but I fully realize the justification of the geneticists' objection to this term. I am also quite aware, and always was, of the implications that experimental embryology has for the ontogeny of instinctive movements, exactly in the way which Dr. Beach has just expounded to us.

As a morphologist, I dare to assert that a provisional labeling is a necessity which we cannot do without. Like the baby giving names to things, we rely, at first, on our Gestalt perception, feeling that it *is* a natural unit, and we attach such a label to it. With sufficient observational basis, this method has never led anybody astray. Like anatomists, we respect the priority of a label given by someone else, yet, as in systematic zoology, it often happens that we discover that there are double, synonymous labels; Frank McKinney and I just found a very misleading example of this when we met recently in Madison, Wisconsin.

The natural unit of innate motor co-ordinations was paradoxically discovered by men who were looking for something entirely different. Charles Whitman was investigating, in detail, the phylogeny of pigeons and Heinroth was doing the same work with Anatidae. I lack the time here to show, in detail, how the task of determining the closer or more distant blood-relationship between two species is directly dependent on the *number* of comparable, homologous characters found and used.

But I must say a few words about the concept of homology. The term homologous, as applied to characters in comparative morphology, means simply "inherited from a common ancestor." If a man, a mole, a bat, and a whale, have a skeleton in which the forelimb, in spite of tremendous differences in function, consists of a humerus, a radius and an ulna, a set of carpal and metacarpal bones and a corresponding number of digits, this very complicated conformity is, and can only be, explained by the assumption that these characters are, in all four creatures mentioned, inherited from a mutual ancestor that possessed them. As to the term "inherited," may I make this clear: In spite of the fact that nothing whatsoever is known about the genetics of the process, we nevertheless know that the pattern of our skull bones has been transmitted to us from the coelacanth fishes which first evolved it, and that the pattern of our limb skeleton has been transmitted to us, as a *pattern*, from the stegocephalians of the carboniferous era. However the genetic process of this transmittance has taken place and however great the role of epigenetic factors in the individuation of these characters, we know that they are transmitted as *whole patterns*. The only alternative assumption would be that the conformity in different groups of animals is pure chance, which, of course, is nonsense.

While Whitman and Heinroth were looking for more and more comparable characteristics, in order to give their reconstruction of the phyletic process more and more accuracy, they accidentally hit upon a whole set of such characteristics that had been, hitherto, quite unexploited by phylogeneticists. They discovered that there are motor patterns which vary from species to species, from genus to genus, and even between the largest systematic group categories, and vary exactly the way that morphological characteristics do. In other words, there are behavior patterns, whose geological age is obviously as great as that of the most conservative body characteristics. These behavior patterns are in the same sense constitutive properties of a species, a genus, an order, or a class as are the structure and form of bones or any other organs. The comparative method, to which we owe all or most of our knowledge concerning the evolutionary history of living creatures, is just as applicable to these behavior patterns as to any organs.

As is to be expected, the evolution of motor patterns and of organs often proves to have run parallel and in strict correlation. Good examples of this can be found in the courtship movements and feather structures of many birds, for instance, in the highly ritualized "sham-preening" of many Anatidae. In surface-feeding ducks there is a correlation between a certain preening movement and the development of secondary and tertiary feathers. The drake moves its bill over the

inside of a slightly raised wing, thus causing the brilliantly colored secondaries and tertiaries to vibrate and to emit striking light reflexes. The movement is concentrated mainly in the brightest parts of the wing. In the American wood duck and in its Asiatic cousin, the mandarin, the preening is transformed into a highly ritualized motor pattern whose origin we should hardly recognize if we did not know the intermediate stages of differentiation in other ducks. In both of the species, the movement of the bill is directed at one particular tertiary feather which is made to wriggle in a peculiarly striking manner. In the mandarin, this is the beautiful, huge, fan-shaped last tertiary. In the wood duck, the homologous movement and structure are even more elaborate. In this species, it is the next to the last tertiary which is brightly colored and is moved in the act of ritualized preening. This feather, which has a bright brassy sheen, is normally hidden under the last tertiary which is broad and of a sooty black color. The drake puts his bill behind the wing and causes the brass feather to pop out from behind its black diaphragm for only a fraction of a second, emitting one single, surprising flash, invariably aimed in the direction of a female.

This is only one example, but I can assure you that I could easily cite many others. In very many of these it can be shown that a movement has a slightly wider distribution and an indubitably greater phyletic age than the structures correlated to it. The general assumption of comparative morphology, that the more widely distributed characters are the older ones, certainly holds true here. The correlation between movements and feather structure can be shown, in many cases, to be nonepigenetic; in other words, structure and movement, closely as they may be correlated in one function, are *transmitted independently* from each other. Jean Delacour had a mandarin drake which, for some reason, never grew the fan feather but persisted in performing the ritualized preening movement in the air, an inch above his back where the feather "should" have been.

I think the statement that these movements are transmitted as patterns and are of great geological age is no longer a matter of controversy. What is more controversial are some of their properties, which we may sweepingly call physiological properties. Neither Whitman nor Heinroth ever offered any theory concerning the physiological nature of the newly discovered type of movements. Whitman simply called them "instincts," whereas Heinroth called them "species-proper drive activities." As you see, Heinroth thus avoided, with the fine intuition of the good taxonomist, implying any genetical hypothesis in the term he chose. It was only Whitman's great pupil, Wallace Craig (4), who

began to approach the physiological analysis of instinctive movements.

I must add that Heinroth's concept of species-proper drive activities, as well as Whitman's and Craig's concept of "instinct," is much broader and more loosely defined than our concept of instinctive movements. Both concepts comprised orientation responses and Wallace Craig even regarded the whole sequence of appetitive behavior as a "constituent" of instinct, though he very clearly developed the concept of the "con-summatory act," which alone is equivalent to our notion of the instinctive movement.

Yet, in their considerations of taxonomic interrelations of species, Heinroth as well as Whitman used chiefly or exclusively true and pure instinctive movements as the dependable characteristics on whose comparison they based their phylogenetic conclusions. Courtship movements particularly were chosen for this purpose, and with very good reason: Less than most other instinctive motor patterns they are overlaid by spatially adaptive orientation responses. All that sometimes happens is that a bird first orients its whole body into a certain spatial relation to the female, but when it "releases," all the succeeding behavior is practically pure instinctive movement. My duck film illustrates this. Thus, in the courtship movements, an important source of error can be excluded which, in other cases, would hamper our study of instinctive motor patterns.

Mayr: I would say the second reason is that, these movements, more than any others, are specifically selected for species differences.

Lorenz: Yes, exactly; I am coming to that very soon. The reason you mention also explains why we find, in courtship movements, the most convincing series of differentiation of a single, homologous movement in closely allied species. As one of the courtship movements' functions is to prevent hybridization in exactly the same way that Charles Sibley (5) has shown for nuptial plumage patterns, they are, so to say, made to make the taxonomic relations between species clear, even to the females of these species. They are species-characteristic in the extreme!

In their use of pure instinctive motor patterns as taxonomic characteristics, Whitman and Heinroth emphasized, without really intending to do so, one particular property of these movements, their extreme lack of modifiability. The very "rigidity" of instinctive movements is one reason why, at an early stage of my endeavors to understand animal behavior, I concentrated my attention on them: It is always a sound plan to start the investigation of a system by ascertaining and studying its least variable parts first. In the intricate interaction within the whole, it is necessarily the least variable part that appears most frequently as a cause and least frequently as an effect. For no other reason,

you will find that anatomy, in teaching as well as in research, invariably begins with the skeleton of the organism being studied.

I think that theorists on learning, particularly Prof. Hebb (6) in his criticism of Dr. Tinbergen's work and mine, have not quite realized the extent of this rigidity. Of course, it is formally quite correct, if Hebb states that species-predictable behavior depends not only on invariable heredity alone, but also on an environment equally invariable in most or all important matters. There is always an environment, as Jean Piaget said at the last WHO meeting, which many of those now present attended. The difference of opinion between Prof. Hebb and us is merely quantitative and concerns what you happen to regard as the "important matters" in the organism's environment.

I think that most unprejudiced people, having read these statements of Hebb, would be surprised to hear that for the performance of a weaverbird's very complicated weaving movements, the plant fibers which are attached to a twig in the process of nest-building by these very same motor patterns, are definitely not an "important matter" in the bird's environment; he performs the same movements, in photographically identical co-ordinations with or without their functional object. The performance is dependent on a lot of environmental factors. If you want to keep a weaverbird in order to see these movements, you must be a pretty experienced bird-keeper in order to procure for the bird all the environmental "important matters," e.g., food, vitamins, housing of the right kind, enough light and warmth and not too much, and so on. Your bird will not weave at all, unless he is in very good condition and it is not at all easy to keep him so. But, provided the inner conditions of the bird are all right, the instinctive movement in question will go on with or without the adequate object, which, in my opinion, clearly shows that no stimulation emanating from the object influences the co-ordination of the movement.

Still more surprising is the analogous phenomenon in cases where a part of the animal's own body is the functional object of an instinctive movement. I have already mentioned Delacour's old mandarin preening the nonexistent fan feather. Similarly Heinz (7), a pupil of Prof. W. Jacobs (8) in Munich, found that in many flies a *whole* wing was not an "important matter" in the organism's environment for the performance of wing-preening movements. In insects whose wings had been amputated immediately after emergence from the chrysalis, the wing-preening movements persisted, exactly as they do in wingless mutants of *Drosophila*. Particularly interesting are Heinz's experiments of substituting a bit of tissue paper for the eliminated wing, by sticking it onto the fly's thorax where the wing would

ordinarily be, or even in a slightly different place. He found that he could make the fly perform the movement about half a millimeter higher or lower than the natural position of the wing would have been. If no substitute wing was attached, the movement went on in the middle, in the normal position of the wing.

Moore: Does it move the wing? Can you train it to do so?

Lorenz: No; the leg movement simply persists in its original place. Heinz could not deflect its direction. There simply is no taxic component, no orienting influence exerted by proprioceptor or exteroceptor stimulation emanating from the wing itself.

We can show many other cases in which instinctive movements prove highly independent of factors which, one might naively assume, must be perceived either by proprioception or exteroception. Even in cases in which proprioception is certainly known to exist, this independence remains. Consider the weaverbird whose behavior I have already described. He is certainly in a position to "know" whether he has a strand of grass in his bill or not, and will try hard to get one if he wants to perform nest-building movements. But if he fails to get one, he performs the movements "*in vacuo*," and their co-ordination will be the same. A bird reared in isolation, never having so much as seen a blade of grass, will also do the same. A psychiatrist watching a bird do this would be likely to think that the bird is suffering from an hallucination of a blade of grass, which, of course, would be highly unscientific because we cannot "introspect" into a bird.

Liddell: The experience of the phantom limb seems to have nothing to do with conditioning. Is it not related to the matter you are discussing ?

Lorenz: It may well be. No, on second thought, I do not think so. The phantom limb certainly arises from misinterpreted stimulation emanating from proprioceptive nerve stumps. On the other hand, I think that the phenomena I have been discussing are the very opposite: they are highly independent from afferent control in general and proprioception in particular.

I have said that it is not at all easy to keep an animal in a state of bodily health sufficiently good to make it perform all the motor patterns characteristic of its species. The inadequate environment of captivity may cause the disappearance, to be more exact the nonappearance, of many instinctive movements, or it may, with more subtle damage caused by the unnatural environment, cause some instinctive motor patterns to work at less than normal intensity, even cause them to fail in performing their function. But you never see a *qualitative* change of instinctive movements. If you keep a mallard drake on very

poor food in too small a pen, he does not get into breeding condition and you will not see more than a few half-suppressed hints of his courtship movements. But those you do see are identical with low-intensity movements to be observed in a normal drake. The only difference is that your experimental animal simply lacks some of the high-intensity motor patterns. You will find, in that experiment, that you have wrought many more changes in bodily characteristics of the bird than in its instinctive movements: It may turn dull brown instead of showing the beautiful colors of its normal nuptial plumage; it may become small or hunchbacked, and so forth.

In theory, it might be possible to rear a mallard so rickety that it develops a strong scoliosis of the neck vertebrae, so that this unhappy bird would perform the "grunt-whistle" (and other motor patterns that are normally performed in a vertical plane) in a crooked manner. But we have, hitherto, not the slightest indication that it is possible to change the form and co-ordination of an instinctive movement, even through the most massive environmental influences.

I would like to emphasize that this very remarkable rigidity is to be found exclusively in such motor patterns as show the typical distribution in the zoological system and the geological age of which I have spoken before. These two properties always coincide.

From the physiological point of view this rigidity is not so very surprising after all as we know that the central nervous system tissue is the least modifiable and least regenerative of all tissues.

Fremont-Smith: Is there also selection pressure that protects these movements from environmental change?

Lorenz: Selection pressure does not protect it from environmental change; it protects it from phylogenetical change. Selection pressure is forever narrowing down the breadth of variation.

Fremont-Smith: Doesn't it take advantage of environment?

Mayr: I think I would like to disagree here. It is quite possible that selection pressure can affect the amount of phenotypic variability of any organism; in fact there is good evidence for it. If such motor patterns serve as intraspecies signals, there will be high selection pressure for reduced variability, because standardization is of high selective value. For instance, let us say a male performs the wrong signal; he will simply not get a female and will not leave any offspring, or at least the probability that he will have a female and offspring will be very much lower.

Lorenz: Quite right. I did not see that for the moment. It is quite a convincing point.

I would like to add at this point that, of course, the existence of an

IRM which is susceptible to a supernormal stimulus or object may exert superlatively strong selection pressure in one direction all the time. That is exactly how such very bizarre differentiations, like the plumage of birds of paradise, the peacock's tail, or the secondaries of the argus pheasant, have originated. They have a high negative survival value for the species as a whole. Intraspecific selection, such as the competition of the males to be chosen by a female, often effects evolutionary changes which are definitely unadaptive as concerns the interaction of the species with its environment. Heinroth always said that the wing feathers of the argus pheasant and the hustle of modern man were the best examples of how bad and unadaptive characteristics could be brought about by intraspecific selection. It is a crude but wonderfully apt way of putting it.

But let me resume: All these motor patterns which show *a*) organlike distribution within the zoological system and *b*) extremely small modifiability, also show a third property which is at least as important and characteristic as the first two mentioned. I would like to pay tribute, at this point, to Wallace Craig who was the first to realize the inferences of this property. He (4) sent me his classical paper *Appetites and Aversions as Constituents of Instincts* at a time when I was biased by my grudge-fight against vitalism and still persisted in the theory that all instinctive movements must be chain reflexes. I did not yet know Erich von Holst's work (9, 10, 11) either. In Craig's paper, I read a simple statement that struck at the foundations of the reflex theory — that it is obviously nonsense to speak of a reaction to a stimulus not yet received. It was Wallace Craig who showed clearly that the instinctive movement, the as yet unused activity, is a source of stimulation in itself and causes, in the animal, a general kind of motor excitation which, in turn, increases the likelihood that the organism will meet the adequate stimulation eliciting the movement in question. In its simplest form, this excitation produces only random movements; in its more highly differentiated forms it results in appetitive behavior, including conditioning and the learning of ways and means to find the stimulus situation in which the consummatory act can be released.

Tinbergen: May I interrupt? I think that formulation you used just now ("the unused activity, is a source of stimulation in itself" etc.) should be worded differently.

Lorenz: Some source of stimulation ?

Tinbergen: I mean that this formulation may give rise to misunderstanding. Ought we not to be more precise in asking what makes the animal show appetitive behavior, and what makes it change over to the next movement in the series? What you really mean, I believe, is

that something which ceases to exert its influence as soon as the end act has been released, makes the animal show appetitive behavior and makes it go on showing it until a new or proper stimulus impinges. Then the appetitive behavior comes to an end, and the next appropriate movement appears. I think it is confusing to express this by saying that the end activity acts as a source of stimulation to behavior prior to its appearance.

Lorenz: I was actually quoting Wallace Craig who meant exactly what Dr. Tinbergen has just expressed.

Beach: May I interject very briefly that this same concept bothered Lashley in his article called *Experimental Analysis of Instinctive Behavior* (12)? He refers to this as "reaction to a deficit."

Lorenz: The point I would like to make is that these movement patterns have no influence at all, although they behave in their rhythmical reappearance exactly like reactions to tissue needs.

Lehrman: I think we are confusing two things in the formulation of what Wallace Craig (13) meant. You cannot have a reaction to a stimulus which is not yet there. Of course, that is true. When there is no external stimulation causing an action, you say it is not a reflex in the sense of a response to an external stimulus. That is one point you are making. But you are also making a point that something inside the animal is *urging* it to act, and this is not due to or through a response.

Lorenz: It is a *physiological impulse within* the animal which is the motor factor.

Lehrman: Yes, but that also implies something more. One should be careful not to state the very true proposition in such a way as to imply that one has also demonstrated the other thesis: that there is no relationship between the central nervous system and the periphery, within the animal. That is, when you speak of a chain reflex or when you speak of a stimulus being applied to the motor, it is true the stimulus does not come from outside the animal. It could come from inside the animal, although not necessarily inside the central nervous system.

Lorenz: We know it does in very many cases.

Fremont-Smith: We are a little inclined to say the animal is urged to behave, and that this urge is not dependent upon an external environmental stimulus. But we do not add the phrase: *at that moment*, and I think it is very important to bring out the time factor, probably a time lag or elapse of time, and the fact that there have been external-internal environmental interactions in the past of the organism which made it possible for the animal to have this urging. Therefore, if one takes into consideration the time-binding concept, it is entirely appropriate to seek in the past history of the animal the internal-external environmental

interaction which leads through growth to the particular urging at this time. That, it seems to me, might be a way out of our dilemma, since it would not put us in the position of saying that any action takes place independently of external environment. It simply implies that an external environmental influence may have existed, and probably did exist, sometime in earlier history.

Lorenz: Yes.

Fremont-Smith: Maybe this is too obvious to be important.

Lorenz: It may even be very important. But I think you would have to go into the phyletic history of the species to explain the things I mean now. I think I had better proceed to examples in order to make myself clear. We have many cases in which an instinctive movement, or a set of activities in which instinctive movements predominate, is performed with a very high intensity the first time it occurs in the animal's life. Later on, even after a pause of many months, that activity never reaches more than about 60 percent of the intensity it had the first time. Robert Hinde (14, 15) has investigated this "fading" or "waning" in detail, in the mobbing response of the chaffinch. This waning phenomenon troubles us enormously.

On the other hand, we have instinctive activities which rise in intensity with repetition, though of course, with pauses of recuperation between performances. And we know some few cases, in which a true atrophy can be brought about by very long inactivity. We have a confusing interplay of multiple factors. But there is no case in which the spontaneous endogenous generation of readiness to perform a given instinctive motor pattern does not play its part. You can go about the investigation of this spontaneous increase of internal readiness in two ways. Even before I knew the work of Wallace Craig, I had found that the threshold of stimulation eliciting an instinctive movement underwent regular fluctuation. When I discovered that any instinctive movement was easier to elicit, the longer it had not been elicited, I interpreted this phenomenon simply as a lowering of the threshold.

You see, I was still thinking in terms of reflexes at that time. I found that a cichlid or a Betta kept in isolation would react to a rival with much more intensity and would accept, after a still longer spell of solitary confinement, even very inadequate plasticine dummies and fight them as if they were rival conspecifics. If I wanted a fish to react to a dummy, I simply isolated it until it would. Even earlier, in trying to breed hybrids, I used the isolation device to make the animal react to the proposed inadequate partner. As a boy in high school, I knew that it was difficult to mate old male cichlids that had lived in isolation for a time, because they would fight the female as though she were another

male, and even then I had discovered the trick of letting such an old fighter "lower his threshold" by making him fight his own mirror image until he was exhausted. After this, he would be ready to court a female instead of killing her. It was in the search of a technique for breeding cichlids, not in a search for knowledge as such, that I discovered these phenomena, and I still clung to the chain reflex theory at that time. Therefore no one can accuse me of having had a preconceived theory which directed and biased my experiments.

I must now proceed to expound an important complication in the motor co-ordination of an "instinctive movement," which I have not yet mentioned, for the sake of clarity. If, for example, I have spoken of "fighting" in cichlids, as if this were just a single motor co-ordination, I must now hasten to explain that "fighting" is really what we call a "set" of motor patterns, correlated to each other in a most peculiar way. In the normal course of the entire performance of such a function, the single patterns belonging to such a set follow upon each other in a definite temporal sequence. A cichlid fish, confronted with a rival, 1) first assumes nuptial coloration, 2) then raises the vertical fins, 3) then stands parallel to the antagonist, 4) then depresses the gill membrane, 5) then gives what we call the tailwhip, 6) then performs a short frontal threat display, and then 7) rams the rival.

There is no law that the sequence must be performed in its entirety. The opposite of an all-or-nothing law holds true of most instinctive movements, and the series may fade out or break off at any given point. But we can state a law: The higher numbers of the series cannot be performed until after the lower numbers have been carried out. If we interrupt the fighting at 5, for example, and let the fish simmer down to complete quiescence, the fish has to begin at 1 again if we confront him anew with a rival. This law suffers only the kind of exception which proves the rule: If we take an animal, in which the internal readiness for a set of instinctive movements has been raised to an abnormally high value, and put it under a superlatively strong and adequate releasing stimulation, it may occasionally happen that the sequence is broken and that all the movements belonging to a set break out simultaneously, resulting in what Dr. Tinbergen has called a *cacophony* of movements or what Grey-Walter would call a *fit*.

Even the few things I have said up to now, should make one interpretation of these phenomena rather obvious: The single motor patterns 1, 2, 3 and so on, respond to one kind of excitation, but do so with different thresholds, that is to say, with a series of thresholds the values of which rise with the sequence of the single motor patterns. Normally this excitation mounts gradually and reaches the threshold values of the single

motor patterns one by one and, only in the abnormal case of the fit, floods all of them simultaneously.

One common quality of excitation which elicits all the movements belonging to a set — and no others — appears more than probable because of the two following facts: The first is that the fluctuation of threshold, of which I have already spoken happens to the thresholds of *all* the single motor patterns simultaneously and parallel to each other. If we find that movement can be released by an exceedingly weak stimulation, we then know with certainty that the thresholds of all the other patterns belonging to the same set are correspondingly low. If, on the other hand, we find that we need quite a strong dummy to release number 1 or 2, we can predict that we shall fail in releasing number 5 or 6 even with optimal models.

The second fact is that the performance of any of the motor patterns belonging to a set raises the threshold of all the others in the same degree as it raises its own. Thus it is possible to prevent specific excitation from ever reaching the thresholds corresponding to the higher numbers in such a series. If, for instance, we *crowd* male cichlids into a tank where they are forced constantly to encounter each other, they will react pretty nearly continuously with slight fin-spreading, gill membrane-depressing, but will hardly ever reach the level of excitation necessary to perform a tailwhip, still less a ramming thrust. This is why it is perfectly possible to keep twenty cichlids in a tank quite peacefully, whereas only four or five might otherwise fight each other to death in a few minutes.

The regularity of parallel fluctuation and mutual influencing of threshold is a very strong bond between the single motor patterns of a set, and incidentally is really the basis for much of our ability to predict animal behavior. The observation of low-threshold patterns in a set makes it predictable that those of higher thresholds are going to appear within a short time, provided the rising excitation will reach their thresholds. This again is predictable, providing you know your animal, from the speed with which the lower rungs of the intensity ladder are reached by the rise in specific excitation. If they follow each other swiftly, it is predictable that the swiftly rising excitation will keep on rising for a longer time than when the animal spends a very long time performing one low-intensity pattern. An amusing example of all this is shown in a film I have made of fighting Andean geese. A gander, in the first scenes, in which he has failed to "work up" to rushing his antagonist, takes a long time in getting flatter and flatter, while with a stronger stimulation, the threat and the rush follow each other immediately.

The internal build-up of a specific readiness to perform a certain set of motor patterns makes it necessary to measure *simultaneously* the effectiveness of external stimulation and of the internal threshold values prevailing in the organism at the moment. You can get an absolutely identical response, either with a weak dummy in a subject whose thresholds are at the moment extremely low, or with optimal stimulation in an animal whose thresholds happen to be very high.

The internal build-up of the readiness to instinctive movement was discovered in intact animals by Wallace Craig, but the very same phenomenon had been discovered in neurophysiology, from an entirely different point of approach, by A. C. S. Sherrington.

In criticizing a new paper by L. Franzisket (16), Erich von Holst read a very old paper by Sherrington and found that he had been quite aware, in all the important detail, of the phenomena about which I am now speaking. This is mildly distressing to us in a way, but it is very reassuring in another, because we find that physiologists are less liable to doubt Sherrington's statements than ours.

I shall give you an example of what Sherrington called a "spinal contrast." It will illustrate the close affinity of the phenomena he was studying and the ones I am talking about. The seahorse is a little fish whose main locomotor organ is a very beautiful dorsal fin. In quiescence, this fin lies folded up between two rows of spines along the sides of the fish's back. If a seahorse is decapitated, then made to breathe artificially, and if the preparation is allowed to recover from shock, the dorsal fin exhibits very curious behavior. This fin, instead of remaining tightly folded, as in the intact fish, rises gradually up to a sort of half-mast position and remains thus. It never shows either the undulating movement of swimming, or the folded rest position of the intact fish. Obviously, some influence which causes the fin to be depressed into its groove, and which is exerted by some function of the brain, has been removed by its elimination. We can supply a rude substitute for this function, though; if we compress, with two fingers, the neck region of the spinal seahorse, the dorsal fin immediately snaps back into the normal "rest" position in the groove. We do not quite know how this is effected, nor is it particularly interesting. What is interesting is what follows upon the removal of this fin-depressing stimulation. The dorsal fin springs up, as soon as we relieve the pressure on the neck of the spinal seahorse, and assumes a position which is more erect than the half-mast position it held before. The longer we depress it, the higher the fin rises and the longer it stays up before sinking back into its previous position. That is why the phenomenon is called *contrast*. If we depress the fin for a very long time, it not only rises, after removal of the neck pressure,

to the maximum extent, but proceeds to perform the undulating movements of normal swimming, if only for a short time, after which, as in the afore-mentioned experiments, it sinks back, in an asymptotic curve, to the half-mast position.

Erich von Holst's interpretation of this phenomenon is identical with our provisional interpretation of the threshold-fluctuations observed in instinctive movements. The first assumption is, in both cases that "something" is accumulated during the rest period of the activity which is destroyed in its performance. Holst thought that this "something" might be humoral, a theory which was independently proposed by J. B. S. Haldane* at the symposium on instinct recently in Paris. The second assumption is that the higher levels of brain function hold the continuous and spontaneous process under control, under an inhibition which is removed only when the instinctive movement should be performed.

Fremont-Smith: May I ask, then, does this mean that the animal in isolation that is not exhibiting a certain behavior because he is in isolation, is in fact inhibiting this behavior by virtue of his higher centers?

Lorenz: Yes.

Fremont-Smith: This is very important. This introduces a different concept, I think, than we have had; that is, that we have a positive inhibition of a behavior which would spring into activity if released.

Lorenz: If you cut off his brain.

Fremont-Smith: Therefore, the threshold is lowered.

We know from the work of Erich von Holst that fin movements, in all respects closely akin to the fin movements of the seahorse of which I have just spoken, are independent from afferent control in general and from proprioceptors in particular. Gray and Lissman (17) have also shown this to be true for the swimming movement of the dogfish (*Scyllium*) and Weiss (18, 19) for the walking movements of the *Amblysloma* larva. I need not go into particulars, as I think the point is no longer controversial.

We must make a sharp division, however, between the question of stimulus coordination independent of afferent stimuli, and of stimulus generation independent of afferent stimulation. Perhaps I should tell the story of the only two cases in which the latter was irrefutably demonstrated. The first concerns the creeping movements of the earthworm. Von Holst isolated the ventral ganglion chain of this animal completely, suspended it in Ringer's solution, and connected every ganglion with an electrometer. He found rhythmical impulses going out which followed each other in exactly the same sequence in which the muscle segments

* Haldane, J. B. S.: Paper read at *Colloque Internationale sur l'Instinct*, Fondation Singer-Polignac, Paris, 1955.

contract in the normally creeping, intact earthworm. It was known earlier, that after the removal of the supra-esophageal ganglion the otherwise intact earthworm would go on creeping incessantly. Again, it is the higher function of the brain that keeps the instinctive movement in check.

It was still doubted by some critics, that this rhythm of impulses, spontaneously generated by the ganglion chain, was really identical with that of creeping. Holst responded by repeating the first experiment, but leaving, in addition, several ganglia in connection with their muscular segments. Now these segments beat in time with the timing of those that were still connected with the other ganglia.

The second instance in which endogenous generation of stimuli was irrefutably established was Paul Weiss' (18, 19) classical experiment in which he implanted a piece of medulla and a limb bud into the back of an *Amblystoma* embryo. You will remember that this limb started "walking" rhythmically and perpetually as soon as the first motor nerves had grown out to reach it, at a time when afferent nerves could not yet function, and could not function because they had not yet connected with their end organs, as subsequent histological examination showed.

Therefore I think we can accept it as a fact that the central nervous system can generate and co-ordinate nervous impulses without any afferent inflow. The point is important with regard to the point of view that learning enters into everything; how could that piece of *Amblystoma* medulla learn to move the leg when it does not even have information about what is happening in the periphery?

Fremont-Smith: This follows Coghill completely, doesn't it?

Lorenz: Oh, yes. And so do many results obtained by Leonard Carmichael (20).

Now, I would like to go on with some cases in which a nervous inflow is necessary for the *generation* of impulses, but not for their coordination, as is probably the case in the swimming movements of most fishes. Gray's and Lissmann's spinal dogfish (*Scyllium*) made beautifully co-ordinated swimming movements as long as two or three posterior roots remained intact. When these were cut, the movements ceased altogether. In another example, Holst took an eel and, to show that its undulatory swimming movements were not based on chain reflexes, not only de-afferented, but completely isolated a stretch of the spinal chord in the middle of the fish's body. The snake-like swimming movements now started, as in a normal fish, at the front end, disappeared in the paralyzed part of the body, much as a train disappears into a tunnel, and reappeared at the rear end of the paralyzed section slightly sooner than the wave would have reached the corresponding point in

an intact fish. Without the effect of some feedback from the muscles, the waves proceeded slightly faster than normally.

Fremont-Smith: The feedback would slow them up a little bit?

Lorenz: Yes, although nobody knows how it does so.

I mainly wanted to present to you today the facts with which we are concerned. Let me add what little theory we have, as so much has been said and written lately about our alleged "theories." All these theories consist in the belief that instinctive movements are physiologically closely akin to the neurophysiological phenomena of endogenously generated and centrally co-ordinated movements as described by Sherrington, Paul Weiss, Erich von Holst, and so on. It seems only plain common sense to look for a physiological explanation in that direction rather than in the area of chain reflexes and learned responses.

Consider for a moment the most unexpected properties of instinctive movements: their surprising rigidity, their independence from afferent control in general and from proprioception in particular, which makes possible such phenomena as the weaverbird weaving without a strand. Consider their tendency to rhythmical recurrence and to "explosions" when releasing stimuli fail to arrive. All these characteristics of instinctive movements cease being paradoxical and become naturally expectable the moment we free ourselves from the preconception that "the reflex" is the basic and only elementary neural process, and that learning *must* enter into everything that takes place within the central nervous system.

We may have been too sweeping in our statements about the unimportance of proprioception and reflexes. If we have, we may ask to be exonerated since others against whom we have been arguing insisted that "instinct" was *all* reflexes and proprioception, plus conditioning. There may be of course, species-predictable instinctive movements which are interspersed with, or which interact with, true reflexes. One example of this which I suggested to Dr. Lehrman as a good subject for investigation is the courtship movement of the common domestic pigeon. In this movement, the male pigeon alternately stands very upright and bows down deeply toward the female. During the upright phase, it inflates its crop by queer little pumping movements which also emit a sound like the stroke of a small air pump, "wongwong, wongwong," and so on. During the downward phase, the crop is deflated while emitting the well known "cooing." In the normal wild *Columba livia* L. and in most of its domestic varieties, one "wongwong" is sufficient to inflate the crop sufficiently to let a "coo" follow, so that the sequence is "wong-wong-coo, wongwong-coo" and so on.

Now, there are some varieties of domestic pigeons, the so-called

pouters, which have been bred to develop an enormous crop and which give more "wongs" to one "coo" than the wild variety. What is most interesting is that those with the biggest crop need the greatest number of "wongs" to inflate it, before emitting one gigantic "coooo."

Incidentally, it is amazing that English pigeon fanciers use this peculiarity to assess the value of the birds: The judges at pigeon shows actually count the "wongs" necessary to inflate the crop and the bird with the highest number wins.

What makes these differences between pigeon varieties important to us is the following speculation: We know that endogenous motor coordinations of true instinctive movements are usually conservative. The variability which we encounter in the pigeons suggests that there is a variable link (that is, controlled by afferent stimulation) between the "wong" and the "coo." It is a likely guess that, when the crop inflation has led to a certain tension, this tension stimulates some proprioceptor and elicits a true reflex setting off the "coo." Dr. Lehrman once had the brilliant idea of inserting a little valve into a pigeon's crop and trying to find whether or not it is possible to elicit a greater number of "wongs" by letting out some air, and a greater number of "coos" by adding some.

The point I would like to make is that we do not deny at all that there are species-predictable motor patterns which come about mainly or even exclusively through the mediation of proprioceptors much in the way suggested by Dr. Lehrman (21).

But we do contend that there are other important factors too, which are entirely independent of afferent stimulation. And I am still very firmly convinced that these phenomena are based on the same elementary processes as Holst's central co-ordination and Sherrington's spinal contrast. This last sentence contains practically all of what I should call our "theories."

Before I finish, however, I would like to ask a question, particularly of Dr. Beach. It concerns the influence of the instinctive movement, especially on what Wallace Craig called the consummatory act. To illustrate what I mean, I must begin with a simple behavior story.

One of the most universal instinctive movements that are most universal in the class of birds is the nest-building movement. The bird takes a bit of nesting material, a twig or a blade of grass between its mandibles and, executing all the while a strong trembling movement, shoves it sideways against the substratum. We have labeled this movement the "tremble-shove." I quite agree that it needs further physiological analysis, but you may rest assured that it is transmitted as a whole pattern

(as much so as that of our skull bones) and that it is a true natural unit. It *is* the same in birds as different from each other as Corvidae and herons, or pigeons and eagles.

Once I had a brood of young black-crowned night herons, reared from earliest babyhood, some even prior to hatching, which had always been kept in an electric brooder. When they were old enough to live without artificial heating, I moved them into a box filled with straw almost to its upper rim. As soon as the birds were in this new substitute nest, one of them bent over the edge, looked about searchingly, grabbed a splinter of wood sticking out from the unplanned boards, broke it loose, and built it into the straw at the edge of the box with a perfect tremble-shove. This bird had never before seen any material with which this movement could be performed, nor had it seen another bird do it.

In the night heron, the response to a twig suitable for tremble-shoving is entirely innate. That young bird would not have accepted the splinter, if a good twig had been available, and a good twig is so greedily accepted and tremble-shoved into the nest by night herons in their late nestling period that I used to present them with twigs in order to get them positively conditioned to my person more quickly. Even at that time (1931) I must have had some idea that the mere performance of an innate motor pattern, without supplying a tissue need, had the effect of a "reward."

In jackdaws, the material to use in tremble-shoving must be learned by trial and error. Inexperienced birds, when getting into breeding condition and beginning to build, use the most impossible materials, such as cakes of ice, brass settings of electric bulbs, etc., and only after much experimentation arrive at using twigs and branches of adequate length, and even prefer those that have little side branches that make them stick more firmly in the nest. The choice of a locality for building, on the other hand, is entirely dependent on unlearned preferences which need not concern us here.

In the night heron all this is different: While reacting by unlearned preferences to the nest-building material, this species must learn, by trial and error, where to build. It will take a twig, fly into a tree, and start performing the tremble-shove at random, very often on a smooth horizontal limb where there is absolutely no chance that the twig will stick and form a firm basis for a nest. But once it has, by pure chance, found a place in which a twig will stay put, it quickly concentrates its efforts on that locality, as quickly as a Skinner-conditioned animal would.

Now, the question is: What effects this conditioning? We get some

information about it if we watch our bird closely. When the bird, in its tremble-shoving movement, encounters resistance, the intensity of the performance is increased, and if the twig really stays in place, the bird reaches a real frenzy of maximum intensity but then ceases abruptly, giving way to complete relaxation and a temporary disinterest in twigs. If, on the other hand, no resistance is met, for instance if the bird attempts to build on a smooth horizontal limb, such a peak of intensity is not reached and the movements die out gradually, until the twig is dropped, after which the night heron very soon finds a new twig and resumes its activity.

These two endings to the performance of an instinctive movement, the orgasmic discharge with a sudden ending on the one hand, and the gradual petering out on the other, have opposite effects upon what the animal does next; it will tend to repeat all activities that have led up to the first, and it will tend to discontinue those that led to the second type of ending. In other words the orgasmic discharge of a consummatory act has the effect of a very potent reinforcement. This reinforcement is much more effective than the punishment exerted by the dying down of the activity in the unsuccessful situation. Indeed, if the non-attainment of discharge of the orgasmic consummatory act were a real punishment, it would discourage the organism from trying again and again, which obviously would be of negative survival value. But it is the positive reinforcement that leads to survival. It would, therefore, be much more descriptive of what really happens, if we spoke of the animal as learning by "trial and success" rather than through "trial and error."

I could give you many more examples of animals learning through the reinforcement exerted by the consummatory act. Occasionally an instinctive movement has no other survival value than the choosing, by trial and success, of a certain situation or a certain object. Common pigeons or *Columba livia* (I do not know whether blond ring doves or *Streptopelia risoria* do it), always build nests of strictly similar twigs. This is effected by trying a peculiar shaking movement on all potential nesting materials. They take a twig from the ground, shake it a few times and then, if it is too light or too heavy, drop it again. But they carry it to the nest, if it affords what we might anthropomorphically call a "satisfactory" shake. I think that the real survival function of the shaking movement is to assess the weight or the size of nesting materials to be used.

Lehrman: That is a very good example of the way in which field observation makes you find out things you could never discover in the laboratory; I never saw that in the laboratory, but I am sure it is because

in the laboratory the birds always get the same size nesting material.

Lorenz: And they are also too near to the nest. I think they do it only when they fly with the nesting material. It would be interesting to follow that up.

One more example of an innate motor pattern which, although it has another function too, plays an important role in teaching the organism some essential thing. You will find that the nests of warblers and other song birds are usually built in a whorl of little branches. If you watch a whitethroat or a goldfinch going house-hunting, you will see that males as well as females tentatively perform the movement of cup-moulding in different potential nesting localities. The movement consists in pushing the breast forward and downwards and the wing shoulder outward, while scraping or pushing backwards with the feet. Thus, the nesting materials are pushed symmetrically outwards at five points at once, and by performing this movement repeatedly while slowly turning on a vertical axis, the bird moulds the circular nest-cup. The above-mentioned anticipation of this motor pattern, the moulding of a nest-cup where no nest-cup as yet exists, is essential for the choice of a place where the nest has a sound support: The locality finally chosen is invariably one in which the bird finds a maximum of tactile stimulation on all sides while turning to and fro executing trial cup-moulding movements.

I think that this is one of the rare cases in which it is perfectly permissible to extrapolate from introspection, as long as we maintain a clear-cut separation of what happens physiologically and what happens in our experience, without attempting to tear holes in the granite wall of the body-soul problem.

We know from personal experience that what is rewarding to us in the consummation of an instinctive activity is proprioception of our movements as well as exteroception from the releasing situation. It is not only the proprioception of chewing and swallowing that is agreeable, but also the taste of the food, the tactile perception of its crisp-ness, and so on.

These special reactions to very special stimulus situations certainly imply something like an IRM on the physiological side; why one type of stimulation is rewarding and agreeable and another is not agreeable, is not clarified yet by our physiological interpretation and must still be explained.

Now, my question to the learning theorists, which is actually of a psychological nature, is this: How can performance of a movement leading to reception of certain stimuli come to be a re-enforcement of

learning, since no tissue need is fulfilled and nothing is changed? For example, what changes when we sneeze? We might say there is some change. If the bird only performs a good, rewarding tremble-shove, gets an effect from it, and walks away contented, what is the re-enforcement, how does it come about, and what has it learned? This is my question.

Schneirla: I would like to take exception to that statement that there is no change in tissue need, or any tissue need under those conditions. It must be admitted that very frequently we cannot readily identify the tissue need or its equivalent in cases where we are inclined to suspect one is present and is changed by an act. The tissue need in the case of the tremble-shove may not be too apparent, but to say there is none, is going too far.

Lorenz: Dr. Schneirla, if we assume there is tissue need, you are assuming that there is a special humoral basis for the whole occurrence.

Schneirla: Perhaps humoral or not, but at any rate, some physiological events demanding investigation in relation to external adjustments. The problem is great, and I am probably as mystified as you are about it, but we are not going to find out as much as we should about it if we insist on a split between the role of so-called tissue needs in better known cases of learning, and their presumed absence in cases which may at first sight seem very different.

Lorenz: As I understand it, the question is: How is it possible for the mere performance of an instinctive movement as, in my example, the performance of the tremble-shove, to act as a re-enforcement to a whole series of appetitive behavior which gets the bird into the exact situation in which the one tremble-shove was successful and then led to a peak and a refractory period?

The same question really arises about any reward or punishment producing a reinforcement or the contrary. But somehow it seems more natural that the piece of meat which a Pavlovian dog gets as a reward and which supplies a tissue need is a reinforcement and that an electric shock which does actual tissue damage is avoided afterwards; both have rather profound consequences permeating the whole organism. The question is, how can a mere performance of certain movement patterns have the same effect? That it does have that effect, is an indubitable fact. But how this effect is brought about, that is the difficult question. What is so hard to see, is how the "successful" or "unsuccessful" performance of the consummatory act can have an influence on the behavior which has preceded it, often preceded it by a considerable stretch of time. The night heron has done a lot before doing its tremble-shove; it has gone to a certain place, collected a twig, flown up into a tree,

performed the movement in a certain place—and all of this sequence is reinforced by the consummatory act.

Fremont-Smith: You mean is a reinforcement to that behavior?

Lorenz: No; the performance of the tremble-shove behavior is a reinforcement, is a reward, teaching the animal to go again through the long chain of behavior which it has just completed.

Lehrman: The question really is, how can the performance of this act be a reward if the performance of this act does not include the reduction of tissue tension?

Liddell: Say it again.

Lehrman: The question is, is this the framework of the type of problem Dr. Lorenz is implying here? A reward is usually defined as the satisfaction of a need or reduction of tissue tension. Here we have a situation where the animal learns only on the basis that when it does the right thing it gets a chance to perform this movement. On this basis, it does what leads up to the situation where it can perform this movement. How can the movement function as a reward if there is no reduction in tissue tension?

Lorenz: What does it do in that way to act as a reward?

Fremont-Smith: Is there a reduction of tissue tension?

Lehrman: That is the question we should have asked.

Lorenz: The answer of Dr. Schneirla was that in some way it does affect it.

Schneirla: That was one point behind my remark. But there is much more to be said. There is first the fact that so-called instinctive activities such as nesting can end apparently in more than one way, but an important way is by reducing the effect of a part of the stimulus situation necessary to set them off or keep them going (22). The internal basis of this change and its relationship to what we call learning are very poorly known.

But more specifically I wanted to call attention to the great possibility that often, perhaps quite often in such activities, there may be events occurring which bear at least a partial relation to learning phenomena. The motor component for instance may have relationships to the autonomic nervous system, and to the viscera and their related processes, which are changed in some characteristic way when the act is ended in some important phase or as a whole sequence. But the key matter may well be how this relationship changes with reference to particular external conditions somehow prominent for the animal. Does the animal's act change its relationship to the external situation in such a way as to admit the neural change hypothetically considered essential

for learning? And are so-called instinctive activities free from related occurrences?

Lorenz: Yes.

Schneirla: I think this is consistent with the kind of learning theory by which Dr. Maier and I distinguished between what we called "selective learning" (traditionally, trial and error) and conditioned-response learning.

We really made the distinction in our book in 1935 (22). Then in 1942 (23), we described as specifically as possible the essential properties of selective learning and conditioning, and circumstances under which each occurs. In *selective learning* the animal's response changes the situation in some effective way with respect to the relationship of prominent stimulus aspects and the animal's condition as altered by the act. Of course many theorists had been concerned with this problem. We tried to suggest a distinction from other types of learning which might lead to fruitful lines of investigation. The theory centered around the effect of "what the animal does" upon the animal's condition in the situation. Its action changes the situation for it in a critical way.

Lorenz: Definitely. Everything is changed afterward.

Schneirla: It is how the carrying out of a particular action may change the relationship of autonomic nervous system and viscera to the rest of the organism through the central nervous system, under sensory conditions focalized by the change. Then the key neural modifications become possible; that is the gist of the idea.

Fremont-Smith: Let me put it this way, and this is pure hypothesis: Is it in the line of thought that the movement of the feather could stimulate the vegetative nervous system to release a hormone which would influence the state of the animal so that he no longer felt the need and had a refractory period, if you like, until something built up again ?

I am not saying this is the actual process, but is this the kind of vegetative hormonal relationship that might be released by behavior?

Schneirla: It depends. This might be a part of a complex of relationships, and might contribute focally to a modification. Or movement of feathers might be focal to the observer and perhaps also to the species mate, yet the act might end without a basis for later modification on recurrence. Feather control is not like limb control in relation to the central nervous system. But whether selective learning occurs or not, requires performing the act in such a way that the animal's functional relation to the situation is changed.

Fremont-Smith: There might be many other things that take part in this.

Schneirla: It is the relation of the behavioral event to the condition of the animal as a going organism, focalizing the conditions prevailing at the time the act is performed.

Fremont-Smith: Then, vegetative nervous system and hormones and back to the total conditioning or condition of the animal is really what you mean?

Schneirla: That is what we would need to consider.

Fremont-Smith: Therefore, this would be an area for study: What is the process that takes place in the animal simultaneous with the movement which moves the feather, of which the feather may be only one tiny piece?

Lorenz: Exactly, the feather need not be there at all. Maybe, Dr. Schneirla, as Dr. Fremont-Smith was not with us at the symposium on instinct in Paris, we might illustrate what he has been saying with Prof. Haldane's theory. Haldane called our attention to the fact that the regulative process of breathing might be studied as a good model of what happens in the building-up and destroying of specific potentiality in instinctive movements. Dr. Barron actually suggested the same thought independently today. There is an indubitably automatic generation of impulses in the breathing center. Its activity is stimulated by the presence of carbon dioxide. This stimulant is accumulated when the activity is not being performed and it is eliminated by the performance, that is to say, by the effects of the motor impulses of the breathing center. Haldane suggested that all the phenomena of threshold fluctuations, etc., of which I have been speaking, might find their explanation in an analogous feedback mechanism. I may say that Erich von Holst, too, tends to believe in the production of a substance stimulating certain functions within the central nervous system and being destroyed by the activity of these centers.

Schneirla: We have to consider that under appropriate conditions the organic effect of performing the act functions not just as feedback or as facilitator to keep it going. It might do so in stereotyped, minimally modifiable activities. But under different conditions, depending on species and conditions, we might get behavior modification, conditioning, or perhaps selective learning.

The metabolic background of acts is not necessarily the same under different conditions but, depending on the organism and the set of relationships involved in the act, may promote one or another type of modification. Maier and I suggested that when learning occurs, the

processes may involve neural (especially cortical) events varying from the more local to the more inclusive. When the act does not sufficiently change extrinsic-intrinsic relationships (e.g., does not stop shock, get food) only a conditioned learning may be expected. A contiguity of sensory events is then presumed to dominate which admits only a localized correlation change between two afferent cortical processes. This is a more restricted kind of learning in which the animal is involved rather passively. But when the act also focalizes a change in the animal's condition, changing its relationship to the situation as a visceral tension-reduction occurs, then the learning is selective, i.e., has a higher type of organization. Classical conditioning and selective learning have different properties in visceral background and in their organismic patterns. From the standpoint of this theory, Haldane's suggestion of a respiratory feedback effect could not be assumed to cover the range of possible learning patterns.

Fremont-Smith: Especially in the absence of hardly any information as to the process at all?

Schneirla: Especially that.

Lorenz: And especially as there is positive information telling us that there are other processes, too, on the receptor side, which run parallel to those which Haldane's explanation covers, and which can be, and actually have been confused with them. There is that interesting process which physiologists have called "adaptation" to a stimulus—we prefer the term "afferent throttling"—which gradually reduces the organism's readiness to respond. My pupils Precht and Margret Schleidt (24) have studied afferent throttling in very different objects. Both have shown that the decrease in the readiness to respond concerns only a very narrow range of stimulation. The slightest change in the stimulus makes the organism react again. Then there is the process of "waning" of an inborn response, extensively studied by R. A. Hinde (25) and possibly related in some way to the one first mentioned. Both of these sets of phenomena must be taken into consideration when studying the internal build-up of instinctive movements. They represent a serious complication to our attempts at analysis.

But there are still other difficulties about Haldane's assumption. One is the displacement activity. P. Sevenster, a pupil of Jan van Iersel in Leiden, has shown in a paper, not yet published but read at one of our symposia, that the performance of a displacement activity lowers the organism's readiness to perform the autochthonous instinctive movements, just as if the movement itself had been performed — a most important fact in itself.

The second objection is that it is extremely difficult to see how similar,

and often actually identical, motor patterns could lower the readiness for different sets of instinctive activities. Let me give you one example of this: Drees (26) has studied the courting and the hunting behavior of spiders belonging to the family of Attidae. Both courtship and hunting begin with the same movements of first running at, and then carefully stalking, the object. Running at and stalking a prey and running at and stalking a female are mutually exhaustive. They are "fed out of the same pot," but the spider can be made to run by other means too, as it is strongly phototactic and runs toward any light. Placed in a tube with light bulbs at both ends, the spider can be made to run up and down many times in succession, covering many yards. The running toward prey or to a female is exhausted after the spider has run several inches. Running toward light has no influence on the readiness to run toward a prey or a female—and *vice versa*. The motor patterns performed in both cases are identical—just plain running—and I do not see how one could find an explanation for the fact that they exhaust two different specific action potentialities, but they do.

On the other hand, the low-intensity patterns of a set exhaust the same specific action potentiality as the high-intensity patterns and as the orgasmic consummatory act. We suspect, though, that they consume quantitatively less specific action potentiality. It is a thing that would be quite easy to investigate, though none of us has done it yet. The tremble-shove should be an excellent subject. One could put a night heron in a cage in which only a very insufficient basis for nesting is offered, for instance, only one very thick and smooth perch, and let it try nest-building. Then one could do the same with a good nest-building basis, for example a nice wicker basket where every single twig that the bird tremble-shoves will stick beautifully. The prediction is that far more time will be spent in tremble-shoving by the bird in the first situation, in which it never attains the full "orgasm" of tremble-shoving, as I described it before. That bird would never get the complete lowering of intensity and the refractory period that follow upon the consummatory act.

Schneirla: But we have to consider the fact that what seems to be the same motor act can occur in very different contexts for the animal. It may exhaust or not, lead to no learned modification or some learning, or lead to learning of different sorts. I do not think you are arguing that "satisfaction" can be used for the terminal organismic condition in these different cases. A simple illustration would be the kind of pleasure a cat seems to get from a good stretch. But admit the stretch only under particular conditions in a problem situation, as against any conditions, and it can have very different relationships to possible

behavior modifications or their absence. This might be used to investigate the properties of that stretch in relation to its organismic background.

Lorenz: I think that stretching and yawning are actually movements of that type, where you work up to a climax, then cannot do it again immediately afterwards.

Barron: They seem to serve the purpose of increasing the venous return.

Lorenz: Of course they do. But that does not prevent you from getting pleasure from them. The tremble-shove serves the function of building a nest, yet the bird obviously gets pleasure from it. The pleasure is the subjective side of the reinforcement effected by the consummatory act.

Barron: But it may be an aspect of this.

Lorenz: The survival value is always an aspect. But the point which is extremely difficult to find is Wallace Craig's great discovery that the survival value of the thing and the goal subjectively aimed at by the animal are something entirely different. My aim, my subjective goal in having lunch, is the pleasure I derive from eating and definitely not the biological consequence of my eating activity—which is to make me still fatter.

Tinbergen: May I bring up a point I have been wanting to make for some time? We have been talking, I think, of two things that may be different and that we tend to treat as one and the same thing. One is: What stops an activity? The other is: What acts as a reward?

Lorenz: Yes.

Tinbergen: Now I think, as long as we have not established that the same factors that stop the chain of movements (the consummatory act) are also the "reward" that reinforces in learning, we should study the two problems separately. My main point concerns the first problem: What stops an activity (in subjective terms, satisfies the animal)? In other terms again: What brings down the specific motivation? Dr. Lorenz pointed out long ago that in current thinking it was the attainment of the "goal" that brought the motivation down, for example, the rat in the maze finding food, or the young. He then said: It looks much more as if it is the performance of the end act itself that brings the motivation down. But then he made a jump, and I think it is important to point out that we are now quite aware that this was an unjustified jump. He said (because he observed vacuum activities) the motivation is obviously brought down by the exhaustion, the running out, of specific motor excitation. But the (rare) vacuum activities showed only that the motivation can be brought down to a certain extent by performance itself; they do not allow one to decide that it brings the motivation down

as much as the performance in the complete environmental situation. For what happens when an end act is performed can be three different things: *a*) motor excitation is used, and as a consequence perhaps the excitatory state of the motor center(s) involved decreases; *b*) the animal receives proprioceptive stimuli informing it that the movement has occurred; and *c*) by performing the end act the animal changes its relation to the environment, and it can receive confirmatory stimuli (consummatory stimuli of Bastock, Morris, and Moynihan, (27)) as a result of this change. Steps *b* and *c* may both act as a negative feedback. Now where Dr. Lorenz originally overshot the mark is that, first, he forgot that the performance of the vacuum activity can do both *a* and *b*; without further experimenting you cannot decide; and second, that the vacuum activity may lower the motivation to a lesser extent than the activity causing negative feedback of type *c* to flow in. In fairness to Dr. Lorenz, it must be said that several ethologists have been stimulated by his raising this problem, even though he drew too simple a conclusion, to do research on it.

As to the relation of this to the problem of "reward": I think that when American psychologists speak of conditioning being dependent on whether the end act lowers a tissue need, they are acting on the assumption that whatever brings the motivation down, also acts as a reinforcement. It is worth stressing that, as long as your only measure of the drop in motivation is whether learning follows, you use a less direct way of studying level of motivation than when you measure motivation by just measuring readiness to act in a standard stimulus situation. Ethologists have developed this more direct method (28) and because it avoids this detour around conditioning, it may be a better method. Anyway, the method deserves wider application.

Lorenz: I think we must. My question actually was, what works backward in time to reinforce what the animal did in the last 5 minutes to get to that situation? That is something which seems awfully difficult to me, physiologically speaking.

Schneirla: If you use the term "reward" as a convenience, I agree. But if it is given any theoretical weight, I disavow it. What I meant were organic changes necessary for the neural changes essential to what we call learning — but not considering these as tied to the meaning of reward or punishment.

Tinbergen: I mentioned the word "reward" only because Dr. Lehrman used it.

Lehrman: I want to comment further on the same general point Dr. Tinbergen raised. I think there is a question here of the parsimoniousness of the explanation. Dr. Tinbergen says, the original formulation

of the notion of central coordination implied that the specific readiness to perform a particular act is built up through nonopportunity to perform the act, as you mentioned earlier, and that this merely represents the accumulation of some specific excitation, as you have said.

Lorenz: As in Haldane's example.

Lehrman: And as the animal performs, something is used up. I do not think this is like Haldane's* example, because Haldane's example is quite different. The CO² is not used up by the performance of breathing.

Beach: Nor is it accumulating in one place.

Lehrman: It is accumulating in a different place and there is a feedback.

Lorenz: We do not know whether any is accumulation here.

Lehrman: Haldane's example was the CO² regulating function, the effect of CO² on the respiratory center.

Mirsky: That was 20 years ago. I thought people were now interested in more basic factors involved, not in the cholinesterase that plays a role in the respiratory center.

Lehrman: I do not think that is really *apropos*.

Schneirla: For instance, you will find this very idea in the paper written by Robert Gesell** for the same symposium and read for him posthumously. Unfortunately there was no chance for discussion of this paper, so I do not know what Haldane's reaction might have been.

Lehrman: The assumption was that something is built up and, in the process of performing the act, this same thing is used up.

The original notion which, of course, will now have to be considerably modified in many cases, was that something is built up in a mechanism or place or organization which has been referred to as a center for that particular instinctive act. I will not insist on the terminology.

Lorenz: I do not quite remember what Haldane specified on this question. My impression was that he thought of some chemical agent pervading the whole organism more or less like a hormone or, for that matter, like CO², but certainly a substance quite specific for one activity.

Mirsky: What kind of activity?

Lorenz: An instinctive movement, or a "set" of instinctive movements.

Fremont-Smith: A particular activity.

Lehrman: It is the point Dr. Tinbergen made. It has relevance to this problem that Dr. Lorenz is talking about now. There are many other

* Haldane, J. B. S: Paper read at *Colloque Internationale sur l'Instinct*, Fondation Singer-Polignac, Paris, 1955.

** Gesell, R.: Unpublished data.

ways, as you can see now, for accounting for the fact that the condition of the animal changes as the result of its having performed an act.

One of the factors, for example, is an adaptation on the sensory side, as Precht (29) showed in his study of the gaping response. The other, as Bastock, Morris, and Moynihan (27) pointed out, was the fact that when the animal performs an act, there is a change in his proprioceptive inflow as a result of this act being performed, and this in turn changes the condition of the central nervous system.

I wonder whether these possibilities should not have an effect on the evaluation of the original assumptions that the essential organization is entirely central, and that there is a central nervous mechanism which is independent of the periphery. I am not convinced of this independence from the periphery, because all of the later information that we get when we come to closer consideration of the physiology, implies that relations between the center and periphery have to be considered. It may not be adequate to do as they did, perhaps 20 years ago, to imply that there is only a central organization of the act, and then—

Mayr: I do not understand why we must belabor that point in such detail after Dr. Lorenz has said twice that he did not think that the IRM is necessarily central and, so far as he knew, had never had that idea.

Lehrman: Because he said it a few hours ago.

Fremont-Smith: It seems to me we have reached the point now of saying because there are alternative conceivable hypotheses, we should not lean very heavily on any *one* of them.

Collias: Perhaps mention of an example on the sensory side might help our communication here. If you take a baby chick from the incubator and expose it to recorded clucking, it does not respond very well at first. Apparently it is listening to the clucking; then if you stop the clucking, this chick is much more inclined to give the distress calls, which are the normal response to a deficit, such as being removed from the mother. So, apparently, mere exposure to the appropriate social signal, the clucking, somehow increases the need of the chick for the appropriate social signal (30, 31). It is just as Dr. Lorenz said with respect to the motor side, where performance of the movement apparently is its own reward.

The problem would then appear to resolve itself into the physiological basis of the increased need that is brought about by the appropriate response.

Fremont-Smith: That is where we need new information. I would like to urge that we move forward.

Peck: I do not know whether this is going to be a movement forward

or not, or even if it bears any relationship at all to the line of concern that has been recently expressed here. To avoid any responsibility I will designate my remarks as an association.

As this question came up again, there kept occurring to me a question that has occurred to me often, namely, why is it that certain kinds of patients seem to do better in a therapy group than in individual treatment? I guess this was set off by mention of the fact that the proprioceptive activity would change the status of the central nervous system. The kind of patient I am thinking of, you may describe in many different ways, but he is the sort of person who in the individual treatment situation has subtle reactions which you suspect contain elements of hostility toward the analyst; however, one cannot discern even in bodily postures, much less associations, anything that might be called a hostile response.

However, in the therapy group situation, because of its very nature, there is often present someone else who may be more easily provoked into overt hostility than the patient. Dr. Redl (32) has talked about this in his work on group emotion and leadership. When this occurs, it may facilitate release of similar reactions by the patient, so that finally he behaves in such a way that other people in the group can observe him in behavior recognizable as hostility. After this is repeated a number of times, one may call the patient's attention to it with some expectation that he can accept it.

Some observers are content to explain such phenomena by saying, "Well, now you can convince or prove to the patient that this is so simply because he did it, and other people saw it," and so on. However, it has often seemed to me that perhaps one very important aspect of this matter grows out of the fact that the patient has been helped to react or behave in a way which is different from the way he has reacted before. Therefore, I suspect what one says to him about what he has just done, is being told to an organism whose neurophysiological status has really been altered.

Fremont-Smith: It is changed by his reaction and, therefore, he is differently receptive to the same thing you said to him before.

Peck: Yes.

Mirsky: I would like to *give* some physiological support to that statement. I might bring this problem back to the original hypothesis: If one exposes an animal, like the rat, to any kind of stimulus which is noxious to the rat, a marked increase in the antidiuretic activity of the plasma occurs. This increase appears to be due to the secretion of antidiuretic hormone by the hypothalamus. For example, if a rat is taken out of its cage and is put into a Skinner box such as is employed for conditioning purposes and which is assumed to have no significance to

the rat, one finds a large increase in the antidiuretic hormone circulation within 2 minutes after the animal has been put in the box. If one removes the rat or permits the rat to get out of the box within 2 minutes, the increase does not occur.

In man, the most potent stimuli which result in an increase in the concentration of the antidiuretic hormone (vasopressin) in the circulation, i.e., which activate the hypothalamus to secrete the neurohormone, appear to be stimuli which mobilize anxiety.

In other words, the mobilization of anxiety, which we can only infer and must prove later, results in a marked increase of vasopressin in the blood and also in the stimulation of the adrenal cortex, as evidenced in the production of 17-hydroxycorticosteroids. Overt anxiety does not appear to be associated with an increase.

Fremont-Smith: This is part of what I think is a very general phenomenon. One of the first demonstrations of it was made by Felix Deutsch (33) in certain hypnotic experiments. The point of his experiment, I think, and of the general phenomenon is, that if an appropriate stimulus to memory occurs, but for one reason or other the expression and recognition of the full memory cannot be brought back to consciousness, you will then get an exaggerated response in the vegetative nervous system and maybe even in behavior which will be reduced promptly on the actual remembering of the experience itself.

I think that this is parallel to the specific situation that you have given, where there is mobilization of anxiety but no discharge. When the mobilization takes place without discharge and discharge is not permitted, then you get a greater vegetative and hormonal response, and when discharge is permitted, it is lesser.

I think this is a very fundamental general phenomenon. It is the basis of most psychosomatic disturbances, and I wanted to generalize from what you had given.

Lorenz: Might we not ask the psychoanalysts present if it is not the basis of all therapeutic efforts to make conscious some repressed form of trauma? Is that not the same mechanism?

Psychoanalysts are always trying to make conscious something which has been repressed into subconsciousness; if so, is not the curative effect of making all that conscious based on the phenomenon which Dr. Fremont-Smith has just described? It might be.

Fremont-Smith: This arouses an argument with many therapists on the basis that the transference or the relationship between the patient and the therapist is the basic thing which makes the cure or the improvement or the release of symptoms possible; my own way of thinking about it, and it may not be at all correct, is that it is the transference

situation that provides the appropriate dosage of free-floating security in which it is possible to re-remember the situation and that the re-remembering of the situation does have in itself a therapeutic effect. I do not think that this is necessarily the only therapeutic effect.

Lorenz: I would like to mention an interesting hypothesis of the French-Swedish philosopher Henri Bergson (34). He held that the subjective emotion correlated to some specific behavior was experienced only when that behavior was in some way prevented from being performed.

Let me put it in an example. Suppose you are crossing the street and see a bus approaching. You will respond by an escape reaction to avoid being run over. But you will not experience "fear," the emotion subjectively correlated to escape, even if you have to jump to escape it. Now suppose that some conflicting motivation prevented, or only counteracted your jumping aside. Suppose a tiny child had fallen down in front of the bus and you had to dash back to save it. Then you certainly would experience fear. I am sure that if you would investigate all this from Dr. Mirsky's point of view, you would find that the adrenals remain quiescent if you merely jump away from the bus unimpeded, but that the whole of "Cannon's effect" will occur when a man jumps in to save a child from under the wheels of that bus.

I think that this is the kind of case in which introspection, if properly used, can tell us a lot about what happens within us physiologically.

Redl: The last one goes further than I think I could accept, because it would really mean there is no emotion ever when you act out.

Lorenz: I am quite sure that Bergson's theory is greatly overaccentuated.

Schneirla: On the interpretative side, too.

Fremont-Smith: You said there was more emotion when the overt activity was repressed or prevented but there was more vegetative or hormonal response. I think this would fit and this would still probably have to be qualified in certain instances, but as a general phenomenon I do believe you can say the most vigorous vegetative or behavioral disturbances are those which occur where there is arousal toward activity and inhibition (and usually psychological inhibition) of the activity. I think this is a generalization which probably will hold within certain modifications as a first working hypothesis around which most of the phenomena of psychosomatic behavior and of neurotic behavior will fall in line.

Schneirla: You were not using vegetative in the sense opposed to interruptive in referring here to autonomic function, were you?

Fremont-Smith: I am using it in the very broadest possible sense,

hormonal and vegetative, meaning the whole sympathetic-parasympathetic nervous system and any others there may be along with the hormones.

Schneirla: That was to be suspected, but I thought it should be clear you were not using it in the more restricted sense.

Liddell: Dr. John Whitehorn (35) showed that when his subjects could communicate through recognized emotions, such as anger, their cardiac perturbation subsided and so did their unpleasant emotional tension.

Lehrman: In regard to emotional response and mobilization of the autonomic system, if you watch a bird performing a threat movement or even nest-building, the subjective impression you get from watching the amount of tension that develops in the body, is that not only the skeletal movements are involved, but also a considerable involvement of autonomic elements.

When you watch Dr. Tinbergen's films of gulls, for example, you do not really get an adequate impression; when you hear the sound at the same time that you see the movements taking place, it enormously increases the impression of emotional tension involved in this act. Is that not so?

Tinbergen: Yes.

Lehrman: It is not action performed by an emotionally neutral animal, as a signal; there is considerable force along with it.

Lorenz: When you say that "tension" is involved in the act I think that you express something which is more literally true than you suspect, yourself. When a goose is exposed to conflicting motivations, wanting to peck at an antagonist and, at the same time, wanting to get away from him, you get simultaneous innervation of the muscles which move the neck forward and those which move it backward, to the extent of causing head and neck to tremble violently in extreme tension between antagonistic muscles. In Canadian geese this is particularly marked because of the length of their necks. They start trembling even if they just want to eat out of your hand and do not quite dare to. The same thing happens in the Cichlid (*Etroplus maculatus*), you will remember that it simultaneously skulls forward with the caudal fin and backwards with the pectorals whenever it gets into a conflict between escape and aggression. I think that whenever we speak of a person as "under tension" we really and naively mean a simple muscular tension arising from similar physiological processes, and not some farfetched analogy to electric tension. The expression was evolved by persons not influenced by electrophysics. I always trust common parlance; if it evolves a special, generally accepted expression to describe a certain process or phenomenon,

one can rely on its reality. Common parlance is a very astute observer.

Fremont-Smith: I think you see the same thing in an individual who is hysterically paralyzed, when you ask him to move his arm; he does not move the limb, but it may begin to quiver, a response in which the muscles for the movement of the arm and the muscles for the inhibition of the movement operate simultaneously against each other and result in great tension. I think you get the same response in a hypnotic experiment if you tell a person to open his hand after you have told him previously that he will not be able to do it. He just sits still and appears to be doing nothing but the myograph reveals that both agonist and antagonist muscles are undergoing tremendous activity. Is this right, Dr. Cobb?

Cobb: Yes.

Lorenz: I think a different phenomenon might be involved in what you have just described. When people have suffered a peripheral lesion in motor nerves, and the nerves have later regenerated and re-established their former muscle connections, one often finds that the patient is still unable to move the muscles in voluntary actions because he has forgotten how to do so centrally. He has, so to say, forgotten which button to press in his pyramidal system. In these cases one sees the whole limb stiffening, with many unnecessary innervations going into action when the patient tries merely to move a toe. He behaves much as we do when we try to perform new and complicated motor co-ordinations. If you ask me to join the fifth and fourth fingers, and the third and second fingers of my left hand, maintaining a large space between third and fourth, I find my hand trembling because I do not quite know how to send out the right impulses and I send out a lot of unnecessary, even contrary, additional innervations to a number of muscles not at all involved in this movement.

The man with the peripheral nerve lesion is in a very similar position. I think that the kind of trembling you may get in hysterical paralysis may also be affected by this particular process.

Fremont-Smith: There are myograph studies on this, aren't there, Dr. Cobb?

Cobb: I wonder if we need to use your example of the man who had a peripheral nerve injury. Those of us who were raised in the Sherrington school, were perhaps a little overtaught about reciprocal innervation. We had an idea if we made a movement, that the protagonist worked and the antagonist was inhibited. That is not so or we would constantly make very awkward movements. There is usually innervation of the antagonist as well as of the protagonist in order to make a smooth

movement. There is a controlling feedback arrangement. Under emotion, as in the neck of your goose, or in anybody who is under emotion and shows a tremor, it is simply, I think, an overflow of excessive innervation into the muscles that we cannot accurately describe as being in the antagonist or protagonist. It is a disorderly overflow into both; this is what happens in reinnervation, until the person learns by re practising. Yes, these phenomena have been shown by myograms.

Liddell: There was an interesting case reported by Dr. Robert B. Malmo of McGill University some years ago. An hysterically deaf girl was given earphones to wear. Suddenly and without warning, a tremendous blast of sound entered her ears. After the sound was turned off she burst out crying, but could give no report of having heard anything.

Pribram: I would like to distinguish between two things that have been said; they are not mutually exclusive, rather one is subsumed by the other. I believe that the problem of tension is more basic than the problem of the autonomic or visceral reaction. The reaction of smooth muscles autonomically innervated has been overemphasized in the last few years, as far as I am concerned. Smooth muscle contraction in emotion is one part of the total "tension" picture which involves striped muscles as well.

Again, Malmo's studies, I think, are very relevant to this point.

Fremont-Smith: That is why I brought in behavior as a whole, which involves the voluntary musculature.

Pribram: I think the example of cutting that you use, Dr. Lorenz, is a good way of pointing up some of the difficulties we have encountered in our thinking about learning and central processes. When one cuts a nerve, what happens? The nerve degenerates and then regenerates. Immediately after regeneration, the nerve fiber size spectrum is relatively flat. After the regeneration process has taken place, differentiation of the fiber sizes goes on until the nerve coming from a particular muscle attains the specific spectral pattern associated with that muscle. If we think exclusively of something going on in the central nervous system, we may miss a lot; adequate performance may just be waiting for the specific peripheral spectrum to be re-established. To jump immediately to thinking in terms of some reorganization of central neural process is, I think, premature.

Liddell: Is there not a latent period of regenerating nerves before they establish functional contact with the periphery?

Pribram: Months.

Fremont-Smith: That reorganization can take so long is shown in the remarkable studies of Margaret Kennard (36, 37).

Spiegel: Some of us are lost over here as to what we are discussing now.

Fremont-Smith: The real or assumed capacity of the central nervous system to

reorganize. I do not quite remember how it came in and why it is important.

Pribram: It is important because Dr. Lorenz used a method of thinking about central neural processes which he has used before: inferring neural events from some behavioral manifestations and behavioral measures. Something may be going on in the central nervous system. You are perfectly right; there is certainly lots of evidence that new learning can take place. When a facial nerve is cut and the spinal accessory nerve is substituted for it, reorganization of behavior does take place. But there are enough data which suggest that peripheral events might be going on as well as central ones to explain this reorganization. That was all I wanted to point out.

Erikson: To approach this from another angle, ever since we saw the pictures of the chicks and the ducklings I have been thinking of some writing that I just finished. Dr. Fremont-Smith asked me to talk about this for a moment.

I have had occasion recently to read carefully the early letters of Freud's, which were found during the War, and were first published in German. Their existence had been completely unknown. They were letters written to Wilhelm Fliess in Berlin during the first years of Freud's private practice as a neurologist, and Freud had asked Fliess to destroy all of this tentative material. These letters now have been published in English (38), and I was asked to write a review of them (39); therefore I am a little preoccupied at present with Freud's early theories. They are condensed in what he called a "project of a psychology for neurologists." To me (and I trust to some others) it is just about the most difficult reading matter, and I would think that many neurologists of today would consider it a somewhat absurd attempt to base a psychology on the physicalistic physiology of his day. But, it was a historically unavoidable conceptual experiment and, after all, Freud never published it of his own free will. At any rate, in the midst of "phi neurons" and "psi neurons," and pathways and blockings of energy, Freud suddenly refers to a group of two persons, namely, a helpful person and a helpless one, or, an "experienced person" whose attention is drawn to a child's condition of needfulness by "a discharge taking place along the path of internal change," meaning the child's crying. He adds: "The original helpfulness of human beings is thus the primal source of all moral motives."

I thought I would quote this little sentence here as a possible anchor

point for the psychiatric discussion of the "smallest group" — when we get around to that. Freud did not say "mother," or "environment," but "experienced person." This, it seems to me, establishes the human element of the matter, for an experienced person is one who is guided by tradition, maturation, and learning, and backed up by a social state. I do not know any similar statement from Freud later; but psychoanalysis has moved in this direction with its interest in the "mother-child relationship."

All this points to the fact that when we speak of human beings, we are speaking of the interlocking of on-going life cycles and not just of one life cycle such as *domesticated* animals have, animals whose environment we have taken over. The human question is not restricted to what happens to the young in regard to mere survival, but in regard to his potential ability to help his young to survive — and prepare the minimal psychological requirements for generations to come.

In that sense, I wanted to ask whether any of the case histories of imprinted animals referred to, also include or will include observations as to what such an animal, for example a duckling or a gosling, will do *with* her young. This is one question which I think would be interesting to us.

Lorenz: It behaves exactly like any wild goose.

Erikson: Like what?

Lorenz: Like its mother whom it has never seen, or like any normal wild goose that was raised by its own parents.

When the question arose whether animals with a higher "cerebration" were more dependent on personal experience and on the social induction emanating from their parents, Jocelyn Crane (40) told us how absolutely independent her spider and butterflies were of these factors. Yet I do not think that one can make any sweeping statement about the correlation between higher "intelligence" — or whatever you chose to call it — and the role played by these environmental and social factors. There is no such general correlation. But if you concentrate on one single function performed by different species and ask yourself for which of them it is of survival value to be able to perform that activity without previous experience, you do find a correlation between this ability and the selection pressure brought to bear on its evolution. In the case of a reed warbler, nesting above the surface of water, it would be fatal to any baby to miss its perch even once after leaving the nest. In a jackdaw this is not at all vital. Correspondingly we find that in the first species a most wonderful distance-assessment is inborn while the jackdaw obviously has to learn it.

You will find that ants and bees which are fed by their older sisters

have opportunities to learn, but Jocelyn Crane's male spider has not the faintest opportunity to be taught from his father how to behave when he first meets a female, and if he fails to wave his front legs in exactly the right manner, at exactly the right speed, he will be eaten the next moment.

Fremont-Smith: Dr. Lorenz, I wonder whether you answered the question. It seems to me the question was if a gosling or a duckling is imprinted, not to its normal parent but to another species, such as yourself, to what extent does this influence its later behavior as an adult?

Lorenz: Yes, maybe that is right. I wanted to make a point clear which I failed to get clear before. Of course the artificial rearing may influence the later social behavior of the individual enormously. It may fixate some of its social responses on entirely abnormal objects. But this object-fixation, imprinting as we call it, always refers to one single function. Therefore it is misleading to say that a gosling has become imprinted to man. Its "following-mother-response" may be thus fixated on the keeper, determined by stimulation emanating from the keeper, while all its sexual responses, conditioned by stimuli emanating from its siblings are attached to members of its own species in a perfectly normal way.

No generalization is possible about what stimulation produces what imprinting. In the greylag, it is indubitably the sibling which determines imprinting; in the Muscovy duck it is the parent. Muscovy ducklings reared by greylag geese became sexually fixated on the latter species. This is an exception among Anatidae; if it were so with most of them, all of Peter Scott's ducks and geese would be sexually fixated on bantams, which he uses as foster mothers.

There is no generalization possible as to whether imprinting will take place at all. While jackdaws are easily fixated on man with practically all their social responses, the magpie, a closely related *Corvidae*, is evidently nonimprintable. I have reared birds of these species again and again, in company of humans and in that of jackdaws, and I have never seen a magpie react sexually to anything except another magpie.

If you get a bird sexually imprinted on man, it is in most cases impossible to breed that individual because it refuses to copulate with a conspecific. This has been observed in parrots, cockatoos, eagle owls, Andean geese, and many others, also in my first jackdaw, "Jock," who was socially imprinted on hooded crows and sexually on humans. Yet, when she was confronted with a baby of her own species, she adopted it, treating it as a perfectly normal jackdaw treats its young. But she did not adopt a hooded crow baby also present at that time.

I should think that you would find similar behavior in most species.

The response to the baby must be inborn, for the same reason that the treatment of the female must be inborn in Jocelyn Crane's spider males; it would be lethal if it were not. A human imprinted Andean goose in the Vienna zoo built a normal nest and incubated normally, but if one had substituted fertile eggs for her unfertilized ones, it is quite safe to say that she would have shown quite normal parental care to the goslings that hatched. The misimprinting of the sexual functions would certainly not influence the parental care functions at all, just as they did not in my old jackdaw, Jock.

Fremont-Smith: Did she ever go back to normal sexual patterns?

Lorenz: No, never.

Fremont-Smith: This was a life imprinting.

Lorenz: This was a lifelong imprinting, and we know from several cases that secondary conditioning to the normal object could be produced; that is, imprinting to the inappropriate object was not brought about.

My friend, Hellmann in Rotterdam, did this. He got a male bud-gereegah imprinted on himself. The next year, he imprinted a female of the same species on himself. They were both sexually imprinted on humans. You may know, budgereegahs are very good at accepting substitute objects. Normally imprinted budgereegahs will take a celluloid doll for a substitute female, try to feed it, and attempt copulation. Now, when Hellmann put these two birds together in a garret room and shut them up, they gradually became conditioned to each other and finally accepted each other as substitute objects, copulated and even reared young. None of them had ever successfully copulated with a human being; indeed it could not.

Now, the point is, that after these budgereegahs had been together until they had reared two broods successfully and were about to rear the third brood, we exposed them to human beings. I was standing there, and the partition was removed. The budgereegahs saw a human being again after a very long time, after having been "married" successfully for a very long time. Both at once went into a frenzy of courting directed toward the humans. Then, they had a terrible fight between themselves and let their present brood of young die of hunger because their whole reaction to each other had been disrupted by the re-exposure to humans. The experiment was over and we did not want the young to die, so we retired immediately, but it was too late; this brood of young starved to death.

I think in this case where successful readjustment to the biological object was achieved by true learning, the irreversibility of imprinting is more striking than in any other case.

J. Portielje, director of the Amsterdam Zoo, had an analogous case (41) in a South American bittern, *Tigrisoma*. This bird was slightly ambivalent in his reactions; still he preferred Portielje to his female. In order to breed them, Portielje put the pair into a ground glass cage in which they could not see any living being except each other. This was necessary because the male at once wanted to court human beings and chased the female out of the nest. I was very impressed when Portielje entered the cage. The human-imprinted male immediately drove the female off the eggs and invited Portielje, by ceremonies, to sit on the eggs. Portielje is a man a head taller and also much bigger than I. It was very funny to see that wisp of a bird inviting and emotionally urging Portielje to sit on his nest.

I would not say that imprinting is not re-related to other types of learning or that there are no intermediates between them. But still, consider those budgereegahs that had *learned* to accept each other as substitute objects, but still remained object-fixated in the human species, with which they could never attain the reinforcement of a consummatory act.

I would like to mention the particular characteristics of imprinting that separate it from other types of conditioning, mainly because they were not mentioned in Dr. Beach's account. One is that the fixation takes place at a time when the response thus fixated is not yet functional, when you cannot condition any not-yet-functioning response in the ordinary way. The second is the limitation of imprinting to a short ontogenetic phase. And the third is the irreversibility of the process.

Tinbergen: As the complete evidence on imprinting has not been published, could you mention the exact evidence? Have the animals in which sexual imprinting has been observed really been screened from further contact between the time of exposure to the other species in early youth and the onset of sex behavior? That is essential is it not? If you allow them to stay together with the species that brings them up, you are not excluding reimprinting at a later stage. I imagine that the sex behavior got conditioned when it began to show.

Lorenz: Anyhow, these budgereegahs were only isolated from human beings after they had attempted copulation with the humans whom they had been courting; but it is different with the Muscovies. Those Muscovies were with their foster parents for about 5 weeks only and from then on they were in the company only of their brothers and sisters. So there was certainly no overt sexual activity in them, not the slightest intentional movement or anything like that at the time of their being imprinted.

I think in human beings — in pathological cases — there are instances where something very similar occurs. Many of Krafft-Ebbing's (42)

cases of fetishism give that impression. In normal cases the function of falling in love with somebody is a process which bears some resemblance to this, because it does not involve any conditioning consummatory act, but works by just being exposed to a certain type of stimulation. This may seem a big jump, and it may lead nowhere; but I was looking for an example of behavior of simple exposure without any overt behavior. Evidently the process of "falling in love" also fixates behavior on an object with a certain irreversibility.

Hess: You do not mean with overt behavior? For instance, ducks do not become fixated on ducks just from seeing them?

Lorenz: I want to say what Dr. Hess has not mentioned yet. The independence of acting is not found in the imprinting of Hess' ducklings: Their imprinting only starts when they start following. Hess could show that the effect of imprinting was not correlated to the time spent with the mother-object but to the time spent in following it! This is a very important finding, I believe. We must do the same thing with the goslings, because in goslings I think we have evidence that greeting alone imprints following as well. Again, goslings have a reaction, an overt reaction to the parent substitute, because they give the greeting reaction at a time when they cannot walk yet.

Mayer: Goslings?

Lorenz: Goslings only. Then, after that they can be imprinted to the human but not yet quite irreversibly. That is another question. There are two questions concerning imprinting that must be clearly kept apart. One is: When do young organisms first react to the object to be imprinted? The second is: For how long a period of time can one still imprint or transimprint? We need not go into that here.

Barron: You may interpret this example as you like, but it is a part of my own experience. The observation relates to the question: Can conditioning or imprinting take place before there is the capacity to express this in a motor act? Now, I have phrased this very poorly, but I believe this is the point we were discussing. This relates to a female child born on June 23rd, 1936. I ask you to keep these dates in mind because they are relatively important.

This child was born to a French-speaking mother who during the course of the early antenatal care was entirely responsible for the management of the child and as a part of the nursery room activity always spoke French to her. The child began speaking in August, 1937. On December 18, 1937, an individual who did not understand French was taking the baby, then about a year and a half old, for a stroll in a pram when the first snowfall of that year took place in the locality. The child kept repeating the word or the sound, "Neige, neige, neige" (snow).

Upon returning, the adult who had been taking the child for the stroll inquired of the mother what the word meant. There had been no snowfall between August and December and there seems to have been no opportunity for this child to have spontaneously uttered this

word. The only explanation that appears to be open at the moment (unless someone can suggest another) is that the child, during the time it was unable to make a response in this form, had conceived the capacity for the word and then on the proper opportunity and the first opportunity, had uttered it.

I thought this was an example of just the kind of learning we were discussing and the only one that I know to have occurred in a human child. This is simply what I wanted to bring out.

Crane: What about a picture book? Would the child have been capable (I do not know enough about young children) of forming a visual impression and carrying it over until she saw the real thing and so interpret it?

Barron: I could not vouch for the fact that all possibilities have been excluded. But so far as one can see in checking the circumstances, there seems to have been no opportunity for this child to have encountered snowflakes or anything pertaining thereto between the time she began to talk and the time of the occurrence. As to the possibility of books, during that interval the child was no longer in her nursery but had actually been taken on the continent of Europe, where she was deprived of opportunity for the normal nursery surroundings.

Pribram: May I give an example of that kind, too, from chimpanzee behavior? At Orange Park, all chimpanzees are bred and raised in the laboratories; nest-building behavior is usually not seen in any of these cage- and nursery-reared chimpanzees. At Yale, I had an opportunity to observe two adult chimpanzees living together. A baby was born to this pair and for the first time I saw nest-building in chimpanzees. Inquiry showed that these chimpanzees could not have been any older than one and one-half years when they arrived in the laboratory. There had been no opportunity in the 10-year intervening period for these animals to observe nest-building. Something seems to have happened in the first year and a half of these animals' lives in their original environment which was different from that which happened to animals reared at Orange Park in the laboratory environment. This difference may well account for the nest-building of the two animals at Yale.

Fremont-Smith: Dr. Lorenz, won't you tell the song story?

Lorenz: Heinroth was writing a book on bird songs, which was to be accompanied by a set of phonograph records. For the purpose of this book, he borrowed a blackcap (*Sylvia atricapilla*) from a bird fancier,

and kept it exactly one week to take the record; then he sent it back to the owner. In that one week, which is recorded in his diary, this bird was kept in a room together with a nest full of young nightingales, from the twelfth to the nineteenth days of their life, just about the time they left the nest, when a nightingale is still far from being able to sing and can only utter a few chirps, begging notes, and so on. Among these three nightingales there was one male. Heinroth need not have taken his own record, for this nightingale had done it too. In January, it started singing loud enough so that Heinroth could recognize the song.

Fremont-Smith: What was the difference in time?

Lorenz: It was exposed to the blackcap's singing at the end of May when nightingales are nesting, and it started to sing in January. It was just good luck that Heinroth had the record of that blackcap, because thus it could be checked that the song of the nightingale was in every detail the exact replica of the *atricapilla's* song.

Frank: This conversation is very uncomfortable to me because it gives a certain plausibility to dianetics.

Lorenz: What?

Frank: There was a cult that went through this country a few years ago called dianetics, which was based entirely on the idea that infants, even prenatally, got imprinted with certain things they heard in the womb or heard afterwards and this affected them later on.

Spiegel: I wanted to ask a question to clarify just that sort of issue. It is not at all clear to me exactly what the difference is between imprinting and conditioning, and especially, whether or not reinforcement and extinction play a role in imprinting. I wonder if there is a way of answering that, whether it could be discussed from the point of view of psychiatry, for example, in the traumatic neurosis or any traumatic situation. We had a little discussion of that earlier with reference to cure. We know now that with a traumatic experience, there is a very high degree of visual and auditory memory retention. To some extent, the reason for the vivid retention of the sensory impression, even if repressed for a time, is due to the fact that there has been no abreaction or expression of the sort Dr. Frank was speaking of. We also know that cannot be the whole story, because there can be abreaction and adequate physiological expression of all the feelings, but still this sensory impression together with the accompanying anxiety is retained rather vividly for long periods, sometimes for the rest of a person's life.

Now, my question is: Is the retention of these strong visual, auditory, and kinesthetic impressions in memory an example of imprinting, or what system of neurological physiology can one use to explain this phenomenon? Is this not a question that should be raised?

Lorenz: I think that it is just a question of definition of imprinting. Hitherto we have called the strongest of these phenomena, imprinting. We are quite aware that they are of

varying degrees, passing over into other types of learning or conditioning. Anyhow, I believe the question whether imprinting is conditioning, is to be answered, "yes." Imprinting is definitely one type of conditioning. This typical imprinting tapers off into learning, like the learning processes in Hess's experiments in chicks, where the learning to aim can be brought about only during a short sensitive period.

Erikson: I have a question for Dr. Tinbergen. What came up today in discussion was the question of the emotional state of these birds when they, let us say, make a threatening gesture. I know you have not put little measuring devices on them, so I am merely asking for an impression. I mean the following: If one watches these birds fluttering around, one could think they are wasting an enormous amount of emotional energy, unless quite a lot of what they are doing is really ritual behavior and is, as it were, "institutionalized" in that group of birds. On the moving pictures at least it seemed to me that when one bird was attacking the other, and the other made off, the interaction was so smooth and graceful that one often had the feeling it was only a signal, a convention. One did not have the feeling that the birds had to develop the whole emotional gamut of pugnacity or of fright.

Now, this is, of course, important because of the things which this group will get to later on, namely, to what extent individuals in a group suffer if the emotions do not find a conventional way of mutual interlocking, an institutionalized expression which in the over-all "culture" would permit of a certain parsimony of excitation. I merely wondered, Dr. Tinbergen, to what degree the examples in the pictures you showed previously were social play comparable to a ritual of gestures, and to what degree they were truly emotional states with idiosyncratic forms of individual discharge ?

Tinbergen: If I judge the intensity of the emotions on the basis of movements observed, which is the only thing we can do in the field, my guess would be that all these gestures are the outcome of a very strong motivation, and are accompanied by very strong emotions. For instance, judging from the accompanying expressions when a gull flees from another gull that attacks it, however smooth the response looks, I assume that this fleeing gull is greatly afraid. You get the impression that these animals reach a pitch of emotion which we ourselves reach only in exceptional circumstances, and I recognize myself in them only when I remember the War years. The years of war suddenly were driven

home to me; in it we experience emotions of an intensity which, in our sheltered everyday life, we never experience.

But this is pure guess work. I did not bring this problem up at all, because we intentionally take the resigned attitude that we cannot know anything about subjective phenomena in animals.

Lorenz: Beach found very much the same in young children who are very, very serious when they cry or laugh.

Evans: I wonder if I could try to make a point in connection with what little I have observed of sea gulls. As Dr. Frank Fremont-Smith and I sat together in a bird-blind on a sand bar, it seemed to me that there were a lot of intention movements. The entire flock of perhaps 2,000 birds inhabited that particular sand bar; however, the flock was plainly composed of smaller units of 200 or 300 each. We noted that each unit operated separately. Any disturbance, such as the approach of a human being closest to a particular unit, set off intention movements in that unit alone; the rest of the flock ignored the disturbance. But as the human moved toward the next unit, it rose screaming into the air while the first one settled down and became quiet.

It seems to me that Dr. Spiegel was asking for help, so to speak, on how to apply these signs and symbols to human relations. Care must be taken in comparing animal with human behavior, because many types of animals have evolved in an ecology which is quite different from the human.

I remember particularly Dr. Lorenz's work mentioning the signs that the goose seems to make, signifying "I am going to fly, I am going to fly," which keep up until the whole flock is doing it; then they go off together. We see that, of course, in the baseball game—the intention movement of the entire Cleveland stadium, for example. The audience is waiting for Dusty Rhoades to step up and smack the ball out of the park; the sigh that goes up when it comes through and the game is over—that *is* an intention movement.

Apart from that, I think one must be very careful in drawing too many conclusions from animal behavior for comparison with human behavior because of the very high degree of specialization developed by each species for its own ecological niche.

Mirsky: Are there any evidences of what you call imprinting in man?

Lorenz: I would answer your question by saying, "Please judge for yourself." Go through Heinroth's and my own chance observations on imprinting; read Eckhard Hess's publications (43) on the subject and then compare them with what Krafft-Ebbing (42) writes about case histories of fetishism. You will find amazing parallels. But whether or not the phenomenon of object-fixation occurs in the same manner in

healthy persons, and whether or not it is identical with imprinting, must be decided by a psychiatrist knowing both sets of phenomena by personal experience. I know only the most basic and simple process and cannot judge what more complicated events may take place in humans, which I do not know at all from my own basis of induction. In all inductive natural science, extrapolations proceeding "upward" from the lower, more generalized field of knowledge in the direction of a more specialized one, are extremely dangerous if not outright illegitimate. The opposite process is the legitimate one; analysis must work its way from the special case toward the general laws. The man working on the lower and more general level can only offer his findings, as a possible explanation to what I always call "the man upstairs." The organic chemist offers his findings to the physiologist of metabolism. He need not know anything about the physiology of metabolism. But the physiologist, on the other hand, is lost if he does not know all about organic chemistry. That is what I always tell psychiatrists: I do not know much about psychiatry, but I contend that psychiatrists should know a lot about ethology. Some do; John Bowlby does. Of course we dare to extrapolate to such an extent that we call the attention of psychiatrists to such observations which we think that they should be interested in, such as imprinting, and displacement activities which certainly are akin to what is called the "neurotic symptom."

Tinbergen: Part of what you see described as neurotic symptoms are, after all, just displacement activities; others are not.

Liddell: Doctor Lorenz, in field studies do you ever encounter anything similar to the panic causing people to be trampled to death in a theatre fire or similar to the stampedes of the old buffalo herds on the plains?

Lorenz: In jackdaws we have. The explanation of the panic is roughly this. Under normal circumstances, the response of any bird to the intention movements of escape in a conspecific are so finely triggered that, if one bird is frightened by some external stimulus and shows the outward signs of beginning escape response, any other on perceiving these signs reacts with an escape response of approximately equal intensity. Thus, the individual which has actually seen danger, transmits an alarm signal of such exact dosage that all conspecifics present will react exactly as it does itself, in other words, as if each of them had itself perceived the cause of alarm. If, however, a slight threshold-lowering of escape activities has taken place—for instance if, in semicaptivity, no cause for alarm has occurred for weeks—any bird seeing an alarm signal in another will react with a stronger response than that other has shown. So, in every transmittance of alarm from one individual to another, the

intensity of the flight response increases. You can easily observe this in a flock of tame jackdaws. One individual treads on a loose twig that jumps up and causes it a very mild alarm. Its expression movement induces a stronger alarm in the next bird, and so on. Before the transmittance has gone around the circle and reached the first bird again, it has snowballed into a stampede. You can observe the same thing in flocks of common sparrows.

I have made films of courtship movements of the mallard duck *Anas platyrhynchos* L. showing the separate motor patterns, the initial head-flick, the grunt-whistle, the head-up-tail-up, and so on. And I have made two other films containing the same material but arranged in two different ways. In the first of these, a number of species, the pintail, the Bahama duck, and so on, were treated in the same way, giving as complete an inventory of every species' courtship movements as we could achieve.

In the second film, the same shots were arranged from a different point of view: All the comparable movements of different species were put together, so as to afford the possibility of immediate comparison. This film showed all the initial head-flicks of all the species, one after the other, then all the grunt-whistles, and so on.

I would like to point out one result from the phylogenetic comparison of the motor patterns in these films. They are extremely similar in species which differ widely in external appearance. The courtship movements in the Mallard, are found again, with slight variations, in very many of the other species of surface-feeding ducks. One important point is that these variations often do not concern the form of co-ordination of single motor patterns, but their combination (Figure 26).

Let me give you a few examples of this extremely interesting phylogenetic process of recombination of behavior patterns. Take the head-up-tail-up movement of the mallard. After a greater or lesser number of head-flicks, the drake suddenly pushes its head and its tail up beyond the vertical, so that its body is bent into a crescent. In the Bahama, the head-up and the tail-up movements are identical with those of the mallard, but they are not performed simultaneously; the bird first does a very marked tail-up movement and follows it up with a typical head-up. Furthermore, this sequence of movements is, in the mallard, always followed by turning the head toward a female, then by the bridling movement, in which the bird sits straight up in the water and draws its chin inward, and finally by nod-swimming and turning the back of the head toward the female. In the Bahama, the movements already described are always preceded by one more particularly emphatic head-flick, and followed by turning the head toward a female; there is no bridling, no

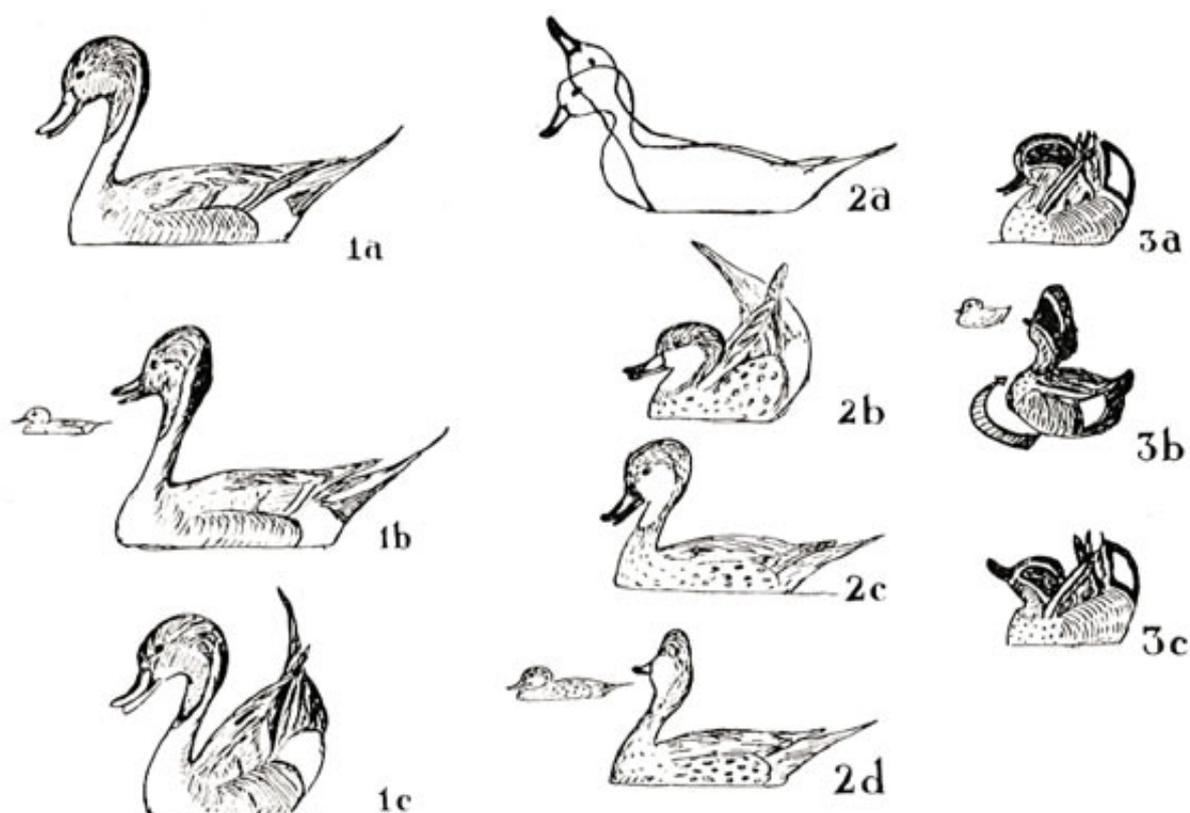


Figure 26. Different linkages between identical motor patterns in courtship movements of dabbling ducks: (1) common pintail, *Anas spinipectus* A) head-up movement, followed by B) turn-to-female and C) head-up simultaneously with tail-up, also followed by B) as above; (2) Bahama pintail, *Anas bahamensis* A) to D) obligatory linkage of A) initial head-flick, B) tail-up, C) head-up, and D) turn-to-female; (3) European teal, *Anas crecca* A) and B), simultaneous head-up and tail-up, followed by pivoting of the whole body toward the female, and C) isolated tail-up, as in the Bahama, but not followed by any movement.

nod-swimming. The bridling, however occurs in the Bahama duck exclusively in another combination, that is to say immediately after copulation. The same principle is repeated many times. The elementary motor patterns are more widely spread among the species than their combinations.

Now the point is this: In comparative phylogenetics we always judge the age of a characteristic by its distribution among allied species. If the head-up pattern alone occurs far more widely spread than the head-up simultaneous with tail-up plus look-to-the female plus bridle, plus nod-swimming, it definitely means that this combination is phylogenetically younger than its elements. This is entirely born out by checking it with other comparable characteristics and their distribution. In other words, we can conclude that the combination and recombination of the single motor elements are the latest steps in the evolution of these behavior patterns of Anatinae! In my opinion, this most important conclusion is

strongly confirmed by the fact that we occasionally find new combinations of older motor patterns in domestic strains of duck. I had khaki Campbell ducks in which the head-up-tail-up was welded into a unit with the down-up movement following immediately afterwards. The same combination, incidentally, is characteristic of the gadwall, *Anas (Chaulelasmus) strepera* L. This is an important fact, as it undoubtedly is a step in the evolution of a behavior pattern that has taken place within historical time. It would be interesting to know whether it is due to a single mutation.

An interesting item I have not mentioned and would like to mention is that very often these species' or sub-species' differences are only in quantity of movement, that you see more of one movement and less of another movement. What we have to search for is individual differences in wild species. We must get many shots of mallards, see how great is the distribution of variation between individuals, and measure them for quantitative differences.

Fremont-Smith: Would slow-motion pictures help with that?

Lorenz: We should get slow-motion pictures in exact profile so that we can get a fairly correct curve of this. You must photograph some background against which you can reorient your pictures, otherwise the jumping of the picture disturbs the curve. We have tried to do this.

Then, you might take two points on the bird's body, for example, the eye and the tip of the bill, and draw the curve of such a movement and then extract the constants for different shots; furthermore, we must see how curves differ in different species and so on.

That would be very helpful but we will need a number of further details as well.

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