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ETHOLOGY, THE COMPARATIVE STUDY OF ANIMAL BEHAVIOR

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ETHOLOGY is an approach to the study of animal behavior, derived from the discovery of instinctive movements. Anticipating the modern viewpoint, Spalding, as early as 1873, proposed, on the basis of his experiments, that besides learned behavior there existed inborn behavior patterns, the "instincts." He kept nestling swallows in such narrow cages that they were unable to practice any flying movements. Nevertheless, these birds were able to fly excellently, on their first opportunity, when released at the age when swallows normally fly. Spalding's experiments were forgotten until Whitman (1899, 1919) and Heinroth (1911) independently called attention to these innate behavior patterns. Each of these authors explored the systematics of a group of birds—Whitman, the pigeons; and Heinroth, the ducks. Since morphological characters proved inadequate, they each sought other genetically constant characters upon which to base their classifications. They thereby discovered behavior patterns, such as courtship display movements, with specific taxonomic value.

Craig (1918), through his own researches, made the first step from the purely descriptive to the nomothetic stage, when he discovered a certain lawfulness in these fixed patterns of behavior. Lorenz (1935, 1937) developed these beginnings of Craig's further, and published the first general work program which led to further ethological contributions by other investigators. More and more, interest concentrated on these instinctive acts, which we will discuss later in detail.

The method of ethology is the same which every scientific discipline uses when exploring an organ or organism. It starts with the description of behavior forms, which leads to the systematic cataloguing of these forms, and may then proceed to a physiological causal analysis. The method of explanation includes both comparative morphology and physiology, the ultimate aim of which is the causal understanding of the observed regularities and lawfulness; but emphasis is placed on the evolution, ontogeny, and survival value of behavior.

Although classical physiology is today fully aware that there are various levels of integration and coordination, in the past this discipline concentrated mainly on the analysis of simple muscular contractions. The ethologist emphasizes these various levels of integration and tries to describe, analyse, and understand the lawful interplay and succession of very different muscle actions. The entire organism, rather than isolated nerve-muscle units within the organism, is the object of study. It is an approach which includes the relations of the organism to its environment (Ecology) and to the members of its own species (Sociology). The ethologist is particularly interested in the phylogenetic origin of the observed patterns of behavior, and tries to trace these by comparing related species. Indeed, it is this phylogenetic constancy, i.e., the presence of similar behavior forms among related species, which establishes the validity of the phenomena with which he deals.

Ideally, the start of any analysis is an inventory of innate behavior patterns, the ethogram, obtained by observation of captive and free-living animals. Although recent ethological investigations, such as those of Marler (1956) on the behavior of the chaffinch and of Morris (1958) on the reproductive behavior of the ten-spined stickleback, sometimes begin this way, older ones often began with chance observation and subsequent interest in the origin or function of a particular animal movement.

The ethologist is interested in the survival value of observed behavior patterns, not with a view towards answering the finalistic question "for what?" but rather to understand in the service of which function selection pressure has determined the evolution of a certain structure. It should be pointed out that ethology does not restrict itself to the study of innate behavior patterns alone, as is sometimes critically implied. All ethologists are aware that in higher animals innate and acquired patterns of behavior are nearly always linked together in a unified functional system, which may be explored as isolated partial systems (both physiologically and psychologically) and as a single system (ethologically).

Behavioral phenomena have been generally considered within the province of psychology by American investigators, but all behavioral processes fall equally within the scope of physiological explanation. Whereas physiologists and psychologists, when dealing with animal behavior, have primarily emphasized reflex theory, conditioning, and learning, the positive contribution of ethology has been its emphasis and exploration of those mechanisms which are innate, i.e., those reactions and states within the animal upon which conditioning and learning depend.

Ethological investigation is concerned with the behavior of many diverse groups of animals, and its experimental tests are designed to explore specific aspects of behavior observed under natural conditions. In this it also differs from American psychology which confines itself to a few selected laboratory animals. Consequently, ethologists have refused the historical term "animal psychology," without in any way minimizing the individual contributions of this and other behavioral disciplines.

THE INSTINCTIVE MOVEMENTS

Many papers have confirmed the constancy of instinctive behavior patterns first demonstrated by Whitman and Heinroth. It is only necessary to mention a few of these studies—that of Lorenz (1941), dealing with the courtship postures of 16 species of ducks, of Crane (1949, 1952) dealing with courtship and threat display in 15 species of salticid spiders, and the defense display of 15 species of mantids, Baerends' and Baerends von Roon's (1950) cichlid studies, Fulton's (1932, 1951) studies of the songs of crickets and katydids, Jacobs' (1953) studies dealing with the stridulatory behavior of grasshoppers, and the detailed studies of Faber (1919, 1932, 1936, 1953) on grasshoppers over a period of three decades. In Great Britain, Sladen (1899, 1912) early utilized behavioral differences in his taxonomic studies of bumblebees; and in his taxonomic studies of termites and their nests, Emerson (1938, 1956) emphasized the biological significance of the study of the phylogeny of behavior. The fact that the instinctive behavior movements of all individuals of a natural systematic group (species, genus, family, etc.) expresses itself in the same way, suggested that the time sequence of the individual muscle actions involved in a movement is an inherited trait. Lorenz therefore termed these movements "fixed patterns" (Erbkoordinationen). These movements sometimes evolve phylogenetically more conservatively than morphological characters. The scratching movement with the hind leg found in all amniotes (reptiles, birds, and mammals) is one example (Heinroth, 1929), the synchronized wing-leg and double wing-neck stretch movements found among birds another (Fig. 1). A certain variability within the species derives from the superposition of fixed patterns (see p. 196) and especially by the fading of intensity, to which all such movements are subject. Some intraspecific variability may also be due to learning superimposed on an innate behavior pattern, as in the nut-opening technique of squirrels (see p. 199). There are all gradations from intention movements, which indicate what an animal "wants" to do, up to the fully executed patterns of behavior. A fixed pattern of behavior is frequently combined with a taxis, forming a natural unit which is designated the instinctive act (Instinkthandlung). [An instinctive act may include appetitive behavior and releaser mechanisms, as well as a taxis and instinctive movements.] The prey-catching reaction of a frog is composed, for example, of a directed orientation movement in line with the prey (turning towards it), followed by the fixed pattern, "snapping." The greylag

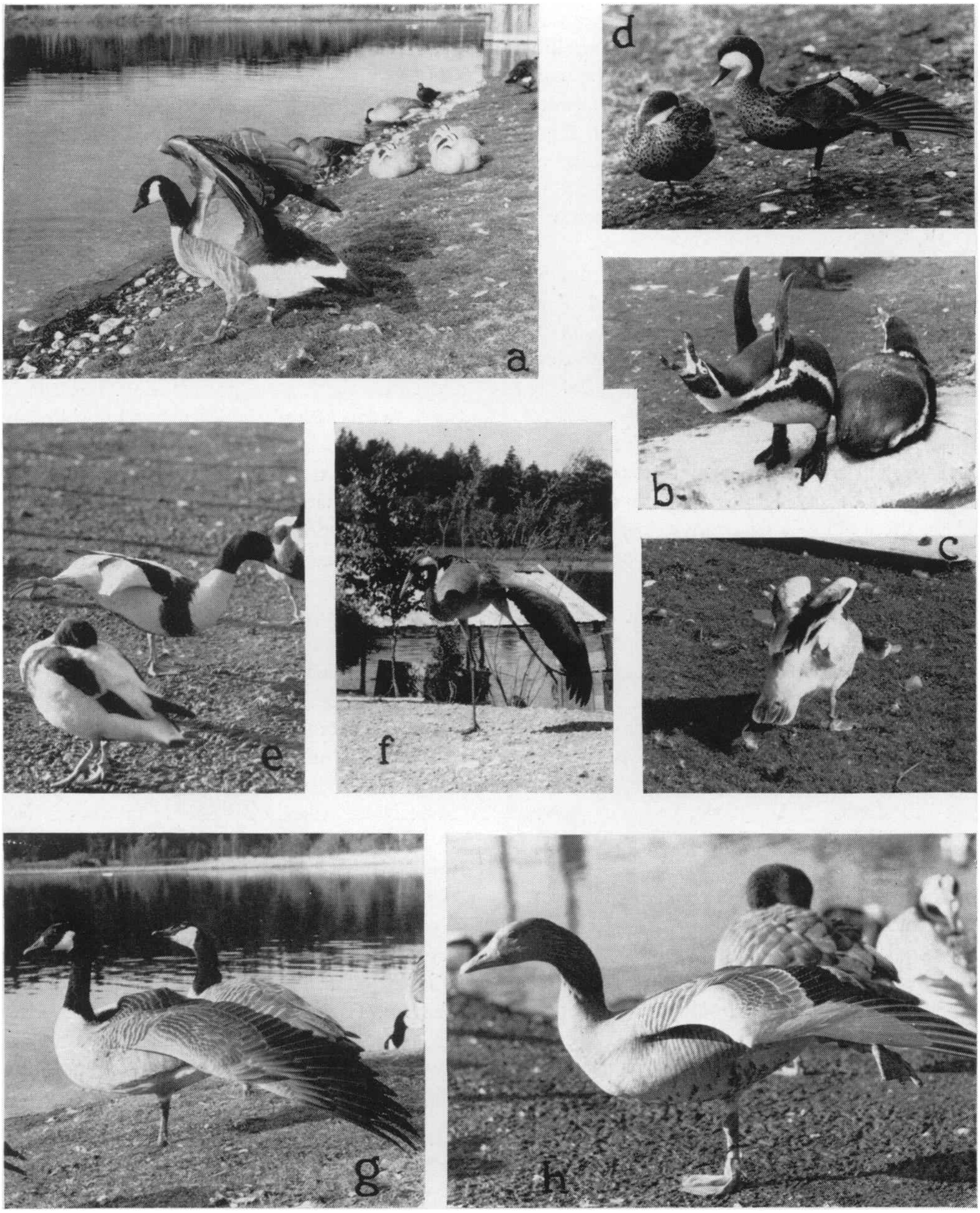

FIG. 1. INSTINCTIVE STRETCH MOVEMENTS

These fixed behavior patterns, found throughout the class Aves, are often performed soon after hatching. *a*, The beginning of the double wing-neck stretch in the Canadian Goose, *Branta canadensis*; *b*, the forelimbs of penguins have undergone considerable morphological modification, but as seen in this species of *Spheniscus*, the double wing-neck stretch is retained; *c*, double wing-neck stretch in immature Sheld-Duck, *Tadorna tadorna*. Leg-wing stretch movements are shown in *d*, the Bahama Duck, *Poecilonetta bahamensis*; *e*, the Sheld-Duck, in which the right wing has been clipped; *f*, the Crane, *Grus grus*; *g*, the Canadian Goose; and *h*, the Greylag Goose, *Anser anser*. (Photographs: S. Kramer.)

goose, *Anser anser*, which rolls a displaced egg back to the nest, prevents the sidewards rolling of the latter by following it with looping contact movements of the beak. If the egg is suddenly removed once the movement has started, the fixed pattern "egg-rolling" continues almost as a vacuum activity (Leerlaufreaktion). In the latter case, no sidewards balancing movements take place.

Experiments with animals isolated from members of their own species and deprived of other learning possibilities (Kaspar Hauser tests) have shown that these fixed patterns may develop independently of a specific pattern of previous reinforcement, i.e., learning. Grohmann (1939), without knowing of Spalding's experiments, raised pigeons in cages so small that they were unable to make any wingbeat movements. Nevertheless, these animals could fly as perfectly as the control animals which had the possibility of "learning" to fly. Whitethroats (*Sylvia communis*), which Sauer (1954) raised in isolation in soundproof chambers, developed all 24 species-specific calls, and the sequence of development in all these isolated birds was the same. Likewise, the sequence of species-specific behavior patterns associated with display and brood-rearing has proved to be innate in squirrels and hamsters raised in isolation (Eibl-Eibesfeldt, 1951b, 1953). In many behavior patterns of invertebrates, it is obvious that learning is excluded. Courtship behavior, which occurs on the first meeting of an adult male spider with a female in the requisite physiological state, inhibits their usual predator and self-protective behavior. In one species, at least, (*Eustiromastix* sp.), it undoubtedly prevents the male from being eaten by the female before copulation. In this latter case there is clearly no time for learning, and no evidence was found of display learning among other species (Crane, 1949). Therefore, these patterns are termed "innate," i.e., they are inherited and not learned as the result of imitation or exercise. This is not to say that external environmental stimuli play no role in their normal development. They certainly do so, but in the same way that they influence morphological structures. Just as the male mallard duck inherits its green head, a morphological character which develops as a releaser just before it is sexually mature, it also inherits its grunting whistle (specific behavioral character).

A good demonstration that behavior patterns can be inherited was recently given by von Hörmann (1955). She traced the inheritance of fixed behavior patterns by crossing two closely related species of *Gryllus* differing in four specific characteristics of their behavior. It was found that in three characters, the inheritance was monofactorial. Earlier, Fulton (1933, 1937) had shown the value of utilizing behavioral characteristics for interpreting the relationship of three ecological races of the cricket, *Nemobius fasciatus*. These races, *N. f. fasciatus* (De Geer), *N. f. socius* Scudder and *N. f. tinnulus* Fulton, showed no distinctive morphological characteristic, but possessed distinctive songs. Crosses between *socius* and other races gave no offspring, but those between *fasciatus* and *tinnulus* gave hybrid offspring from seven pairs out of eight. On maturity the hybrids proved to have an intermediate type of song which had never been detected in nature. Fulton concluded that these results indicated that the so-called races constitute natural groups which maintain their integrity in nature.

Observation of the intact animal shows that behavior is not always the response of a passive animal to an external stimulus. When in a state of special readiness to perform a specific activity, the animal often actively seeks a stimulus situation which will permit the performance of this behavior. Craig (1918) called this characteristic activity "appetitive behavior." The term appetitive behavior is not always used in the same way. Van Iersel (1953) termed all courtship behavior appetitive behavior for fertilization, as he considered fertilization to be the terminal consummatory act. Such a broad definition is of little value, as it includes fixed patterns, taxis, and learned behavior. The use of the term appetitive behavior is here restricted to the unoriented seeking behavior, as utilized by Roeder (1955). It usually brings the animal to a satisfaction.

[The goal of the animal is the performance of an act. The dog does not kill "in order" to eat—he may often kill independently for the satisfaction of releasing the innate movements of catching and killing.]

What factors are responsible for this special readiness to act? There are, of course, external factors which have proved to have a stimulating influence. Van Iersel (1953) showed that the eggs of the stickleback not only release fanning, but stimulate the broodiness of the male stickleback. Furthermore, there are inner sensory stimuli, for example, those reporting the state of a storage organ (stomach, bladder, intestine, etc.), which can build up a certain appetitive behavior (food-seeking, or seeking for a place of defecation). Important inner stimulating factors are also the hormones (Beach, 1947, 1948), which, together with external stimuli, induce such phenomena as rutting behavior. With testosterone, for example, one can obtain sexual activity in vertebrates long before sexual maturity, or outside the normal sexual cycle. Progesterone specifically influences the nest-building behavior of female white mice (Koller, 1952). Hormones, it is known, have inhibiting influences as well as stimulating ones. Kilak and Beach (1955) have shown that estrogen inhibits aggressiveness in both sexes of the golden hamster. A real understanding, however, of the mechanism by which hormones induce or inhibit specific behavior is lacking.

Much has been written concerning hormonal influences on behavior, but relatively little attention has been given to those behavioral factors which influence hormone production. Lehrman (1958a, b) studied the effects of courtship and nest-building behavior on the induction of broodiness (egg incubation) in the ring dove, *Streptopelia risoria.* His experiments led him to conclude that participation in both courtship and nest-building brings about the physiological changes underlying the onset of the readiness to incubate. Subsequent comparison of the effects of progesterone and estrogen on incubation behavior with the effects of participation in courtship and nest-building led him to suggest that courtship stimulates estrogen secretion and that estrogen stimulates nest-building behavior, which in turn encourages progesterone secretion leading to incubation. These studies draw attention to the neglected fact that behavior exerts an influence on physiological processes and metabolism, as well as the other way around (see also Beach, 1948).

The main completely unsolved physiological problem regarding instinctive movements lies in the fact that there are lawful fadings of the inner readiness to act which cannot be explained by any of the above-mentioned factors. Thus Lorenz (1937) described that his tame, well-fed starling, which was deprived of normal fly-catching, reacted more and more unselectively to outside stimuli (lowering of threshold) with certain predatory activities and finally, if adequate stimuli (flies) did not appear for a long time, the whole sequence of fly-catching went off in vacuo. The starling suddenly flew up, snapped at nothing that could be seen, went back to his perch, performed a characteristic killing movement, and finally swallowed. Similar examples are given by Koenig (1953). On the other hand, increases of threshold, in which the fixed pattern is harder and harder to release, have also been observed. This spontaneity of behavior, known for many fixed behavior patterns, was interpreted by Lorenz (1937) upon the hypothesis that every instinctive act is fed by its own mechanism of excitation in the central nervous system. In this Lorenz was influenced by the papers of von Holst (1935, 1936, 1937) which demonstrated a central nervous system automatism for locomotion. Accordingly, while an inhibitory mechanism exists, preventing discharge, the excitation is built up in the central nervous system. When the specific stimulus situation is encountered, the inhibition is removed. The performance of the fixed behavior pattern uses, in part, the built-up energy and hence the concept of the "consummatory act." In which way, and specifically what is stored and consumed, is still completely unknown. One can think of biochemical processes through which a higher energy level is built up and discharged roughly comparable to the processes in working muscles. As will later be pointed out, there are also neurophysiological results which confirm spontaneity in the central nervous system.

By special experiments on intact animals, Drees (1952) and M. Schleidt (1955) have shown specific central nervous fatigue of fixed behavior patterns. Nevertheless, a fixed behavior pattern does not end by complete exhaustion of the central nervous mechanism—it normally ends through the performance of the act which activates a special switch-off mechanism. The consummatory stimuli can be initiated by the proprioceptive system as well as by other sensory organs, as has been suggested by Bastock, Morris, and Moynihan (1953). In many rodents, for example, escape reactions come to an end when certain stimuli of the shelter, such as darkness and smell are reached (W. M. Schleidt, 1951), and certainly not as a specific central nervous energy is used up. Prechtl (1953), in studying the gaping reaction of song birds, Franzisket (1953) the wiping reaction in the hindleg of the frog, and M. Schleidt (1955) the gobbling reaction of the turkey, all found evidence of fatiguing in places other than the motor center. For example, M. Schleidt was able to show that when the gobbling reaction was repeatedly released by a certain tone, the turkey stopped reacting, but immediately continued when another tone was used as a stimulus. This indicated that the motor center was not exhausted, and as she could exclude specific adaptation of the sense organ as well as a learning process as a possible explanation, she termed this special process afferent throttling (afferente Drosselung). Prechtl and Franzisket had previously shown similar phenomena, which the former termed adaptation and the latter termed afferent fatigue.

NEUROPHYSIOLOGICAL CONSIDERATIONS

There is considerable controversy regarding the elementary processes in the central nervous system, upon which fixed patterns of behavior with the above described properties can be based. Many still cling to the reflex-hypothesis explanation of all behavior, which Lorenz discarded in 1937. Therefore, in what follows, certain neurophysiological facts will be presented in brief, and their relationship to fixed patterns of behavior will be discussed.

According to the classical reflex theory all behavior is a response to external or internal sensory stimuli. An afferent nerve receives a stimulus from its sensory end-organ and carries the excitation to the spinal nerve cord, whose gray substance forms a "reflex center." Here the excitation is transferred to an efferent nerve. These three elements comprise the so-called "reflex arc." More complicated behavior patterns are nothing more than chain reflexes. When an eel swims, according to this theory, the contraction and relaxation of one segment mechanically stimulate the proprioceptors of the following segment, and these, in turn, stimulate the reflex arc which leads to the contraction of this succeeding segment.

Even at an early date there were findings which could not be put into this scheme without constraint. Graham Brown (1912) discovered that in a decerebrated cat two completely deafferentiated antagonistic leg muscles made rhythmical contractions. This led to the conclusion that there exists an endogenous automatism of the central nervous system independent of external stimuli. Weiss (1941) implanted a piece of embryonic spinal cord and an embryonic limb bud in the axolotl. This implant becomes innervated in the course of its development by the implanted embryonic spinal cord. In this process, the motor neurons grow faster than the sensory neurons, and reach the leg before the latter. At the moment that the efferent connection is made the leg starts to move. Although these movements were not completely coordinated walking movements, nevertheless, they showed the primitive form of coordination involving the alternate contraction of antagonist muscles. This, too, demonstrated the endogenous automatism of the central nervous system. This automatism has also been demonstrated by electrophysiological methods. Adrian and Buytendijk (1931) found in the isolated brain stem of the goldfish rhythmical electrical discharges which corresponded exactly with the frequency of breathing movements (movements of the operculum). Roeder (1955), who demonstrated spontaneous activity in the isolated ganglia of the cockroach, refers to a number of additional examples of automatism.

Von Holst (1953) has pointed out that our present knowledge of the relation of the central nervous system to the peripheral senses and muscular movement is meager in comparison to what is *not* known. The method utilized in such investigations determines in large part the extent of our knowledge and the nature of our conceptions. Heretofore, the most popular method consisted of artificially inactivating the central nervous system and then, through peripheral stimulation, evoking a peripheral response. It is largely on the basis of this one-sided methodology that the central nervous system is held to be only a reflex mechanism.

Rather than making exclusive employment of a methodology which begins with peripheral stimuli, von Holst (1935a,b, 1936, and 1937) has centered his experimental investigations on the central nervous system itself. He demonstrated that in the isolated ventral nerve cord of the earthworm there are salvos of rhythmical impulses exactly corresponding to the contraction of segments in the normal creeping movements of this animal. Earlier, he totally denervated a section of an eel so that this section could no longer contract. The wave of movements which began in the head region disappeared in this denervated segment, but it appeared again in the region behind this area, completely coordinated at the correct phase. The same was observed when a section was mechanically fixed. The process of coordination in such locomotion, therefore, takes place through the spinal nerve cord, but not as a result of "chain reflexes."

Similar phenomena have been demonstrated in other vertebrates. Tadpoles, in which the dorsal roots of the spinal cord were destroyed, were able to swim (Weiss, 1941). Deafferentiated tenches could swim in a coordinated manner as long as two nerves from the spinal roots innervating the pectoral fins remained intact. The same applied to the "spinal" dogfish (von Holst, 1936; Lissmann, 1946). A completely deafferentiated toad is able to swim in a coordinated fashion, according to Gray and Lissmann (1940), as long as both labyrinths are intact. After removal of both the labyrinths it was no longer able to do so. Here, a minimum afferent input appears to be necessary, but "chain reflexes" are likewise inadequate for the explanation of the locomotory pattern in these cases. It has been suggested that a certain input of sensory excitation may either remove an inhibiting mechanism or may raise the general level of central nervous excitation—we do not know.

In the relative coordination movements of many animals, including invertebrates and vertebrates, as well as man, there are central regulating mechanisms which lead to the final action. The fact that in certain situations, as for example, in motion, the "optomotor reflex" or the "postural reflexes" no longer operate, has been explained by classical reflex theory with the assumption that these reflexes are inhibited or blocked during motion. These assumptions, to which reflex theory frequently takes recourse, have largely gone unchallenged. Von Holst and his colleagues have succeeded in showing, however, that it is possible to subject such conceptions to experimental investigation.

Let us take two examples. Mittelstaedt (1949) has shown that if the fly *Eristalis* is placed in a striped cylinder, and the cylinder is rotated to the right while the insect is at rest, the fly changes its position by likewise moving to the right (Fig. 2a). This response has been termed the "optomotor reflex." If the fly begins to move spontaneously in such a cylinder, it no longer responds to the changed position of the stripes. In the latter case this reflex does not interfere with the fly's movements. According to reflex theory the optomotor reflex is inhibited during locomotion. Mittelstaedt succeeded in rotating the fly's head 180° around its axis and fixed it in this position, so that the right and left eyes were reversed (Fig. 2b). If the cylinder is then moved to the right while the insect is at rest, the fly responds by moving to the left. Theoretically, if the fly now begins to move spontaneously, it should move unhindered by any "optomotor reflex." Actually, however, when the fly begins to move spontaneously, it now moves alternately to the right and left in small circles until exhausted. The assumption that the optomotor reflex is inhibited during locomotion is clearly contradicted by this latter experiment.

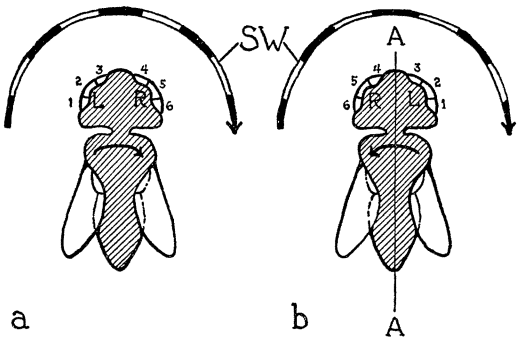

FIG. 2. THE TURNING RESPONSE IN THE FLY, *Eristalis*

a, Normal animal; *b*, animal after rotation of the head 180° around the axis A-A. R, L, right and left eyes (the ommatidia are schematically numbered). The arrow in the animal, around which a striped cylinder SW is moved to the right, indicates the direction of its active turning response. (After Mittelstaedt, 1949.)

The utricular statolith in the labyrinth of vertebrates is influenced by gravity. As von Holst et al. (1950) have demonstrated, if a passive fish resting in its normal position is tilted, say to the right, the increasing shearing force of the statolith on the sensory surface of the labyrinth on this side results in increased activity in the postural center of the central nervous system, and this sets in motion the motor movements that bring the fish back to its normal position. Under such experimental conditions this postural reflex works untiringly. During the normal activity of the fish, as in the search of food, however, spontaneous tilting movements frequently take place. Why, in this case, does the postural reflex fail to pull the fish back automatically to its normal position? According to reflex theory, the postural reflex is blocked during spontaneous movement. It can be shown by experiment that this is not the case. By placing the fish in a constant centrifugal field, it is possible to double the shearing force which the statolith exerts on the sensory surface of the labyrinth. Now, if one measures the frequent, spontaneous tilting movements which the free-swimming fish makes, one finds that they have decreased in magnitude, and that the tilting movements become less the heavier the statoliths are made. Thus, the righting reflex is not blocked during spontaneous movements, but is dependent upon or regulated by the afferent feed-back which they cause.

These, and a number of similar phenomena and experiments provide the basis of the reafference principle which von Holst and Mittelstaedt (1950) have suggested as a more accurate explanation of what takes place. In brief, this principle may be stated as follows: the sum total of all impulses produced by stimuli in any receptor are referred to as the *afference*, and the whole of the motor impulses as the *efference*. Afferent stimuli, however, may have two different sources: those produced by external energy changes, or the *ex-afference*; and those produced by internal energy changes in the muscular system, or *re-afference*. If we abandon the concept that all muscular activity is initiated by ex-afferent stimuli, we may now ask: "What takes place when efferent stimuli emerge from a particular motor center?"

According to this principle, each command, or fixed alteration of the impulse stream descending from some higher center *Zn* (Fig. 3) in the central nervous system to a motor center Z_1, causes here an efferent impulse, *E*, which gives rise to an activity change in the ganglionic mass, which is termed the efference copy, *EK*. The efferent impulse, *E*, induces not only the movement in the motor end organ, but also a reafference from that end organ, *A*, which returns to the motor center. The actual movement of the end organ is regulated by the reaction of the efference copy *EK* with the returning reafference, *A*. If we arbitrarily denote the value of the efference and its copy by a plus (+) sign, and the reafference by a minus (−) sign, the command descending from *Zn* flows out unhindered, and gives rise to constant efferent impulses, *E*, when *EK* and *A* exactly nullify each other. But if, as a result of some external influence, the total afference is too large, or too small, there remains in Z_1 a (+) or (−) residue. This residue continues upward to a higher center, or centers, as a report *M*, which may decrease or strengthen the initial descending command. This in turn modifies the efference emerging from the motor center Z_1. In this scheme, the (+) or (−) residue in Z_1, which continues flowing as a report, and originates as a result of outside influence via proprioceptors or exteroreceptors, is an *exafference*.

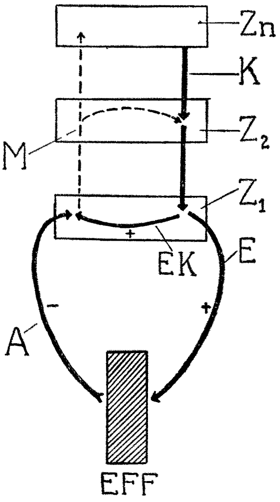

FIG. 3. ILLUSTRATION OF THE REAFFERENCE PRINCIPLE
See text for explanation. (After v. Holst and Mittelstaedt, 1950.)

The reafference principle not only enables one to predict the magnitude and direction of movement which an outside influence will exert on behavior, but it provides insight into known phenomena which have hitherto lacked an explanation. The visual phenomena which relate to space constancy may be included here. For example, whether a car moves across our field of vision, or we rotate our head or eyes about a car which is standing still, the image of the car moves across our retina in both cases. Only in the former case do we see a moving car—in the latter case we have a phenomenon known in the field of psychology as "space constancy." It is known, from cases of people in whom the eye muscles are paralysed (this has also been demonstrated by experiment), that every impulse to move the eyes, say, to the right (which cannot be carried out) results in the objects in the field "jumping" to the right. Since nothing has actually moved this is clearly an "hallucination," but it demonstrates the fact explainable by the reafference principle, that as a result of an unmatched efference copy an intended but unfulfilled movement may cause a perception.

Von Holst has emphasized the fact that the reafference principle is not meant to explain *all* phenomena in the central nervous system, but can in predictable fashion explain certain phenomena which reflex theory explains erroneously. It is only one of many central nervous mechanisms. Here it need only be mentioned that it illustrates in precise manner the errors that may arise if we insist upon explaining behavioral data from one area of investigation with as yet limited theoretical constructions in the field of neurophysiology. As von Holst has indicated, until our knowledge of central nervous mechanisms is more adequate, each field must be left to develop along its own lines. Behavioral data, which do not fit into existing

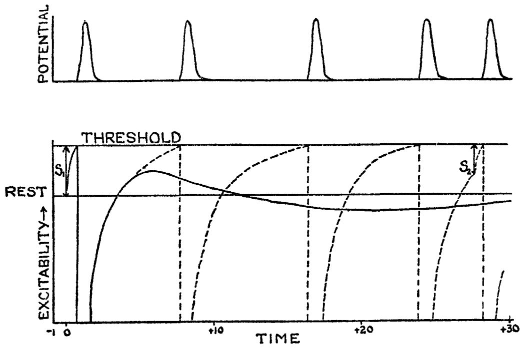

FIG. 4. EXCITABILITY CHANGES IN STABLE (STIMULUS-RESPONSE) AND UNSTABLE (SPONTANEOUSLY ACTIVE) NEURAL ELEMENTS

(Lower graph) Solid curve represents excitability sequence in elements such as mammalian A fibers following stimulus S_1. Broken curve represents predicted excitability sequence in elements with a lower threshold and, hence, repetitively active following stimulus S_1. S_2 is the stimulus interpolated at some point in the spontaneous excitability change, causing premature discharge. (Upper graph) Nerve impulses that would arise from the excitability changes shown below. Time units would have different values for different types of excitable tissue. In the case of mammalian A fibers the units would be milliseconds. (After Roeder, 1955.)

neurophysiological theory, provide us with extremely valuable focal points for further investigation.

The spontaneous activity which has been demonstrated in isolated parts of the central nervous system certainly provides some basis for spontaneous behavior of the intact organism. Roeder (1953, 1955), who taught neurophysiology on the basis of reflex theory for many years, has recently arrived at the same conclusion, after seeing the complete inadequacy of the reflex theory for explaining certain phenomena in the behavior of insects. Roeder has suggested that those individuals who attempt to present ethology, together with its concept of endogenous activity, as a vitalistic philosophy should read the voluminous literature on the physiology of the heart, "a spontaneously active, but certainly not a supernatural organ."

Roeder has indicated that existing neurophysiological findings support the concept of spontaneous activity. He, too, pointed out that in the neural elements underlying spontaneous and reflex behavior only gradual differences exist as regards their threshold of excitability. His theoretical explanation is as follows. In the stable neurons, the excitability remains at a constant resting threshold. A stimulus is necessary to bring the excitability to the level of discharge. After discharge the excitability falls to zero, gradually rises again, and briefly passes the resting threshold ("phase of higher irritability"), then again falls to the normal resting threshold (see Fig. 4). In the unstable neurons the excitability, and with it the readiness for response, builds up until the threshold of release is reached by itself and a spontaneous discharge takes place. Between the extremes of these two types of neural elements, there are all gradients. Whenever the physiological state of an organism causes the resting and response thresholds to become approximated (and this has actually been accomplished in varied ways experimentally) one stimulus may lead to a self-perpetuating sequence of discharges as the curve in the phase of higher irritability will repeatedly reach the releasing threshold.

Actually, very little is known about the anatomical basis of the "centers" responsible for fixed patterns of behavior. We know that coordination in the spinal cord is based on the interaction of unstable cells, which are often far from each other. The coordination apparatus would therefore seem to be little "centralized." Those "centers" which have been localized until now, through destruction or stimulation of parts of the central nervous system (Aronson and Noble, 1945; Huber, 1955; etc.) may be considered as initiating areas. Such initiating areas have been demonstrated by Hess (1948) and Hess and Brugger (1943), who drove fine electrodes into the diencephalon of otherwise intact cats and with simple electrical impulses were able to release highly integrated fighting, threatening, sleeping, eating, and defecating responses together with appropriate appetitive behavior.

Another important approach to an understanding of the central nervous system was made by Coghill (1929, 1933), who utilized the embryonic behavior of *Amblystoma* as a clue to the functional development of the neuromuscular system. It was Coghill's conclusion that the developing pattern of embryonic behavior in vertebrates consisted of the expansion of a growing, primarily integrated, total pattern of action. Within this total pattern, partial patterns, such as reflexes, arise later in development by individuation, through restriction of both the field of motor activity and the field of adequate stimulation. It is in a field of almost total inhibition that the local reflex emerges. Since inhibition is an active process, the mechanism of the total pattern participates in every reflex. The fallacy of the traditional conception of the chain reflex, that one initial reflex stimulates the next in series, and this the following, etc., became more apparent, Coghill felt, when one studied the ontogeny of behavior.

Spontaneous activity is a familiar phenomenon to the vertebrate embryologist who observes behavior. *Myogenic activity*, which originates within the muscle tissue itself, spontaneously and usually rhythmically, occurs not only in the developing heart but also in the trunk musculature of certain vertebrate embryos. Since motor neurons usually establish functional connections with their muscles before their sensory connections are established, one also observes *neurogenic activity* of muscles due to discharge of the motor neuron, either spontaneously or under the influence of stimuli from outside. *Reflexogenic activity*, in which a receptor sensory neuron, one or more intercalated neurons, and an effector motor neuron are involved, only occurs relatively later in development (Hooker, 1952).

The results of these diverse investigations amply confirm the fact that our present knowledge of the relation of the entire organism to the central nervous system, and in turn the relation of the central nervous system to muscular movement and behavior, is far from complete. We require fuller knowledge of the many behavioral responses of which the animal is capable, if our neurophysiological explanations are not to remain restricted to isolated, special systems within the animal.

THE INNATE RELEASING MECHANISM (IRM)

The conception of a continuous production of central nervous system excitation, normally blocked by another inhibitory mechanism, led to the assumption of a special afferent apparatus which removes this inhibition at the biologically appropriate moment. With the arrival of a specific key stimulus the innate releasing mechanism opens the way for the above impulses to their appropriate motor organs. Although these key stimuli are, as a rule, quite simple, they normally characterize the biologically adequate situation in unmistakable fashion. We can often ascertain such stimuli by experiments with dummies. If a bundle of red feathers is presented to a male robin (*Erithacus rubecula*), it will immediately attack this crude dummy, while it would ignore the stuffed skin of a rival male from which the red breast feathers had been removed (Lack, 1943). Sometimes the animal reacts to configurational properties or "Beziehungsmerkmale." A flight silhouette of a predator bird cut out of cardboard has a flight-releasing effect only when moved in one direction (Tinbergen, 1948). When moved in the opposite direction it has no effect at all (Fig. 5). To the human observer, such a silhouette appears more like a flying goose than a bird of prey, when the direction of movement is reversed. Often several key stimuli work together. In such cases, each of these stimuli are capable of a releasing action, but the effectiveness of a dummy proves to be proportional to the sum of the stimuli used (Seitz, 1940). Such innate reactions are differentiated from learned or conditioned responses which are released by complex stimulus situations. If something is changed in such a learned "Gestalt" the animal has to relearn the new situation. Tame birds become shy when the investigator or keeper wears glasses for the first time, or changes his usual clothing.

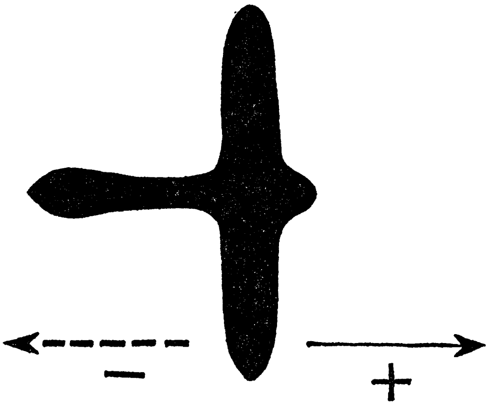

FIG. 5. EXPERIMENTAL MODEL USED TO RELEASE ESCAPE REACTIONS

Model of bird of prey releases escape reactions (flight) among young gallinaceous birds, ducks and geese when moved to the right. Moved to the left (broken arrow) it has no releasing function. In this case shape in relation to the direction of movement provides the active sign stimulus. (After Tinbergen, 1948.)

When referring to innate behavior patterns and innate releasing mechanisms, the term "innate" includes two different concepts. In the first case it indicates that such a motor pattern was not learned by exercise, and in the second case that the reaction to the stimulus was not conditioned.

The innate releasing mechanism has been defined in purely functional terms. Its neurophysiological basis remains unknown. We will deal with the behavior patterns of structures which have been developed for a releasing function (so-called "releasers") in more detail below. It might be appropriate at this point, however, to draw attention to two types of errors made in behavioral explanations. The first of these consists of the use of isolated neurophysiological data as a general explanation of all behavior. On the other hand, investigators familiar with specific behavior patterns have as often interpolated existing neurophysiological data towards the explanation of such behavior. In both instances the link between the two types of data, valid as each may be in itself, is frequently not established.

The increased selectivity of the innate releasing mechanism by learning processes

The specificity of such releasing mechanisms varies greatly. Often an animal reacts unselectively to a few key stimuli. In the common toad (*Bufo bufo* L.), for example, nearly every object between 2 mm. and 20 cm. in length releases prey-catching behavior. Moving pebbles, pieces of wood or paper, flowers, etc., are snapped at by young adults as if they were insects or worms. The upper size limit of such prey may vary. With larger objects the direction of movement often decides what the toad will do. If the object moves towards the toad, the toad will flee; but the toad will follow the same object if it moves away.

The wide variety of objects towards which an innate releasing mechanism will be directed also becomes selectively narrowed through learning. After negative experiences with unpalatable food, the toad quickly learns to avoid such objects (Eibl-Eibesfeldt, 1951a). Polecats follow and bite every fleeing object which is smaller than the animal itself. For example, they attack a fleeing rat immediately, but if the rat sits quietly in a corner the polecat merely sniffs at it curiously. If the rat runs towards it, the polecat runs away. But after one rat-killing experience, it will recognize and attack a rat under any circumstances. The orientation of the killing bite to the neck of the prey is also learned. The inexperienced polecat grasps the prey at various parts of the body, but is successful only if it grasps the neck, and this it learns in a few trials (Eibl-Eibesfeldt, 1957b).

Imprinting

Imprinting, which is one form of conditioning, may be to some extent considered as an unselective innate response which becomes directed towards a specific object. It resembles the above-mentioned narrowing down of an innate response through learning, but differs in at least one, or sometimes two important points. First, such imprinting takes place during an extremely short sensitive period in the life of the animal. Newly hatched goslings from an incubator immediately follow the human being who is their keeper and stick to this human object relationship. If they have once followed him for a few hours, they will then refuse to follow their own mother, no matter how often they are placed together with her thereafter (Lorenz, 1935). Hess (1955) has shown that imprinting in the Mallard is restricted to the period between 12 and 17 hours after hatching. Lorenz (1955) allowed a greylag goose (*Anser anser*) to raise Muscovy ducklings (*Cairina moschata*) as her own young. After five weeks he separated the ducks from the goose. Although from that time on the Muscovy ducks showed special reactions only to the members of their own species, with the onset of sexual maturity they chose greylag geese for sexual partners, thus proving to be imprinted to the latter. Fabricius (1951) has carried out additional extensive studies on imprinting in anatids. Similar imprinting phenomena are known for mammals (Grabowski, 1941).

The second characteristic which sometimes distinguishes imprinting is its apparent irreversibility. In certain instances it has been shown that if a behavior pattern is once fixed to a given object, this object fixation persists. It is possible for an imprinted animal to react to a substitute object, but in a situation of choice, it will prefer the object to which it has been imprinted. Hellman (cit. by Lorenz, 1955) raised budgereegahs artificially. When these birds became sexually mature he enclosed them in a covered cage, so that they could not see their keeper. The birds paired, brooded, and cared for their young, but when Hellman, together with Lorenz, uncovered the cage, both animals showed courtship display towards these men. Thereafter, they no longer showed pairing behavior towards each other, and neglected the care of their young.

Betrothal ceremonies are performed by juvenile bullfinches (*Pyrrhula pyrrhula* L.), as a rule between siblings of the same nest. Sooner or later these sibling betrothals are dissolved, each partner finding a new mate of the opposite sex, even if the original sibling pair was a homosexual one. Bullfinches reared in isolation usually accept the human keeper as a substitute for their sibling partner. If, during autumn and winter, the bird finds opportunity to make the acquaintance of a conspecific of the opposite sex, its relation to the human gradually dissolves and normal betrothal takes place. If, however, the bird continues in human company during this period, it later accepts a human being as a permanent mate, and it is only then that the sexual imprinting to humans becomes irreversible (Nicolai, 1956).

Hinde, Thorpe, and Vince (1956), studying the following responses of young coots (*Fulica atra*) and moorhens (*Gallinula chloropus*), were able to show that this response can be released by a number of objects quite different from each other in size and shape (viz., model of moorhen, black box, small colored ball, colored hides, man, etc.), but having in common the character of being in motion. The response takes place independently of any prior learning. "Imprinting" occurred when the birds followed the moving object and was not dependent on brooding, feeding, or any other activity normally directed by the parent to its young. These birds, however, could be trained to follow different models on successive runs—and it appeared that birds trained on one model would generalize to others presented in the same circumstances throughout practically the whole period in which they would follow at all. The investigators suggested that this response is "self-reinforcing" and that learning occurs when the birds maintain, by means of locomotion, a more or less constant spatial relation with a moving object. As a result of these experiments they concluded that the learning process in the following response of coots and moorhens was not irreversible, and that there was no evidence that imprinting in these cases was fundamentally different from other types of learning. The effects of this type of imprinting on adult behavior was not studied in these experiments.

Other types of restricted learning periods

There are certain forms of learning processes which have in common with object-imprinting the restriction to a definite sensitive period, which is often considerably separated in time from the effective demonstration of what has been learned. Heinroth (cited by Lorenz, 1955) once made a tape-recording of Blackcaps (*Sylvia atricapilla*) which he kept together in a room with 12-day-old nightingales for one week in May. At that time the young nightingales were only able to give a begging call. But when they began to sing in January, much to Heinroth's surprise, they showed a song which was in every detail comparable to the recording of the Blackcap song.

Utilizing a sound spectrograph, Thorpe (1954) studied the song-learning process in the chaffinch (*Fringilla coelebs*). In the first series of experiments, birds, which were reared normally by their parents, were isolated from them from their first September onwards. Such birds acquire normal songs when isolated from sight of other singing chaffinches, or even when subject to an overwhelming barrage of alien songs of other birds. They attend only to the normal song of their own species, which they hear outside. In this lack of general imitation the chaffinch differs from the bullfinch (*Pyrrhula pyrrhula*) and the greenfinch (*Chloris chloris*), which can learn complete songs from alien species. If such birds, isolated as juveniles, are prevented from hearing all bird song from September until May, but are allowed to hear each other, we find some difference between their songs and those in the first series of experiments. The first two phrases of their song are practically normal, but there is a slight tendency for the third phrase to be abnormal.

In the third series of experiments, birds which have been hand-reared and completely isolated from experienced singers since the first few days of their life show a song in which the first two normally distinct phrases are inseparable, the first half of the third phrase is always lacking, and the second half of the third phrase is either lacking or curtailed. The difference between the second and third groups of birds is explicable, according to Thorpe, only on the basis that some characteristics of the normal song have been learned during some sensitive period in early youth, before these birds are themselves able to produce any kind of full song. Thorpe concluded that the normal chaffinch song of three phrases has a very restricted inborn basis, amounting to little more than the ability to produce a song of normal length (2.3 seconds), and that the refinements have to be learned. Nevertheless, the innate basis of this song is sufficiently selective to ensure that the bird does not normally acquire notes or songs from any species other than its own.

THE RELEASER

Hand in hand with the development of selective receptive apparatus (the innate releasing mechanism), the corresponding signaling apparatus has evolved. These so-called "releasers" regulate intraspecific behavior as well as other interspecific forms of communication (for example, in symbioses).

Very different things may serve as releasers. Often morphological structures are developed as signals, such as the nuptial plumage of male birds and the courtship colors of lizards and fishes. As these optically effective releasers are easily imitated with dummies, we have learned a great deal concerning them (Tinbergen, 1948). In these studies the previously mentioned law of heterogenous summation was discovered. These morphological signals also presented investigators with the possibility of creating supernormal objects. Such investigations revealed that the stimuli which

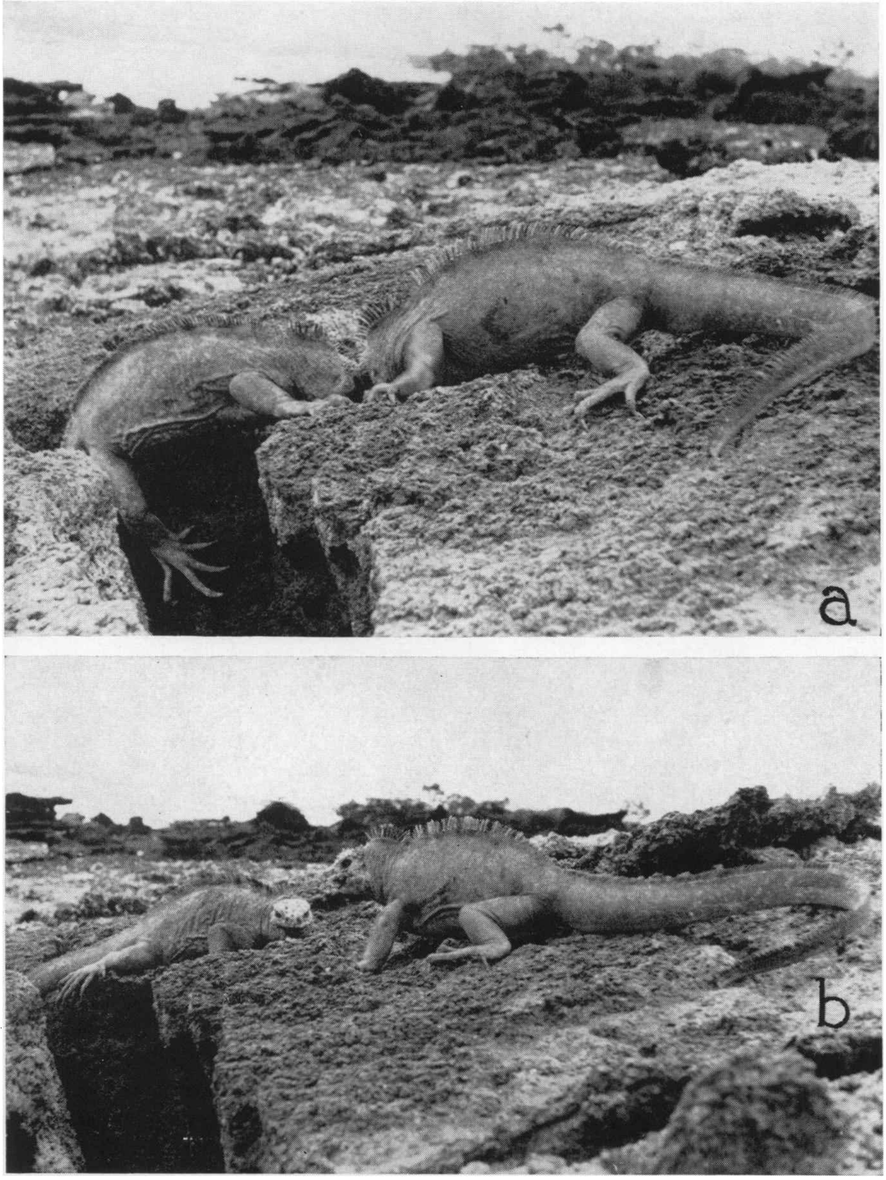

FIG. 6. CEREMONIAL FIGHT OF MALE MARINE IGUANAS, *Amblyrhynchus cristatus*
a, The animals try to push each other from a given spot with their heads. They neither bite nor cause injury but simply pit their strength against each other. *b*, The weaker one assumes a submissive posture by throwing himself flat on his belly. The winner (right) then stops fighting and waits in a threatening posture for the departure of his rival. (Photographs: I. Eibl-Eibesfeldt, Galapagos Islands.)

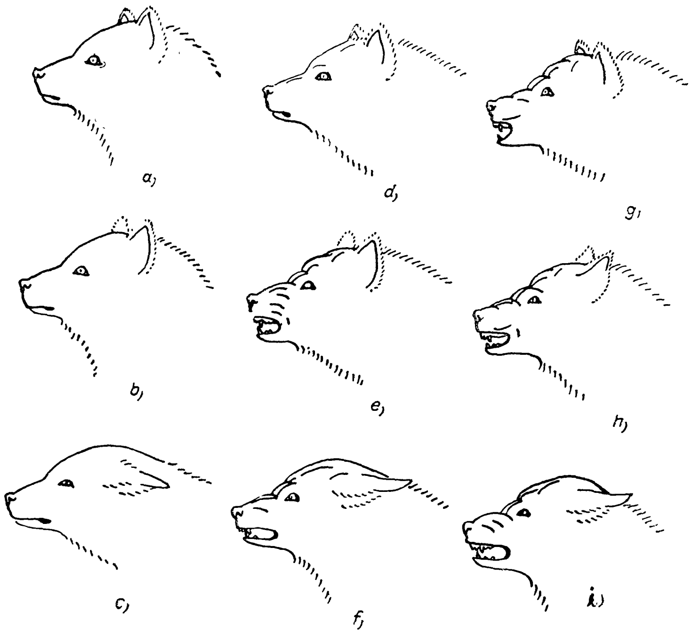

FIG. 7. EXPRESSION IN THE DOG

As the result of the superposition of three intensities of fear with three intensities of aggression, nine different expressions may be seen in the dog. Maximum fear, *c*, is expressed by pulling back the ears and the angle of the mouth; maximum aggression, *g*, is expressed by opening the mouth raising the upper lip and wrinkling of the snout and forehead. (After Lorenz, 1953.)

normally release a specific behavior are not always the stimuli with the optimal releasing function. Very often in such dummy experiments the natural stimulus situation is passed by in favor of the supernormal artificial object. Koehler and Zagarus (1937) found that ringed plovers prefer heavily contrasting, artificially spotted eggs to their own, which are lightly spotted. Similarly, Magnus (1954) succeeded in constructing supernormal ("überoptimale") female dummies of the butterfly *Argynnis paphia*. The innate releasing mechanism therefore proves to be open to exaggeration in a given direction, which is certainly of the greatest importance for the evolution of releasing structures (for example, in sexual selection).

Besides these morphological characters, chemical substances may also act as releasers. In the newt (*Triturus*), species-specific odors release the courtship display of the male (Zippelius, 1948). Many symbionts recognize the host by its odor (Davenport, 1955), and in many social fishes, as well as in tadpoles, there exists a chemically released flight reaction (von Frisch, 1941; Schutz, 1956). A chemical substance isolated from virgin females of the cockroach, *Periplaneta americana*, will cause courtship and copulatory behavior among the males (Roth and Willis, 1952).

Very often behavioral traits, keyed to various sensory organs of the partner, serve as releasers. Crickets, grasshoppers, frogs, birds, and many other animals locate their partners by species-specific calls. In anurans the recognition of sex and the synchronization of spawning and ejaculation are mainly based on tactile stimuli (Eibl-Eibesfeldt, 1955c). Threatening postures and many movements involved in courtship are optical releasers. Expressive movements also attain a high degree of differentiation in invertebrates, particularly in bees (von Frisch, 1950). Various reports on the social function of releasers have been published recently (Tinbergen, 1948; Eibl-Eibesfeldt, 1956a). These not only release behavior, but may have an inhibiting function under certain circumstances. In wolves, the defeated wolf exposes the part of his neck in the region of the jugular vein to his opponent, which inhibits all further attack of the aggressor immediately (Lorenz, 1943). In marine iguanas the ceremonial fight is ended when the weaker one assumes the submissive posture of lying flat on his belly, which is the opposite of the threatening posture high on its legs (Fig. 6).

Through superposition and combination of a number of expression movements with different intensities, many degrees of expression are possible. Three intensities of flight reaction, combined with three intensities of aggressive expression, give nine possible mimic expressions in the dog (Lorenz, 1953) (Fig. 7). By various combinations of call signals, the bearded tit (*Panurus biarmicus* L.) has a multitude of expressions at its disposal (Koenig, 1951). Polecats are able to combine movements which express a readiness for social contact with repelling movements. Thus a pregnant female makes biting intentions toward the male, but at the same time utters a call which normally invites social contact. In this way she repels him, but appeases any aggressiveness which biting movements alone would provoke.

Innate expression movements also play an important role in human beings. Human mimic responses have been shown to be akin in all races, although sometimes varying in degree. Smiling, crying, and fear are such basic expressive patterns, which are present in the newborn infant (Ahrens, 1953; Koehler, 1954a). Some expression movements of man can be derived from intention movements, as has been shown by Darwin (1872) and discussed in greater detail by Lorenz (1952).

Innate expression movements regulate not only intraspecific, but interspecific, contacts as well. Predators are often driven away by certain threatening gestures. Social contact is initiated in certain marine fishes which invite cleaning behavior on the part of their symbiont fish. Other gestures result in the withdrawal of the symbiont fish (Eibl-Eibesfeldt, 1955b).

A series of recent papers is concerned with the question of the phylogenetic development of expression movements. Lorenz (1941, 1951) first pointed out that certain intention movements, as well as various behavior patterns characteristic of conflict situations (displacement activities), may evolve into expression movements, provided that they do so with sufficient regularity to characterize these states. One movement in the courtship of different species of male ducks undoubtedly evolved from displacement preening in this way. In the male Mallard these movements are not very much ritualized. He simply puts his bill between his wing feathers as if he were about to clean them. In the male Mandarin duck, with an identical cleaning movement, a bright orange feather is touched. In a similar way the male Garganey (*Anas querquedula*) points to and exposes a conspicuous group of wing feathers. In like manner, intention movements of aggression have evolved into threatening expressions.

Expression movements can derive their phylogenetic origin not only from instinctive movements but from practically all noticeable phenomena accompanying certain internal states of excitation such as those vegetative epiphenomena responsible for the erection of hairs and feathers, trembling, blushing, urinating, secreting, etc. These latter types of expression may undergo differentiation similar to those derived from instinctive movements. This differentiation always tends to increase the effect of these movements as signals. Frequently this is attained by the help of special morphological structures, as the development of scent glands, special behavior patterns developed in connection with territory-marking with urine or feces, vascularization of hairless body areas, etc. Accompanying, uncoordinated movements, such as trembling, can give rise to new instinctive movements through a process of ritualization. The tail-shaking movements of many rodents offer an example. The hissing sounds produced in defensive threat by so many lung-breathing vertebrates probably originated by a ritualized "mimic exaggeration" of breathing movements, whose increase in depth and frequency is primarily an unritualized epiphenomenon of high excitation (Morris, 1956; Eibl-Eibesfeldt, 1956a).

Insects provide a number of excellent examples of the evolution of secondary biological signals. Luminescence is an accompaniment of a specific metabolic process which occurs among many insect and other animal groups. Among fireflies (Lampyridae) it has secondarily evolved into a mating signal, and Barber (1951) has shown that in 19 species and varieties of North American forms belonging to the genus *Photuris* the male flashing behavior is species-specific. In the females of some fireflies and mycetophilid larvae it has apparently evolved into a prey-luring signal as well. The flight tone (wingbeat frequency) is likewise a secondary accompaniment of flight in insects. It has been shown, however, that among many species of *Drosophila* the flight tone is species-specific (Reed, Williams, and Chadwick, 1942), and in mosquitoes the wingbeat frequency has evolved into the means whereby the male of a given species locates the female (Kahn and Offenhauser, 1949).

The specific problem of how the various physiological mechanism underlying the above fixed behavior patterns have become integrated into a unified system, in the course of their evolution, has remained relatively neglected. Ethological investigation has helped to focus attention upon just such problems. Thus, for example, the evolution of flight in orthopteroid insects is dependent, in part, on the evolution of a musculature with sufficiently high metabolic activity to be capable of the rapid contraction and sustenance necessary for flight. The further evolution of the flight mechanism, as evidenced in such advanced fliers as wasps, bees, and true flies is dependent, in part, on the development of an "asynchronous" flight musculature (capable of a contraction rhythm of up to a thousand contractions per second in the midge *Forcipomyia*; Sotavalta, 1953), which is not wholly dependent on the arriving nerve impulses (Roeder, 1951). The gradual increase in wingbeat frequency which takes place during the first week of adult life in the fly *Phormia* is correlated with a gradual increase in flight muscle cytochrome c and the size of the sarcosomes (Levenbook and Williams, 1956). By utilizing comparative methodology in analyzing the morphological, biochemical, and flight behavioral changes in 18 species of cockroaches, it can be shown that the loss of flight which occurs independently among many genera is accompanied by the ontogenetic failure to develop the pigmented musculature (cytochrome c) and correlated higher muscle metabolism associated with the function of flight (Kramer, in press). Comparative behavioral studies, thus seen, offer a rich and valuable starting point for further physiological investigation.

THE HIERARCHICAL ORGANIZATION OF BEHAVIOR

Observation shows that there are certain lawful relations between different motor patterns. Groups of instinctive movements appear together in a certain situation—they characterize a certain "mood" and show a common fluctuation of threshold. The fatiguing of a behavior pattern *A* also raises the threshold of a behavior pattern *B*, and vice versa, which indicates that both are somehow dependent on a common functional "center." Kortlandt (1955) called such charging "centers," and those locomotor patterns dependent upon them, instincts. If one observes certain complex behavioral patterns one sees a certain regularity in the sequence of instinctive movements. The "ritualized" fighting among conspecific individuals of cichlid fishes, which establishes the spacing of territories, may be taken as an example. Intimidation displays precede most fighting in many bony fishes, and in cichlids a series of differentiations of these intimidation displays can be shown to have taken place. In genera like *Haplochromis*, a furious and damaging fight follows a very short intimidation display; in genera such as *Hemichromis*, a very elaborate intimidation display is followed by a serious damaging fight only if the males are well-balanced, so that neither is frightened off; finally, in *Herichthys* and some *Cichlasoma* species, the damaging fight has disappeared and a highly ritualized intimidation display is performed until complete exhaustion of one of the combatants decides the battle (Baerends and Baerends van Roon, 1950; Lorenz, 1955).

In such ritualized fights there is a specific sequence of movements which begins with (1) the broadside-on display (Fig. 8*a*), followed by (2) the erection of the vertical fins. Then follows (3) the tail beat (Fig. 8*b*) which, by means of the lateral line organ that perceives the pressure exerted, may possibly "impress" the rival with his opponent's strength. This leads to (4) the lining up of the rivals in a head-on position (Fig. 8*c*), followed by either (5) mouth-pulling (Fig. 8*d*) or mouth-pushing, depending on the species. Mouth-pulling continues until one of the fish begins to tire, becomes paler, and finally escapes.

These ritualized fights provide excellent examples of the specific sequence of a set of motor patterns. Tail-beating does not begin before the vertical fins are erected, and mouth-pulling takes place only after a few tail-beats. It is an understanding of such behavioral sequences which the ethologist seeks. An experienced observer can often predict whether a mouth-pulling battle will ensue, as well as its outcome, from the intensity of the early intimidation display and tail-beats, or whether one rival will simply flee before a serious "battle" takes place.

The simple Lorenz-Craig scheme of "appetitive behavior — releasing stimulus — consummatory act," used to describe a common behavioral sequence, sometimes proves to be a special case. An

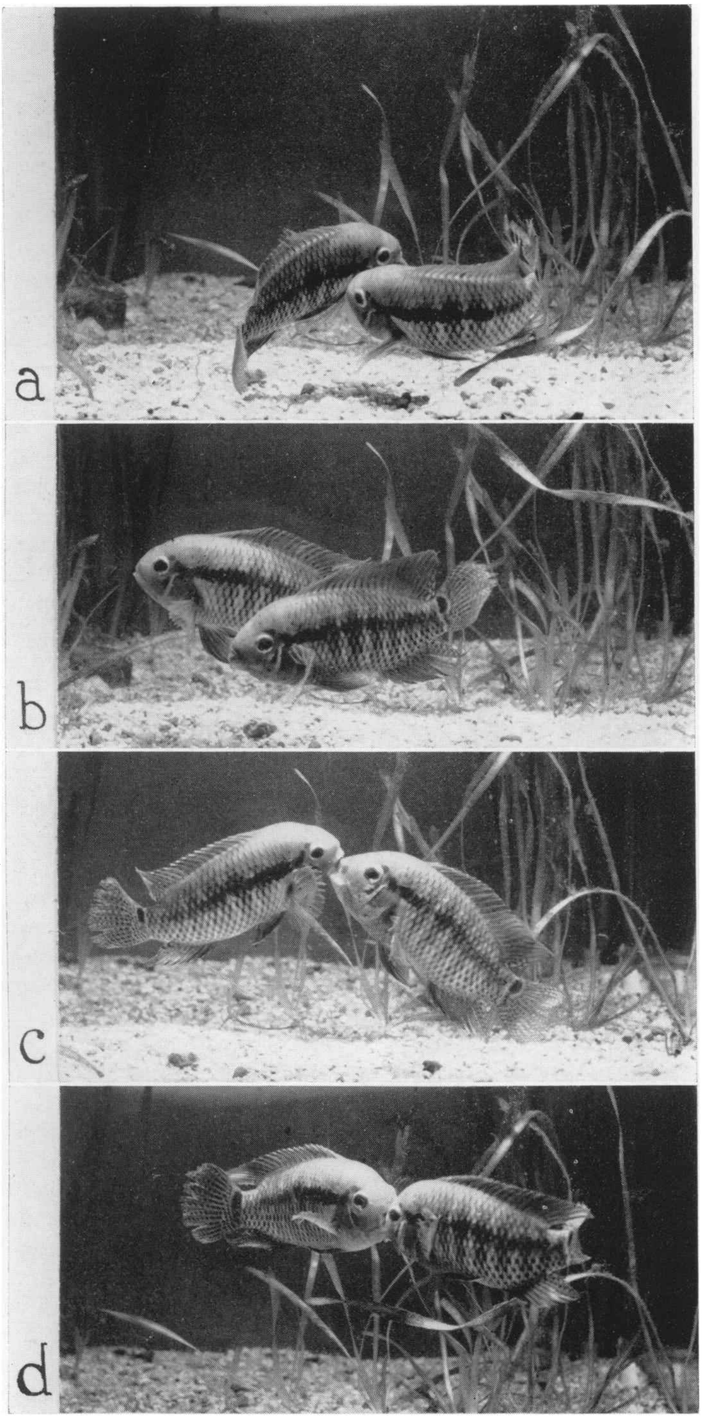

FIG. 8. RITUALIZED FIGHTING AMONG CICHLID FISH

Two males of *Aequidens* (*Acara*) *portalegrensis*. *a*, The rivals first attempt to intimidate one another by presenting their flanks to their opponent, and *b*, by each beating its tail toward the flank of the other. If they are of approximately equal strength and neither attempts to flee, *c*, they approach each other head on and, *d*, grasping each other's jaws, engage in a ritualized mouth-pulling battle until one fish tires and escapes. (Photographs: P. Leyhausen).

appetitive behavior does not always lead directly to a comsummatory act, but rather to a stimulus situation in which the next special appetitive behavior is released. The spring migration of the male stickleback is an expression of an appetitive behavior. The stimulus situation is the shallow, warm water. Here the special appetitive behavior of looking for a territory is released. Only if a suitable place is found does the further appetitive behavior of nest-building, fighting, and courting follow. As a result of such observed sequences, Baerends (1940) introduced the term "hierarchy of appetites," or as this behavior is the expression of a specific readiness to react, a "hierarchy of moods." Tinbergen (1951) interpreted these phenomena by hypothesizing a hierarchy of centers which were subordinated one to another, and which were activated one after the other. According to Tinbergen, then, an instinct is the complete hierarchical organization which responds to certain stimuli with well-coordinated behavior patterns. Such a definition, mainly based on a hypothesis, is unfortunately of little methodological value. The term "center" in Tinbergen's definition is not clearly defined, but as he referred to Hess' experiments (1948) in which various integrated behavior patterns of the cat were released by electrical stimulation of the diencephalon, it is assumed that he referred to nervous centers.

Kortlandt (1955) has shown that in some cases the fatiguing of behavior pattern *A* raises the threshold for this behavior, but does not influence behavior pattern *B*, whereas, the fatiguing of *B* on the contrary alters the threshold of behavior *A*. He concluded that in this special case there were two superordinated charging "centers," one of which feeds *A*, while the other feeds both *A* and *B*, and in his terms this represents a hierarchy of instincts.

The hierarchical organization of behavior has also been discussed by Hinde (1953, 1954). He showed that although behavior patterns in the black-tufted tit may be grouped in a hierarchical scheme, these are not clearly separated. On the contrary, some behavior patterns may be in the service of two or more instincts. Sometimes they are consummatory acts and at other times merely a means towards reaching a consummatory act. These latter have, therefore, sometimes been referred to as "appetitive acts," a term likely to be confused with the term appetitive behavior.

In young animals hierarchical organization is often incomplete and therefore seldom observed. The ontogenetic development of hierarchically organized behavior has been described for the cormorant in detail, and various theories of such behavior have been discussed by Kortlandt (1955). In the cormorant, seemingly meaningless isolated acts appear early in the behavior of the young birds, and only later become integrated into a complex functional pattern of behavior. Besides physiological maturation processes, learning may play an important role in the integration of such isolated behavior patterns, as Marx (1950) has shown in his experiments on hoarding in rats.

A disintegration of hierarchical behavior is very often observed in play, where the single acts become somehow independent of their normal superposed integration centers. During play individual acts belonging to different functions are often freely combined in a way which would normally not be possible in a real situation. Kortlandt (1955) called attention to the out-of-season disintegration, or "dis-maturation," of behavior patterns, which proceeds along exactly the same line, but in the reverse direction, as their maturation. This area of behavior deserves additional attention and investigation.

CONFLICT BEHAVIOR

Until now we have primarily dealt with behavior activated by one kind of motivation. In conflict situations, however, more than one instinct may be simultaneously activated. In such a case it often happens that two distinct fixed patterns of behavior inhibit or overlap each other, as we have mentioned in the discussion of expression movements. Many animals in aggressive mood attack intruders with a sudden jump. If fear is simultaneously aroused, however, the animal does not actually jump at the intruder, but stops suddenly before the intruder. This sudden stop is accompanied by rigid thrusts, or "braking," of the forelegs which continue to stamp on the ground, as in the squirrel, and may be accentuated by sounds and hair-fluffing. This "braking" of an aggressive behavior pattern, together with accompanying autonomic responses, may eventually become ritualized into a threat display or "Imponierbremsen" (Eibl-Eibesfeldt, 1956a).

If an activated behavior pattern is inhibited during its normal course, acts can often be observed which do not belong to the initially activated behavior. Fighting cocks, in the pauses between actually fighting, peck on the ground in an exaggerated way without actually taking food. Many similar examples are known, and such behavior has been termed by both Kortlandt (1940) and Tinbergen (1940) "Ubersprungbewegung" (displacement activity). It has been observed in the following situations:

(a) if two drives counteract one another—i.e., aggression and flight;
(b) if a goal is attained too quickly; for example, when a fighting partner flees too soon, displacement activities may occur in the winner; and
(c) if an "anticipated" stimulus does not occur; for example, when a female suddenly stops following a leading male.

A large number of displacement activities, like the seemingly irrelevant feeding behavior which takes place between fighting cocks, have been observed in a variety of animals. Such behavior includes not only foraging movements, but body-care movements (preening, bathing, scratching, etc.), nest-building movements, sexual movements, food-begging movements, incubation behavior, and even sleep. In the three-spined stickleback (*Gasterosteus aculeatus*), sand-digging is normally motivated as a part of nest-building activity. Kortlandt (1940) referred to such behavior, motivated by its own drive, as "autochthonous" activity. Behavior which is motivated by a drive other than its own, such as the displacement sand-digging which results from the conflicting drives of aggression and flight at the margin of the stickleback's territory, he termed "allochthonous" activity. Tinbergen (1952) simply refers to these two types of behavior, in which two drives utilize a common motor pattern, as the displacement activity and the "example" from which it is derived.

It appears that displacement activities are always derived from or expressed in some form of innate motor pattern. Nevertheless, close observation indicates that there is usually some subtle difference between the displacement activity and its example. Thus, displacement sand-digging differs from true digging in that only in the former case is the ventral spine erected (Tinbergen and van Iersel, 1947). This difference (and perhaps others) enables a rival male stickleback to distinguish between these two types of behavior. Displacement digging thus acts as a kind of signal which is understood by other male sticklebacks as a threat. Displacement activities may thus acquire a social function, and gradually evolve into elaborate signaling devices or expressive movements.

Irrelevant as these displacement activities may seem when observed for the first time, thorough study demonstrates a regularity in their occurrence. Given a particular set of conditions, displacement behavior invariably occurs. Thus, much irrelevant or so-called "random" behavior is not random at all, but determined by specific outer circumstances or stimuli, and therefore lawful.

The inner circumstances or stimuli, which determine the specific motor patterns to be utilized as displacement activities under given conditions, still remain obscure. The widespread occurrence of displacement activities suggests some primary biological significance or function within the animals in which they occur, besides their secondarily acquired function as signals or social releasers. Armstrong (1950) discussed the nature and function of displacement activities in birds in some detail. Tinbergen (1952) proposed that displacements serve a function as outlets for surplus impulses which might disturb or otherwise damage the central nervous system.

Two careful analyses of the mechanism of displacement activities were recently presented at the 4th International Congress of Ethology. Sevenster (1958) undertook an analysis of displacement fanning in the 3-spined stickleback, and van Iersel and Bol (1958) carried out an investigation of displacement preening in two species of terns (*Sterna sandvichensis* and *S. hirundo*). In the latter study it was shown that displacement preening results from conflicts, either between brooding and escape, or between aggression and escape. The frequency and intensity of displacement activity were always correlated with the strength of both of two opposite, conflicting drives.

THE LEARNING HYPOTHESIS

Ethology has placed the exploration of innate behavior patterns in the foreground. In the behavior of higher animals, especially that of mammals, innate and acquired patterns of behavior are blended together into a functional unit, so that is is impossible in principle to explore one without *knowing* the other. Ethologists hold, however, that both elements can be analyzed by careful study, including observation of the free-living animal combined with the experimental approach.

Psychologists often agreed in principle with this formulation. Thus Watson (1924) wrote, "Fortunately in most connections psychology is not called upon to draw a sharp distinction between hereditary and acquired reactions. In making laboratory studies, however, it is sometimes necessary for us to study the details of hereditary response. We find it simpler in such cases to overemphasize for the time the definiteness of the separation. This is unquestionably a legitimate mode of procedure in science. Few biological problems permit of any other treatment."

Nevertheless, this viewpoint is the converse of the contention of some psychologists today, who claim that it is impossible to separate out learning processes from innate responses. It appears to have been a short step from not being called upon to draw a distinction between hereditary and acquired reactions, to the assumption that it cannot be done.

Let us take a concrete example quoted by Lehrman (1953), dealing with the nest-building behavior of the rat. Each adult rat, when raised in isolation, is able to build a nest. We would, therefore, conclude that innate behavioral elements are present, but according to Riess (1954), this is not the case. He raised rats, isolated at 14 and 21 days after birth, in wire cages with powdered food, so that these animals had no opportunity to handle solid objects. When he put them in the testing situation —a wooden box from the sides of which paper strips were hung—none of the animals built nests. They simply scattered the paper strips all over the cage. In the basic experimental group isolated at 21 days after birth there was no nest building, decreased retrieving of rat pups when born, and an infant mortality of 75 per cent due to the absence of suckling. No results of a control, in which rats were kept under identical conditions but permitted to handle solid food, were reported. Lehrman contends that the practice in carrying food pellets is partly equivalent, for the development of nest-building and retrieving, to practice in carrying nesting materials, and in carrying young. Taken with Kinder's (1927) demonstration that nest-building is inversely correlated with environmental temperature, Lehrman suggests that nest-building activity arises from the ordinary manipulation and collection of food (and other objects), under conditions where the accumulation of certain types of manipulated materials leads to immediate satisfaction of one of the animal's needs (warmth).

Eibl-Eibesfeldt (1955a) was able to show in this connection that the results of Riess can be traced to a methodological error in the experimental situation, and that if one avoids this error both innate and learned elements of nest-building may be readily determined. Tail-amputated rats were raised by the Riess' method, but unlike Riess' conditions, these were tested in their *home cage*. All those rats which had a fixed sleeping place (about one-third of the animals) built nests immediately. The others did so after a time of wandering about aimlessly, as the paucity of structural subdivisions in the experimental cage apparently made it difficult to choose a nesting site. In a second series of experiments a vertical tin fold was placed in one corner of the cage, separating off a small area. In such experimental cages, all isolated rats built nests behind the tin fold, before parturition, including those which had sleeping places outside the fold. Apparently the rats used in Riess' experiments failed to build nests, because they were unfamiliar with their testing cages and did not have a definite nesting site. Such a nesting site must first be fixed either by training, or by structures which release an innate orientating mechanism—otherwise, rats do not begin to pile up nesting material. The specific movements of nest building were equal in both control and experimental animals. They are certainly innate and require no handling of solid objects as a preliminary form of learning.

In the films of these experiments, which were shown at the 4th International Congress of Ethology held in Freiburg (Sept. 1957), it was evident that without prior practice or learning the nest-building rats always carried nesting material (paper) toward the nest. Not once did the mother rats fail to retrieve a newborn rat placed outside the nest by the experimenter. On the other hand, learning processes do play an important role in the utilization of various nesting materials. Whereas soft paper is readily utilized, rats must learn to handle stiff straw before they can succeed in building as good nests with the latter material alone.

No ethologist doubts that learning processes are of great importance in behavior. Lorenz (1935, 1937) has often emphasized that learned and innate elements of behavior are closely interwoven. His ravens, for example, had innate nest-building movements but had to learn which material to use for next-building. Eibl-Eibesfeldt (1957a) has recently shown that red squirrels develop individually different techniques of nut-opening on the basis of a few innate patterns such as gnawing and a certain splitting movement. The integration of these movements into a functional unit is accomplished by learning processes in which the special form of the nut favors the development of a definite technique. Far from overlooking learning processes, as psychologically orientated criticisms of ethology imply, Thorpe (1956) has recently devoted an entire volume to the relationship of inherited and learned elements in animal behavior.

Lehrman has criticized isolation experiments on the basis that these do not take adequate account of self-stimulation by the isolated animal, such as its own chirping or licking activity, which might provide a source of differential learning. The implication here is that the results of *all* isolation experiments are questionable. Koehler (1954b) has in turn criticized Lehrman's line of reasoning in detail. Although one may consider that an animal raised in isolation is always exposed to self-stimuli from which learning may follow, there are certainly many other cases in which learning may be excluded. Sauer (1954) showed that whitethroats (*Sylvia communis*) raised in isolation in soundproof rooms develop the species-specific songs in the same sequence and at the same developmental stage as the normally raised controls. The young swift, which hurls itself out of its nest for the first time, and immediately flies to a safe landing, is as little concerned with flight learning as Spalding's swallows or Grohmann's doves. Male ducks reared in isolation show, when mature, all the highly ritualized courtship postures characteristic of the species.

A distinction between innate and learned elements of behavior does, therefore, seem prerequisite for further causal analysis. The learning psychologist who does not know what is genetically determined is in a position equivalent to a geneticist performing modification experiments on genetically unanalyzed material. Seen in this light, a knowledge of the innate behavior of animals, which ethologists have placed in the foreground, would provide the results of learning experiments with greater validity.

Tinbergen has pointed out (correspondence, 1957) that the word "innate" is not the opposite of learned, but of "environment-induced." There are many environment-induced changes which nobody would label "learning." The fact that presumptive trunk skin of a frog embryo, when transplanted into the presumptive mouth region of a newt larva, develops into a mouth, but the mouth of a *frog* tadpole, shows that the words innate or inherent, versus environment-induced, are rightly applied only to influences, not to the characters themselves. This is also true of behavior. Strictly speaking, the application of the word "innate" is a form of shorthand for the differences between species, used in the same way that the geneticist applies this word, and is not entirely applicable to the end result (or "finished product") of structure or behavior.

Schoolland (1942) was able to demonstrate that there are innate differences in the responses of ducks and chicks to water, dust, cries of distress, food, etc., even though both were incubated and reared under identical conditions. (This demonstration of innate response differences, in an experimental approach in which the environment is held constant while the hereditary factors are varied, would be an instructive laboratory exercise). In his introductory statement of the problem Schoolland indicates that since there is no way of determining when the "outer" factors begin to interact with the "inner" factors, one can arbitrarily select a point in the developmental process and study the degree to which development up to this point exerts a determining influence upon subsequent behavior. Those factors present in the organism at birth, which represent development *up to this point* and which are at the same time practical determinants of subsequent behavior he regards as *innate*, or as *representing innate constitution.* Since birth is an arbitrary point in the development process, however dramatic, it should at all times be possible to demonstrate that responses at birth are dependent upon the maturation and integration of a previous structural and functional embryonic organization. To consider such developmental processes as a form of "learning," and to use this as an argument denying the existence of innate behavioral differences, becomes an absurdity. If one were to apply such reasoning to the morphological characteristics which differentiate closely related species, one would be required to conclude, in similar fashion, that such species differences were not inherited (or innate) but were also "learned" in embryo.

Actually, it may be possible to determine when specific external and internal factors begin to react in embryonic development but such study, in view of our relative ignorance of these phenomena, is at present a difficult subject. Thus in *Drosophila* local injuries of the egg effected by ultraviolet light during the first 4 hours after laying cause local defects in the resulting larva, but the imaginal characters are unaffected. If the egg is irradiated similarly 7 hours after laying localized defects are produced in the corresponding region of the adult epidermis without any visible effect during larval development (Geigy, 1931). Recently, Strean and Peer (1956) reported on the basis of a study of 228 cases of cleft palate in newborn infants that such abnormality related to a strong emotional disturbance during the critical weeks of the mother's pregnancy, when the two halves of the upper jaw normally fuse in the palatal arch. They assumed that severe emotional disturbance stimulated the adrenal gland to produce extra hydrocortisone which checks, or may actually dissolve, the formation of connective tissues between the two sides of the palate. They injected cortisone into female mice at the corresponding stage in gestation, when the palates of the embryos were forming, and produced clefts in 87 per cent of these cases. These studies demonstrate that there may be critical periods in embryological development when external factors exert a marked influence on the formation of specific structures and on behavioral responses as well. Such demonstration of external influences on the formation of embryological structures, however, would in no case be ground for asserting that the specific shape of the human palate was devoid of hereditary (innate) influence.

THE COMPARATIVE APPROACH TO BEHAVIOR

As mentioned earlier, it is the phylogenetic constancy of instinctive movements, i.e., the presence of similar, unlearned behavior patterns among related species, genera, families, and even higher taxonomic categories, which provides both the general background and focal point of ethological investigation. The ethologist observes and studies the instinctive behavior patterns of related categories of animals, much as the comparative morphologist examines related categories of animals in an endeavor to "understand" the steps in the evolution of particular morphological structures. The phylogenetic viewpoint was uppermost in Darwin's own thinking when he prefaced *The Expression of the Emotions in Man and Animals* with the following:

> As long as man and all other animals are viewed as independent creations, an effectual stop is put to our natural desire to investigate the causes of Expression. By this doctrine anything and everything can be equally well explained; and it has proved as pernicious with respect to Expression as to every other branch of natural history. With mankind some expressions such as the bristling of the hair under the influence of extreme terror, or the uncovering of the teeth under that of furious rage, can hardly be understood except on the belief that man once existed in a much lower and animal-like condition. The community of certain expressions in distinct though allied species, as in the movement of the same facial muscles during laughter by man and by various monkeys is rendered more intelligible if we believe in their descent from a common progenitor. He who admits on general grounds that the structure and habits of all animals have been gradually evolved will look at the whole subject of Expression in a new and interesting light.... When I read Sir C. Bell's great work, his view, that man had been created with certain muscles specially adapted for the expression of his feelings, struck me as unsatisfactory. It seemed probable that the habit of expressing our feelings by certain movements, though now rendered innate, had been in some manner gradually acquired. But to discover how such habits had been acquired was perplexing in no small degree. The whole subject had to be viewed under a new aspect, and each expression demanded rational explanation.

Enunciation of the theory of evolution by Darwin and Wallace resulted in the increased utilization of comparative methodology in many areas of biological investigation. It provided the stimulus for the growth of comparative morphology, comparative physiology, comparative embryology, and other disciplines, and these in turn enriched both the factual and theoretical domain of biology. Darwin himself made little distinction between the evolution of morphological structure and the evolution of instinctive behavior. In his chapter on "Instinct" in *The Origin of Species* he stated, "The canon in natural history of *Natura non facit saltum* is applicable to instincts as well as to corporeal structures." In his book *The Expression of the Emotions in Man and Animals* he clearly demonstrated that it was possible to reconstruct the history of the muscular movements, together with accompanying modifications of the respiratory pattern, involved in those aspects of behavior termed "expressions." Jennings (1907), in his studies on the behavior of the starfish, likewise pointed out that there can be no greater mistake in physiology than to omit from consideration the history of an organism's responses in attempting to understand its present-day behavior. Yet, until recently, only isolated investigations along such lines had been undertaken.

Apart from the emphasis given such phenomena by ethological investigation today, Darwin's chapter on "Instinct," written almost a century ago, is surprisingly modern in its setting forth of the basic problem of the origin of innate behavior patterns in animals, as well as in the utilization of comparative observation and experimentation towards their analysis and clarification. From an historical viewpoint one may well ask how it happened that neither zoologists nor psychologists developed a truly comparative discipline of animal behavior, as was the case with morphology, physiology, and embryology.

> Ross and Smith (1955), in discussing the current status of animal and comparative psychology, wrote: "We have not developed a discipline of comparative psychology.... It is our conviction that the comparative method in the study of behavior will persist and develop. If this development is not in the field of psychology it will develop in other fields."

Lorenz (1950) has already pointed out that the dispute between the vitalistic and mechanistic schools of behavior study provided a serious obstacle to analytical research. The reciprocal errors of both these schools prevented consideration, as well as any attempt at a causal explanation of innate behavior phenomena—particularly as regards considering the organism as a whole unitary system, as regards the directedness of behavior, and spontaneity. If the vitalists erred by resignedly attributing these phenomena to some unexplainable, supernatural vital force, the mechanists erred by omitting these phenomena from consideration, or claiming that they did not exist. In general, the acknowledged victory in this dispute went to the mechanists, since they succeeded in uncovering a tremendous array of facts and causal explanations for those discrete elements of the organism which they chose to consider, and this tour de force overshadowed for a time such phenomena as they chose to omit. Nevertheless, an *irrational* fear of vitalism still permeates most zoologists and psychologists, effectively screening from consideration those phenomena which were once considered the domain of the vitalist. It is rational for a scientist, whose aim is the causal explanation of natural phenomena, to reject vitalism, which postulates an unexplainable, supernatural vital force, but it is irrational for scientists, whose domain is the whole of living nature, persistently to omit from consideration certain elements of that nature. Biological and psychological science has grown to such proportions today that any scientist may choose whatever area of specialization interests him, but it is a serious scientific breach for any group of scientists to utilize this fear of vitalism to suggest that all other scientists should reject certain kinds of phenomena from consideration, or that such phenomena be only considered within the dogmatic framework of an existing discipline.

Perhaps historical study will eventually disclose both the basis and influence of the attitudes of the zoologist toward the subject of behavior, and how these attitudes have stifled the comparative study of behavior. Some of these attitudes and dogmas which have long prevailed within the field of biology are the following: (a) behavior is too complex to analyse; (b) behavior and physiological processes are two distinct aspects of the organism; (c) only physiological processes are capable of exact, causal analysis; and (d) the realm of behavior properly belongs to the field of psychology.

Thus, not only was the study of animal behavior relegated, so to speak, to psychology, but this was done with the additional implication that such study was neither objective nor completely scientific. It should be noted parenthetically that although zoologists seemed to shun behavior as a subject of serious study, this never prevented them from incorporating such valid explanations of *individual elements* of behavior as Loeb's Tropism Theory, or Pavlov's Conditioned Reflex Theory as a mechanistic explanation of *all* behavior.

Psychologists reacted to this background of attitudes by stressing learning and conditioned behavior, since experiments could be carried out in this area under what were considered objective, rigorously controlled conditions. It would not be altogether erroneous to say that the defensive reaction of psychologists, with which they rigorously pursued "objectivity," was responsible in part for the one-sided development of behavior theory which emphasized learning and conditioning almost to the exclusion of all else. It has already been shown that the validity of conclusions drawn from learning and conditioning experiments, however carefully "controlled," when carried out without knowledge of the animal's innate behavior, is often open to considerable question. The problem of the survival value and evolution of animal behavior patterns has been almost entirely neglected in the psychological study of behavior.

In their quest for objectivity, psychologists also developed that area of investigation known as physiological psychology, which, in part, has emphasized the physiological changes in specific organ systems during emotional change. These investigations have certainly contributed much valuable knowledge. Physiological psychologists are well aware that emotional behavior, objectively examined, expresses itself in specific patterns of behavior, and that such specific behavior patterns have an historical explanation. But again the comparative study of innate behavior patterns in the Darwinian sense of studying related species, genera, families, etc., as the systematist or comparative morphologist does, was overlooked.

THE CRITICISM OF ETHOLOGICAL INVESTIGATION

A number of papers have appeared in recent years which have criticized the ethological approach to the study of behavior (Hebb, 1953; Kennedy, 1954; Lehrman, 1953). These criticisms have been of value in bringing to light the fact that psychologists, and perhaps biologists as well, apply two distinct sets of criteria to biological phenomena, depending on whether innate structure or innate behavior is under consideration. Both the geneticist and taxonomist know that morphological structures which are of taxonomic value, and hence inherited, are subject to environmental influence and change. Mayr (1942) has pointed out that all taxonomic characters which have been described as good species differences have been found subject to geographic variation whenever they have been studied from this point of view. The range of variation which inherited morphological structures exhibit under varying environmental influence is an important area of investigation. It is doubtful that any biologist would contend, as a result of such investigation, that the morphological differences of distinct species are not to be considered inherited, or innate. Nevertheless, this is what psychologists do when they erroneously quote experiments, which indicate that environmental factors influence behavior, as evidence against innate behavior patterns.

It should also be mentioned that to observe the fullest possible repertoire of innate movements of animals in captivity, they must be kept at a peak of good nourishment, health, and vitality. It is well known to animal fanciers and zoo curators that a reduction in an animal's vitality often results not only in the decreased beauty of its scales, feathers, or coat, but also in the diminished number or intensity of instinctive movements which it will display. Even among invertebrates, Crane (1948) found that the displays of salticid spiders must be studied when the animals are at their physiological peak, otherwise the behavior is not typical of the species. Thus it is possible, as a result of altering the environment, to so interfere with an organism's normal development that certain structures or behavior patterns do not appear at all. This is all that the experiments of many psychologists do, when they try to demonstrate that innate behavior patterns are non-existent, as Lorenz (1956) has already pointed out.

In referring to innate behavior, ethologists do not imply that they consider it unnecessary to investigate the ontogeny of such behavior, as Lehrman (1953) claims. On the contrary, one might suppose, the demonstration that instinctive behavior patterns are not the result of learning (although they may later be combined with learned behavior) would lead investigators to focus their attention on those very developmental processes and genetic influences upon which they depend. Lehrman has also suggested that preformationistic assumptions underlie the concept that some behavior patterns are inherited. Not at all. The geneticist, in shorthand fashion, refers to many inherited morphological structures just as the ethologist refers to innate behavior patterns. Neither doubts that the final structure or behavior is the result of an interaction between genetic influence, developmental processes, and the environment.

Hooker (1952), who provided an admirable survey of the origins of prenatal behavior throughout the vertebrates, pointed out that structure and function are directly and inseparably related in any living organism. An embryo develops morphologically in an orderly sequential manner characteristic of the species, and given an appropriate environment an organism's behavior likewise develops in an orderly sequential manner which is also characteristic of the species. The morphological development of all vertebrates follows a fundamentally similar sequence and one might therefore expect the developmental sequence of behavior in different vertebrates to possess certain fundamental similarities, but to differ in particulars in different species. This is precisely what Hooker concluded when, as a result of a survey and studies of vertebrate embryonic behavior, he wrote: "It is evident that each class of vertebrates, perhaps each order, genus and species, exhibit characteristics in the development of behavior which belong to that subdivision of animals alone." This suggests that the developmental sequence of embryonic behavior is part of an inherited pattern, rather than a learning process.

As has been pointed out, the environment, which at all times exerts an influence on the sexual state and the vitality of animals, often determines whether or not a given innate pattern of behavior will be displayed at all. It is the *form* of the behavioral movements, once aroused, which is inherited or constant. Ethologists use as criteria of *fixed behavior patterns* that 1) the behavior be constant in form; 2) it be characteristic of the species; 3) it appear in animals which have been raised in isolation from others; and 4) it develop in animals which have been prevented from practicing it. These criteria, however, should not be so narrowly interpreted as to exclude other pertinent biological considerations. Every geneticist would expect to find inherited differences in structure *within* species. There is no reason why fixed behavior patterns could not possess, within species, the same inherited variability that one finds in morphologically inherited traits.

Lehrman is right in pointing out that the term "innate" when applied to a behavior pattern still leaves many questions to be answered. Some of these are the following.

(1) What mechanism would best explain the observed lawfulness associated with fixed patterns of behavior?

(2) How does the animal achieve the coordination and proper succession of the specific movements, underlying innate behavior patterns, at a particular time in ontogenetic development?

(3) How does the performance of certain behavior not only regulate subsequent behavior, but metabolic activity as well?

(4) How are inherited patterns of behavior transmitted to offspring?

No student of ethology is unaware of the questions which comparative animal behavior raises. Whereas these questions have been largely overlooked by both the psychologist and the general biologist, ethologists have, over the past two decades, actively attempted to answer them.

Critical papers, such as those of Hebb (1953), emphasize the fact that learned and innate elements are closely linked together in all functional behavior, and that we cannot dichotomize mammalian behavior into learned and unlearned, environmentally determined and hereditarily determined. Such papers imply that ethologists are unaware of this relationship, but as has been shown, no ethologist would deny the importance of environmental influences on behavior. Ethologists believe, conversely to Professor Hebb, that such a functional unit is capable of analysis just as any other natural function, regardless of the difficulties, and the previous review indicates how this has been done.

The parallel between certain ideas in ethology and psychoanalysis led Kennedy (1953) to question the objectivity of ethology, as well as to brand it a dualistic and hence a vitalistic approach to animal behavior. Kennedy, who acknowledges that subjective phenomena play some *causal* role in behavior (which the ethologist does not), feels that in science the linking of subjectivism to phenomena, concepts, or theories, is a sufficient deterrent to their serious consideration. Thorpe (1954), in answering this criticism of ethological objectivity, has pointed out that *all* concepts are ultimately subjective in origin. It is usually possible to restate them with whatever degree of respectability may be required by the climate of scientific opinion at the moment.

It should be mentioned that ethological investigation has developed independently of psychoanalytic theory. In fact, Kortlandt (1955) has criticized ethologists for having ignored psychoanalytic theories of instinct in their investigations. Nevertheless, Kennedy's criticism deserves more attention, for it has the merit of openly stating what is often tacitly implied in other criticisms.

Classical biology and academic psychology have largely ignored or rejected those clinical findings and theory which Freud (1938) developed at the turn of the century towards the understanding of various forms of disturbed human behavior. In particular, the lawfulness with which certain events in the ontogeny of human beings led to obsessional, neurotic, hysterical, and psychotic forms of behavior, and the regularity with which such behavior was associated with disturbances in sexual function became apparent. His findings represented an important milestone in scientific observation and methodology, notwithstanding the fact that biologists and psychologists preferred to view his work as so much "unscientific psychology." In this viewpoint they overlooked the fact that Freud had already demonstrated proven research capacities as a general biologist, histologist, and neurologist (Jones, 1953). As a result, biologists failed to ask a significant question, which Freud's clinical findings certainly demanded —namely, if specific events in the early years of infancy result in neurotic behavior and such behavior is associated with sexual disturbances, what is the physiological mechanism through which this is accomplished?

The social fear of the essentially biological problem of sexuality has effectively hampered fruitful inquiry in this area, much as the fear of vitalism provided a serious obstacle for analytical research in the realm of animal behavior generally. As a consequence, it was not the biologists, but that specialized group of psychoanalytically oriented physiologists who developed the field of psychosomatic medicine and provided insight into the regularity with which various metabolic diseases appeared in specific personality types. It is to the work of this discipline that we owe much of our knowledge of the role of the autonomic nervous system in such diseases.

The viewpoint that psychoanalytic findings and theory, which deal with an underlying lawfulness in human behavior, is merely unscientific psychology, has crystallized into an acceptable illusion among many biologists and psychologists. It is not at all unlikely that the independent demonstration by ethologists of lawful behavior in animals threatens to shatter it. If biologists persist in this attitude they will almost certainly overlook another central biological problem dealing with certain mechanisms involved in evolution. Morris (1956) has shown that the feather postures of birds, primarily concerned with temperature regulation and under the control of the autonomic nervous system, may, under thwarting stimulus conditions, take part in secondary responses. It appears that these secondary responses, under the pressure of selectivity, may ultimately become ritualized and evolve into special signals. There is considerable evidence that similar secondary autonomic functions are involved in the evolution of signals among other animals.

It is beyond the scope of this paper to provide a full comparison of ideas in psychoanalysis and ethology. It is only our intention to show that the attitude which accepts lawful phenomena in the realms of physics and chemistry, but assumes that there are no laws in the biological realm of behavior, has seriously curtailed investigation in the past. It should be mentioned, however, that Kortlandt (1955) has presented a detailed discussion of the concept of instinct and its relation to hierarchy theory, as developed both in psychoanalysis and by students of animal behavior. Barnett (1955) has discussed possible relationships between displacement behavior in animals, and both psychoneurotic behavior and psychosomatic disorders in man. In a discussion of the nature and function of displacement activities, Armstrong (1950) likewise called attention to their similarity in man and animals.

Kennedy's second criticism of ethology is that it is dualistic *and hence vitalistic*. The approach of vitalism towards life phenomena was dualistic, but the corollary that all dualism is vitalism by no means follows. The rejection of vitalism from the realm of scientific consideration is not based on its dualistic nature, but rather on its postulation of an unknowable, supernatural agency. A dualistic approach is often a necessity based upon ignorance of connecting links or basic laws. Thus, the separation of the study of matter into the realms of physics and chemistry—the one based on the demonstration of distinct physical laws, the other on chemical interaction and forces—was certainly dualistic. It required the work of many generations of scientists before the quantum theory of Max Planck was able to provide an underlying unifying principle. Moreover, it was the dualistic approach to the study of matter which permitted the gradual technological and factual accumulation of knowledge in both these fields and thereby made the demonstration of a unifying concept possible. That accomplishment might still be denied us today if physical science had been able to dictate to the young, still-suspect science of chemistry the nature of its experiments, methods, and thinking.

[Notwithstanding the unifying concept embodied in quantum physics, some physicists still regard it as a dualistic theory. Thus Einstein and Infeld (1947) write: "The new quantum physics removes us still further from the old mechanical views, and a retreat to the former positions seems, more than ever, unlikely. But there is also no doubt that quantum physics must still be based on the two concepts: matter and field. It is in this sense a dualistic theory and does not bring our old problem of reducing everything to the field concept even one step nearer realization."]

Criticisms of individual ethological experiments, observations, and thinking are to be welcomed. The recent criticisms of ethology as a scientific discipline, however, have indicated that biologists and psychologists frequently start with assumptions concerning behavior which are contradicted by fact.

SUMMARY

In summary, it may be said that ethology does not have a complete theory, but rather has contributed a considerable number of verifiable facts which do not wholly fit within existing physiological or psychological explanations of animal behavior. These are as follows:

1. Certain patterns of behavior, termed instinctive movements, possess taxonomic value among diverse groups of animals, i.e., they often show the same species specificity as shown by morphological structures.
2. These fixed patterns of behavior, like structures, may be studied and, in part, "understood" from the viewpoint of phyletic descent. They have evolved from homologous, ancestral behavior.
3. There exists an hitherto unexplained lawfulness governing behavior which is expressed through instinctive movements, leading to such associated phenomena as displacement activities, intention movements, ambivalent responses, regressive behavior, and an inherited sequence of movements.

Ethological investigation has focused attention not only upon the general problem of the physiological mechanisms underlying behavior, but upon the specific problem of how the various physiological mechanisms, fixed patterns of behavior, and specialized structures have become integrated into a unified system in the course of their evolution. Hand in hand with the systematic work of uncovering the distribution of such phenomena in the animal kingdom, and in addition to conducting many remarkable experiments, ethologists have made and unmade hypotheses. This is part of the growth of all scientific disciplines. As a first truly comparative approach to the behavior of animals, ethology should be of interest to many other fields of study. It is hoped that studenst of biology, physiology, psychology, and related disciplines will first verify the facts concerning animal behavior, and then ultimately contribute to their explanation.

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