

SOCIAL RELEASERS AND THE EXPERIMENTAL
METHOD REQUIRED FOR THEIR STUDY¹

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PART I: REVIEW

SOME years ago, Dr. Rand (1941, 1942) published two short papers in which he criticized some of the hypotheses and conclusions of Lorenz (1935 and 1937), especially the releaser concept. Discussing my paper (1939b) on vertebrate social organization, Dr. Rand (1942:404) goes as far as to argue that "the data available hardly justify" me in assuming *even as a working hypothesis* a social, communicative function for conspicuous and highly specialized structures whose participation in non-social processes cannot be found. Though I am in complete agreement with Dr. Rand when he stresses the need for further experimental research on the function of conspicuous structures and movements, I cannot agree with his statement that "the probable existence of releasers has not been clearly demonstrated in any cases" (Rand, 1941:289). This astonishing statement can be explained only by assuming that a number of experimental facts published in American and European journals have escaped Dr. Rand's attention. In order to make these facts better known, it seems worth while to give, as the first part of this paper, a short review of the experimental and other evidence on releasers.

In addition, the experiments reported by Rand in his 1942 paper, which tend to show that the anal feather circling in nestling passerine birds does not function as a releaser, are not, in my opinion, conclusive (though I admit that they are useful as a warning against over-simplistic views). Therefore, in the second part of this paper, I shall discuss some general problems connected with the kind of experiments required in work of this type.

The releaser concept has sometimes been misunderstood even though Lorenz has given a clear definition of it. Rand (1941:289) is confusing matters considerably when he assumes that a releaser in Lorenz's sense is "that portion of the object which sends out the stimuli to which the bird responds." The cause of this misunderstanding lies in the paradoxical fact that not everything that releases a response is a "releaser" in Lorenz's sense.

A number of experimental studies on the nature of the external sensory stimuli necessary to release innate responses have shown that innate behavior is never a reaction to the environmental situation as a whole, but only to a few parts of it. Other parts—although they may be received by the animal's sense organs—are entirely ignored. This is not

¹ Extension of an address delivered at the Annual Meeting of the Wilson Ornithological Club, Omaha, Nebraska, November 29, 1946.

the place to give a complete review of the pertinent facts, and I must refer the reader to the literature, especially to Lorenz (1940), to Russell's compilation (1943), and to my own paper (1942).

To cite a few examples: The escape reactions of many birds from passing birds of prey are a response to a type of movement and to a special characteristic of shape, namely, "short neck" (Figure 1); any

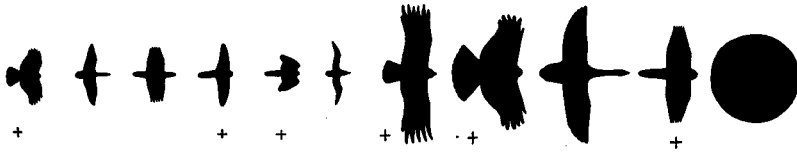


Figure 1. Cardboard models used by Lorenz and Tinbergen to test the reactions of birds to birds of prey. Only the models with a short neck (marked +) released escape reactions.

bird, or even a cardboard dummy, that has a short neck releases an escape response independently of the shape of wings, tail, etc., and of the color (Goethe, 1937b; Krätzig, 1940; Lorenz, 1940). The hunting response of a pike can be released by a shining silvery object pulled through the water. Gulls and many other ground-breeding birds will show incubation responses to many objects other than eggs, provided they have rounded shapes (Kirkman, 1937; Lorenz and Tinbergen, 1938; N. Tinbergen and Booy, 1937); size or color can be varied within very wide limits. Russell (1943) called these influential stimuli (the parts of the environmental situation to which innate behavior patterns respond) "perceptual signs" or "perceptual clues," but for various reasons I prefer the term "sign stimuli."

It should be emphasized that it is only *innate* behavior that is dependent on sign stimuli; as I will show below, many if not all *conditioned* reactions are dependent on quite another type of stimulus situation.

So far as we know at present, every unconditioned reaction of an animal is dependent on its own special sign stimuli, and different reactions respond to different sign stimuli. This shows that the release of every unconditioned reaction is dependent on a special central nervous mechanism, which is called the "innate releasing mechanism."

Lorenz (1935) put forward the theory, based on an unrivaled amount of observational facts, that in animals intraspecific social relations are dependent to a large extent on stimuli sent out by one individual (the "actor") releasing responses in another individual (the "reactor"). As a result of evolutionary adaptation, many species have developed special structures or movements that serve to send out stimuli especially adapted to act on innate releasing mechanisms of

the same species. It is these special structures, the exclusive function of which is to send out sign stimuli releasing social responses, that were called releasers ("Auslöser") by Lorenz.

To use Lorenz's own words: "The means evolved for the sending out of key stimuli may lie in a bodily character, as a special color design or structure, or in an instinctive action, such as posturing, 'dance' movements, and the like. In most cases they are to be found in both, that is, in some instinctive acts which display color schemes or structures that were evolved exclusively for this end. All such devices for the issuing of releasing stimuli, I have termed *releasers* (*Auslöser*), regardless of whether the releasing factor be optical or acoustical, whether an act, a structure or a color" (1937:249).

In the original German paper (Lorenz, 1935), of which the article in the 1937 *Auk* is only a much condensed version, the concept of the releaser is still more clearly defined: "I have used the term releasers for characters which are peculiar to individuals of a given species and to which responsive releasing mechanisms of conspecific individuals react and thus set in motion definite chains of instinctive actions" (p. 143). And again (p. 377): "Structures and instinctive actions that serve exclusively to send out key stimuli reach a high degree of specialization, paralleling the evolution of the correlated responsive mechanisms. We have called such structures and instinctive actions, for brevity's sake, releasers."² The starting point of Rand's criticism is, therefore, a misrepresentation of the basic definition.

As I said before, Lorenz's theories were interpretations of observational data, and although they appealed at once to the majority of field observers, experimental tests were highly desirable. As I hope to show, the experimental facts thus far obtained have confirmed Lorenz's views on the two main points: (1) intraspecific social relations in many animals are largely dependent on innate behavior, and (2) innate social responses are dependent on the display of releasers.

EXPERIMENTS ON VISUAL RELEASERS

Visual releasers have been investigated not only in birds, but also in lizards, fish, and cephalopods. It is well, therefore, not to confine ourselves exclusively to birds, and, since my own experimental work has mostly centered on a fish that has a number of well-developed releasers of different kinds, this fish will serve as my first example.

²"Merkmale, die dem Individuum einer Tierart zukommen und auf welche bereitliegende Auslöseschematen von Artgenossen ansprechen und bestimmte Triebhandlungsketten in Gang bringen habe ich . . . als Auslöser bezeichnet" (p. 143). And again (p. 377): "Organe und Instinkthandlungen die ausschliesslich der Aussendung von Schlüsselreizen dienen, erreichen eine hohe Spezialisierung, stets parallel mit der Entwicklung entsprechender, für sie bereitliegender aus[zulösender Schematen. Wir bezeichnen solche Organe und Instinkthandlungen kurz als Auslöser."

The three-spined stickleback. This stickleback (*Gasterosteus aculeatus*) displays visual releasers of movement, form, and color. Experiments on the function of these releasers have been published by Ter Pelkewijk and Tinbergen (1937) and by N. Tinbergen (1939b, 1940, 1942).

The male stickleback isolates himself in spring, develops a nuptial dress of whitish-blue on the back and brilliant red on throat and belly, selects a territory which it defends against other males, builds a kind of nest, and entices a female to enter the nest and spawn.

The red belly acts as a releaser both to other males and to females. To a male any fish with a red belly is a rival, that is to say, it elicits flight in a male that is outside its own territory and evokes attack in any male that is on its own territory. This is demonstrated by a series of experiments of which the crucial ones may be summarized here.

Two series of models of sticklebacks were prepared, each containing dead sticklebacks and more or less schematic models. The models of series "R" were red on the ventral side; those of series "N" were the neutral color of a male in the non-breeding season and of females throughout the year (silver, with a dark greenish-black dorsal shading).

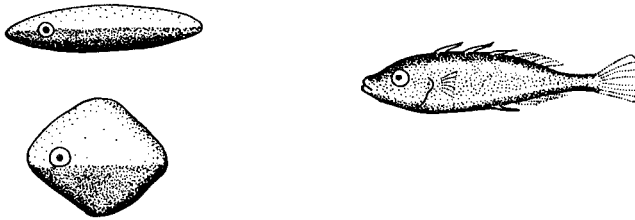


Figure 2. Two models of the R series (left) and a model of the N series (right) for testing the releasing power of the stickleback's red belly. After N. Tinbergen, 1947.

Experiment 1 consisted of bringing a model into an occupied territory for a fixed period. This was done in over 20 territories, and the models were presented in irregular order with due intervals between. Models with a red belly were attacked much more intensely than neutral models.

In Experiment 2 a model was placed in a territory from which the owner had been removed, and the behavior of the neighboring male stickleback in the same tank was watched. A neighbor-male always tries to intrude in a territory as soon as the owner is removed. All R models could appreciably retard the intrusion whereas N models had scarcely any influence.

The females' reactions were tested by trying to induce them to follow a model. In this we succeeded only when playing the models of Series R; no reaction, except occasional avoidance, was obtained with Series N.

A glance at the R and N models (Figure 2) suffices to show that the exact form has little influence, if any at all; models of most realistic form but devoid of red (Series N) had little or no releasive value.

In boundary disputes, a male stickleback often shows a special threatening movement: standing nearly vertically with his head pointing downward, his broad side turned to the rival and (often) the ventral spine on that side erected, he thrusts his snout into the bottom with abrupt jerks (Figure 3), a movement that can easily be imitated



Figure 3. Male stickleback threatening reflection in mirror. Note the unilateral display of the ventral spine. Photo by N. Tinbergen.

with a model. In a group of tests with models from both the R and the N series, each model was presented alternately in threatening posture and in normal swimming position, both in the situation of Experiment 1 and in that of Experiment 2 described above. A "threatening" model, whether from the N or from the R series, had more influence than a model in horizontal position. Also, a male taken from his territory was returned as a captive in a glass tube before the neighbor had trespassed. The neighbor was much more intimidated when the owner was presented in a wide tube that allowed him to perform the threat motion than when he was confined in a narrow tube that forced him to stay in the neutral, horizontal position (Figure 4 A).

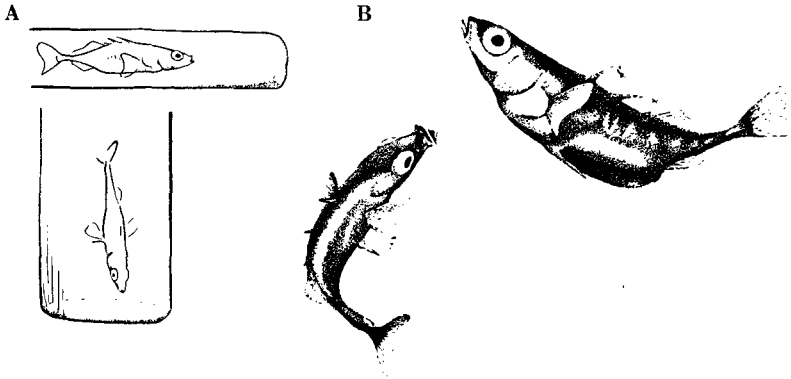


Figure 4. *A*, Tube-test for studying the influence of the threat posture in the stickleback. *B*, Courtship of the stickleback. Male below; female above. After Ter Pelkwijk and Tinbergen, 1937.

Another signal-movement is the "attitude of readiness" in the pregnant female (Figure 4 *B*), and the influence of this posture was also tested with models. A male can be induced by a rather crude model to take the lead and show the nest opening, provided that the model is presented in the right posture. Even dead fish of other species may be effective (Figure 5 *A*). The great importance of the *type* of movement or posture is well illustrated by the fact that it has been possible to induce either fighting or leading with the same model simply by presenting it either head down (which induces fighting) or head up (which induces leading). However, posture, or movement, is not the only signal for leading: shape is of no influence whatever

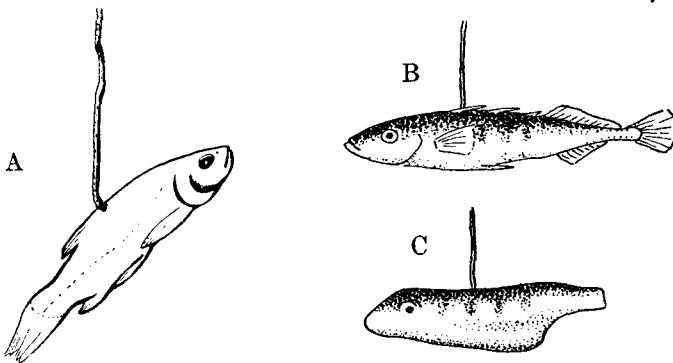


FIGURE 5. *A*, Dead tench, presented in courtship posture of the female stickleback to release the male's courtship. After Ter Pelkwijk and Tinbergen, 1937. *B*, Dead stickleback with normal abdomen. *C*, Crude dummy with swollen abdomen. After N. Tinbergen, 1942.

in releasing the male's fighting behavior, but for courting or leading, the swollen abdomen of the pregnant female has a strong releasing power—as demonstrated by comparing the influence of neutral models with that of “pregnant” models. It has even been possible to change live males into “pregnant” animals by excessive feeding, which caused the abdomen to swell to such an extent that not only the human observer but also the courting male sticklebacks mistook them for females. The relative unimportance of other particulars of form was also shown by comparing the influence of a dead stickleback (Figure 5 B) having a neutral abdomen with a highly simplified model having a swollen abdomen (Figure 5 C). Males invariably courted the “pregnant” dummy, while the dead stickleback affected them little.

The releasing mechanisms of these reactions are all innate. A male that was reared in isolation and built a nest was tested with models before it had ever seen another stickleback. The red belly, the threatening posture of a “male,” the upright posture of a “female,” and a “female's” swollen abdomen had the same releaser functions as in the experiments with normal males.

All these results exactly fit the original releaser theory as outlined by Lorenz.

The English Robin. Lack's results (1943) with the English Robin (*Erithacus rubecula*) show surprising parallels with our stickleback work. The red breast evokes furious attacks in any robin holding territory. It is by far the most effective of all the morphological characteristics of the bird. A mere bundle of red breast feathers is

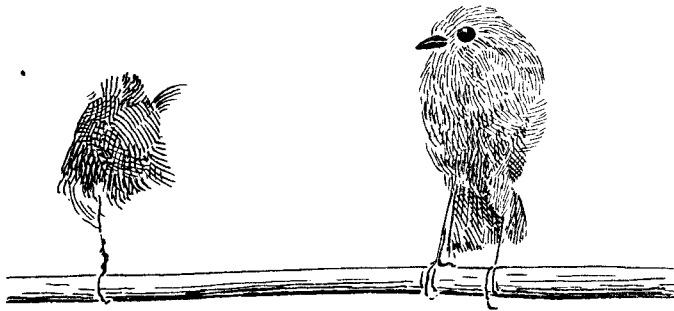


Figure 6. Tuft of red feathers (left) and complete mounted young robin (right).
After Lack, 1943.

attacked, whereas a complete mounted young robin, having a spotted brown breast instead of a red one, is ignored (Figure 6). The red breast is a releaser just as the stickleback's red belly is, although the function of the releaser is not the same in the two cases, since, in the robin, both male and female have a red breast.

The Flicker. Noble (1936) studied the releasing value of the "moustache" of the male Flicker (*Colaptes auratus*). Male and female of a pair in his garden readily distinguished between a mounted male and a mounted female, which shows that morphological characters, though perhaps not necessarily the only means of recognition, were sufficient. When the female of the pair was given an artificial "moustache" by gluing black feathers on the area which the moustache occupies in the male, the female was vigorously attacked by her own mate. After removal of the moustache she was accepted again. It would be worth while to repeat and extend this experiment, but from Noble's descriptions of the male's behavior it seems certain that the moustache has an enormous influence on the male. It is not certain whether the male's response to the moustache is innate or learned. Noble thinks it is learned, but it is not clear on what evidence he bases this opinion.

The Shell Parakeet. The experiments of Cinat-Tomson (1926) with Shell Parakeets (*Melopsittacus undulatus*) are especially convincing. The color of the cere (Figure 7), brown in females and blue

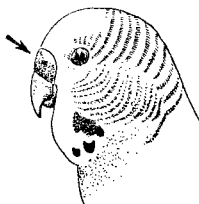


Figure 7. Shell Parakeet. Arrow indicates cere, which is blue in males, brown in females. After N. Tinbergen, 1947.

in males, acts as a releaser. Females with cere painted blue are attacked by the males, males with cere painted brown are courted. It is not known whether these reactions are innate. The color of the cere is used as a recognition mark only in judging strangers—a bird recognizes its own mate, in spite of an artificial color change, as soon as it hears the mate's voice.

The Herring Gull. The red patch on the lower mandible of the Herring Gull (*Larus argentatus*) seems to be a releaser during feeding. Goethe (1937a) presented two stuffed Herring Gull heads to newborn chicks, two of which had been taken from the nest shortly after hatching, while two others were incubator-hatched. One of the gull heads had a bill in natural colors; in the other the red patch was painted yellow of the same shade as the rest of the bill.

In a number of tests the two first chicks pecked 66 times at the red patch and 26 times at the other model. The incubator-hatched chicks reacted 115 times to the red patch and 32 times to the other model. Moreover, Goethe (1937a) observed (as did Heinroth before him) that chicks will often pick at a variety of red objects such as cherries and red rubber soles.

These tests could well be extended; for instance, other colors could be presented, and the color patch could be put at the base of the bill, in order to determine whether the reaction is released by red only and whether the patch has guiding power, but Goethe's experiments proved the releasing value of the patch beyond doubt.

Lizards. Especially interesting work has been done with lizards. In addition to Evans' work (1938), lizards have been studied by Noble and Bradley (1933), by Kramer (1937), and by Kitzler (1941). In *Lacerta melisellensis* the male has a bright red belly; in *Sceloporus undulatus*, the male is blue underneath; *Lacerta v. viridis* has a blue throat in the male. In all three species, the colored underparts act as a releaser; females painted with the colors of the males evoke attack instead of mating attempts. However, in these cases it is not known whether the releasing mechanism is innate; Kramer suggests that it might not be.

Kitzler's work with *Lacerta agilis* and *L. v. viridis* contains a wealth of data on the functioning and the origin of releasers. Experimental proof of the releasing value of the male's secondary characters is given for both species. The blue throat of the male *viridis* has exactly the same function as the stickleback's red throat. A female with the throat painted blue is not only attacked by males, it attracts females. A male with its throat painted green (the female's throat color) is not chased even by the most aggressive male. A painted *agilis* male is treated as a rival by a male *viridis*. A crude yellow clay model with a blue throat is treated as a male *viridis* by both males and females.

Reviewing the results obtained with lizards, it is evident that the experiments should be supplemented. For instance, in Noble's work (Noble and Bradley, 1933) insufficient attention is given to the reactions of the female. In Kitzler's experiments we should like to know how the animals respond to models of other colors, etc. We should also like to know whether the releasing mechanism is innate or not. Nevertheless, in all these papers it is demonstrated clearly enough that the male's nuptial colors release responses in other males.

Cichlid fish. Valuable work has been done with cichlid fish of different species. Seitz (1940) showed that, in the sexually dimorphic species *Astatotilapia strigigena*, the male's fighting behavior is released when he is visually stimulated by another male. The releasing

stimulus situation is very simple, for the male fights against rather crude dummies provided that they are (1) laterally compressed, offering a large surface to the male, (2) glossy silver or blue, and (3) spotted with "jewels." Seitz also tested a male reared in isolation; its fighting response was evoked by exactly the same external situation as that of normal males, showing that the releasing mechanism of the fighting response is innate. On the other hand, the isolated male's courting response could also be evoked by very simple models, such as a silvery ball, whereas the normal males never courted any model at all, however accurate an imitation of the living female it might be. This proves that the releasing mechanism of the courting behavior is changed by conditioning. The female has no structures or movements that could be classified *a priori* as releasers. The splendid nuptial dress of the male, however, appears to be adapted to an innate releasing mechanism and acts as a releaser, a fact which could be predicted from the releaser theory.

In *Hemichromis bimaculatus*, the African jewel fish, male and female are not very different; both have a red nuptial dress and are spotted with "jewels." Seitz (1942) and Noble and Curtis (1939) showed that the red color is an important recognition mark to which both males and females respond, when in mating condition, by fighting and courting. Seitz tested the male's releasing mechanisms of fighting and courting; in both, special movements make sex-discrimination possible; a male will erect and display its fins, a female, after an initial display, has to "break down" and show a submissive attitude in order to be accepted as a female. The releasers on which sex-discrimination is founded, therefore, are not special morphological structures, but rather specialized movements, as could be expected in view of the similar (though not absolutely identical) coloration of the sexes. A further development of this sex-discrimination mechanism occurs during individual life: the fish learn to know their own mates individually; in other words, the releasing mechanism is made more specific by conditioning (Noble and Curtis, 1939).

The cuttlefish. The most striking demonstration of how far convergencies can go in these phenomena, is given by L. Tinbergen (1939) in his study of the mating behavior of the cuttlefish *Sepia officinalis*. Parallel with the development of eyes in cephalopods (convergent to those of fish) the courtship of the cuttlefish has evolved into a typically visual one closely resembling the courtship of certain sexually dimorphic fish, lizards, and birds.

A male *Sepia* in mating condition assumes a strongly variegated pattern of alternating white and dark purple bars, and displays the most conspicuous part, the broad, flattened lateral surface of the fourth arm, toward other individuals (Figure 8). Reactions of males

and females to this display differ essentially: a male returns the display, a female in mating condition keeps quiet and allows the male to copulate. A series of varied experiments with models showed that the male's nuptial colors, and especially the color and display

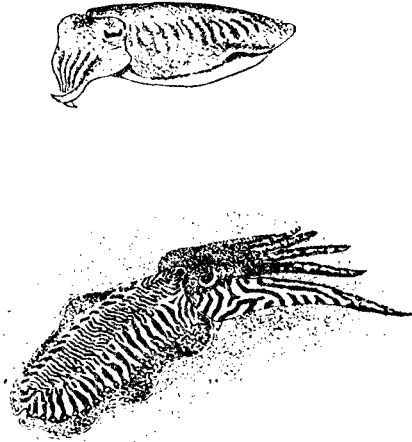


Figure 8. Male cuttlefish in neutral dress (upper) and in display (lower). After L. Tinbergen, 1939.

of the arm, released fighting in other males. The experiments did not determine whether the male's display acted on the female as a releaser. The males treated all models colored and "behaving" like females as if they were females.

This state of affairs closely resembles that found by Noble and Bradley (1933) in *Sceloporus*. In both species the male's display is primarily a means of threatening other males; in both species the stimulating influence on the female is apparently small. The male's nuptial dress is primarily a "gladiator's vestment" (Noble, 1934).

This review of experimental work, short as it is, shows that the releaser theory is not an "ideology" that has to be "accepted blindly" as Dr. Rand thinks. It is true that more experimental work is needed (though not to prove that releasers do occur, since that is clear). A further study of releasers will almost certainly give us an understanding of such diverse problems as the sociological structure of animal communities, the innate releasing mechanism, and last, though not least, the evolution of behavioral elements.

NON-VISUAL RELEASERS

Auditory releasers. There is good experimental proof of the releasing function of the chirping of crickets and grasshoppers. The

most spectacular experiment was carried out by Regen (1913), who kept males and females of *Gryllus campestris* in separate rooms in his house. The male's song was picked up in a telephone receiver which was connected with a loudspeaker in the females' room. Regen had the satisfaction of seeing the females jump right into the old-fashioned, trumpet-like loudspeaker.

So far as I know, no similar experiment has been carried out with birds. However, a number of simpler though nonetheless convincing experiments have been described in the literature, and "natural experiments" have been witnessed by every field ornithologist. Both natural and prearranged experiments concern situations in which a reaction to a call or sound is shown by a bird that is unable to see the calling individual.

The function of song, as the most spectacular of all bird calls, is strikingly similar to the function of the male stickleback's nuptial coloring: it repels other males and attracts females. Instances mentioned in the literature are too well known to need enumeration here, but one instance, from a recent work (Lack, 1943:29), may be quoted:

"On May 27th, 1937, an unringed newcomer robin, evidently wandering without territory, started to sing in a corner of the territory owned by a long-established resident male. The latter, then in a distant part of its territory, promptly sang in reply. The newcomer, which could not, of course, yet know that it was trespassing, sang again. The owner, having flown rather closer in the interval, sang again in reply. The newcomer again sang, the owner again approached and replied, now more vigorously, and this procedure was repeated twice more, the owner finally uttering a violent song-phrase from only some fifteen yards away, but still hidden from sight by thick bushes. At this point the newcomer fled, from an opponent it never saw, nor did it appear again."

It has further been observed in several species of hole-breeding birds that the begging calls of the young stimulate the parents to attempt to feed them, even when the young are concealed from view (N. Tinbergen, 1939a). Some Herring Gull chicks that I kept in my observation hide quite readily responded, by crouching, to the alarm calls of the adult birds; nestling thrushes (*Turdus m. merula* and *Turdus e. ericetorum*) stop begging as soon as the parents' alarm call is heard (Tinbergen and Kuenen, 1939). Further, every bird watcher knows that it is sometimes possible to attract birds by imitating song, call notes, distress calls of the young, etc. Especially in the case of birds whose calls have been mechanically recorded, the opportunity for more detailed study seems to be excellent.

Chemical releasers. In animals in which chemo-receptors are better developed than in man and birds (both exceptionally visual types),

special releasers may be found whose exclusive function is to act on the chemo-receptors of congeners. Several of these cases have been studied.

Von Frisch's classic work on the "language" of hive bees has shown that pioneer workers after discovering a new source of nectar perform a "dance" in the hive which stimulates a number of other bees. These react by leaving the hive and extensively searching the vicinity, eventually gathering on the species of plant that had been discovered by the pioneer. Experiments prove that the bees are attracted to the flower by its odor which was carried in the "fur" of the pioneer that had visited the flower before "dancing" in the hive. When flowers without a distinct odor are concerned, the bees that have been "given the cue" by the pioneer do not alight at once on the flowers when they find them but first perform a long ceremonial flight amongst the flowers while protruding their scent organs, which are located in the abdomen. This ceremony marks the exact spot with a typical scent which attracts other bees. (von Frisch, 1923; see also 1946.)

The male of the grayling butterfly (*Eumenis semele*) has a scent organ on the dorsal surface of the forewing (Figure 9). This is used during an elaborate courtship display, which reaches its climax in the male's characteristic bowing performance in front of the female, when her antennae, which bear chemo-receptors, are caught between the male's wings and are thus brought into contact with the scent organs (Figure 10). These act as the releaser necessary to secure the female's cooperation in coition. Males in which the scent organs have been removed have great difficulty in acquiring a mate in spite of intensive courting (Tinbergen, Meeuse, Boerema, and Varossieau, 1942).

In other animals, scent may be used, in much the same way as song and visual releasers are, as a means to advertise occupation of a territory. This was first discovered in the domestic dog, which erects "scent flags" on prominent places in its territory (von Uexküll and Sarris, 1931). Holzapfel (1939) discovered that the hyena (*Hyaena*) had a comparable habit, and recently Hediger (1944) listed a whole series of similar phenomena in a number of mammals.

Tactile releasers. Even tactile stimuli may serve as specialized releasers—for example, human courtship and human mother-infant relations are partly based on them. The mating of the snail *Helix pomatia* offers another example. As Szymanski (1913) showed, the characteristic movements and postures of each of the partners are reactions to tactile stimulation by the other. The "courtship" culminates in the thrusting out of the "dart" (Figure 11), the only function of which is the delivery of a powerful stimulus; the dart is a true releaser.

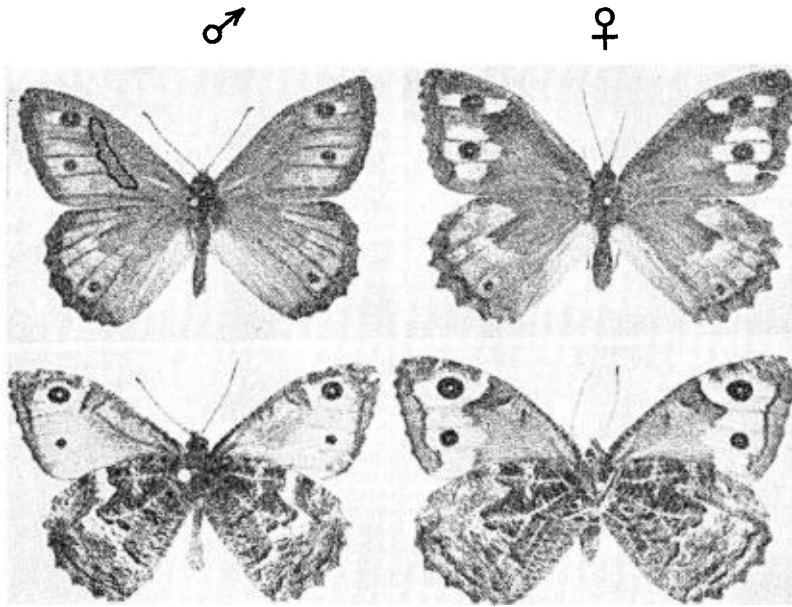


Figure 9. The grayling butterfly. Upper: dorsal side; lower: ventral side. Black line in upper left figure indicates position of scent organ on left wing. After N. Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

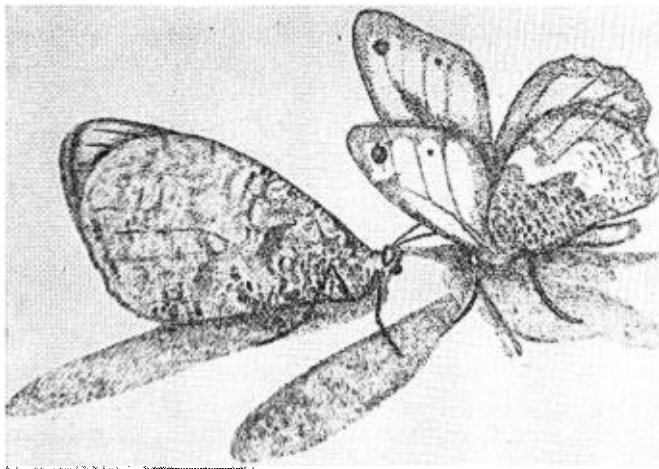


Figure 10. Grayling butterfly male (right) bowing before female, so that the female's antennae come in contact with the scent organ of the male. After N. Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

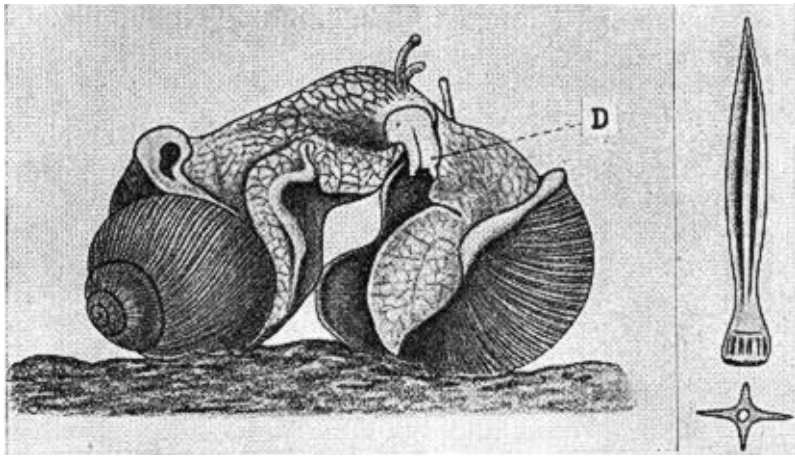


Figure 11. *Helix pomatia*. Extrusion of dart during mating (left). Detail of dart (right). After Meisenheimer, 1921.

These few instances suffice to show that releasers are not confined to the visual domain. It is a significant fact that visual releasers are found in groups with highly developed eyes, chemical releasers in animals with good chemical receptors, auditory releasers only in groups with specialized acoustic organs, and so on. It is even quite possible that in some cases the only function of certain sense organs is as a means of social intercourse. This might well apply to the Homoptera, for example, in which both stridulation organs and tympanal organs seem to be exclusively used in communication between members of the same species.

The visual releaser as a phenomenon, therefore, does not stand alone. It is only a special case of a widespread phenomenon, the existence and function of which has long been recognized. A criticism of the releaser theory as a whole would have meaning only if all categories of releasers were included in the discussion.

NON-EXPERIMENTAL EVIDENCE ON VISUAL RELEASERS

In the foregoing paragraphs it is evident that a "releaser" is part of a complex mechanism involving special movements, special effector organs, special receptors, and special innate releasing mechanisms. The syrinx of song birds, the stridulation organs of crickets and grasshoppers, the scent organs of bees, butterflies, and mammals, the red breast of the English Robin, all are highly specialized, "improbable," specifically adapted organs. Movements, effector organs,

innate releasing mechanisms are fitted together; they act as a wonderful, complicated system the only function of which is the construction of a means of social communication. In fact, such complicated structures are understandable—they “make sense”—only in connection with their function; the coincident presence in the same species of stridulation organs, the stridulating drive, and an innate tendency to react in certain “purposive” ways can be recognized as an adaptive feature only when the releaser function is recognized.

Hence, it is quite justifiable to conduct experimental work on the basis of the releaser hypothesis even when only parts of the whole mechanism are known, that is, for example, when only the effector organ (e.g., a conspicuous structure) is found, with a movement displaying this effector.

It is true, as Dr. Rand remarks, that one has to reckon with the possibility of “maladaptation.” However (apart from the question whether it is satisfactory to consider without proof a highly specialized structure such as the syrinx of song birds or the wing of an Argus Pheasant as a functionless error of evolution), there is a difference between a critical attitude and a defeatist attitude. Any hypothesis aiming at “finding the use” has to be seriously tested before it is abandoned in favor of a purely negative hypothesis. These considerations justify the following enumeration of cases in which only part of the mechanism has been investigated and the releaser function of the whole has not yet been experimentally tested. Since it is especially the existence of visual releasers that is doubted, I will confine myself to supposed visual releasers. The argument applied is: when we again and again observe that a conspicuous, highly “improbable” structure is used as an instrument by an equally conspicuous and “improbable” movement resulting in a display of this structure, we suppose that both structure and movement form part of an adaptive mechanism that has the *function* of display.

I will take the risk of being accused of “following ideologies blindly” and cite as significant the conclusion reached by Heinroth, who worked along these general lines and must in fact be considered one of the founders of modern ethology. This great observer, whose disinclination to formulate general conclusions is well known,³ said, as early as 1900, that conspicuous structures in birds are always used in display. Huxley (1914:523) wrote: “The same instinctively displayed parts—wings and tail, throat and crown—are the parts which are especially singled out for the development, first of special colours,

³ Typical of Heinroth's attitude is the following anecdote, related to me by one of his intimate friends. Heinroth once delivered an address full of interesting facts arranged in such a way as to suggest a special and important conclusion. He did not, however, formulate this conclusion himself, but concluded his speech with: “Na, meine Herren, den Reim dazu können Sie Sich selbst machen.”

. . . then of special colours and structures combined." This sentence, while evolutionary in sense, is based upon descriptive evidence revealing the same general rule as that pointed out by Heinroth. The following facts serve to substantiate this general rule.

Of widespread occurrence is the type of display in which the body as a whole is laterally flattened and enlarged and made as high as possible, often with the help of erectile structures such as fins and feather fans. Correlated with this lateral flattening is an orientation toward the reactor which offers the most imposing view of the body as a whole. Further, the coloration of the body is localized in such a way as to be most conspicuous during the lateral display. Often the color pattern covers both body and extensions, such as fins. This is especially obvious in many fish, where, for instance, black bars or fields of "jewels" extend over the dorsal and anal fins. I often wondered in such cases which part of the coloration would be the re-

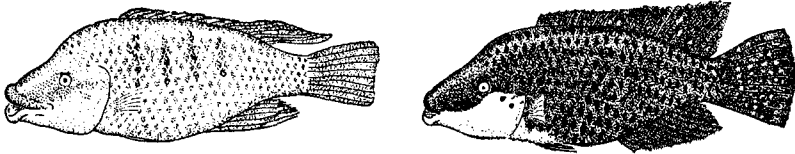


Figure 12. *Tilapia natalensis* male. In asexual (left) and sexual (right) coloration. After N. Tinbergen, 1947.

leaser until I realized that such a fish must be considered as one huge releaser. One could say: such fish "have" no releasers; they "are" releasers (Figure 12).

In fish, the stickleback is only one of the less prominent performers of lateral display. *Betta* (fighting fish), sunfish (Centrarchidae), cichlids, and many others offer extreme examples (Figures 13 and 14). In *Aequidens latifrons*, for instance, the dorsal, caudal, and anal fins, when erected, nearly double the visible surface. The caudal, anal, and hind part of the dorsal fins are also locomotory organs, but the forepart of the dorsal fin has no locomotor function and seems to have been adapted entirely to display purposes.

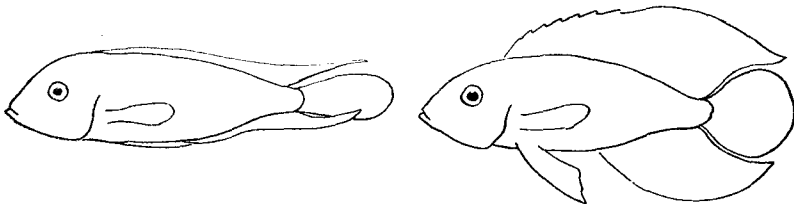


Figure 13. *Aequidens latifrons* male. In posture of inferiority (left) and in threat posture (right).

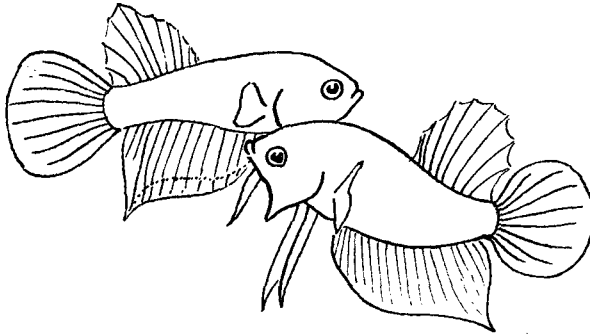


Figure 14. *Betta splendens*. Males in lateral threat display. After Bessiger in Holly, Meinken, and Rachow, 1936.

Orientation in respect to the adversary is very well demonstrated by one of Lissmann's experiments (1932) with *Betta splendens*. Like so many other visual types, *Betta* males threaten their own image in a mirror. When Lissmann turned the mirror on a horizontal axis, the fish followed the movement, keeping its lateral surface parallel to that of the reflection, even turning on its side in order to do so (Figure 15).

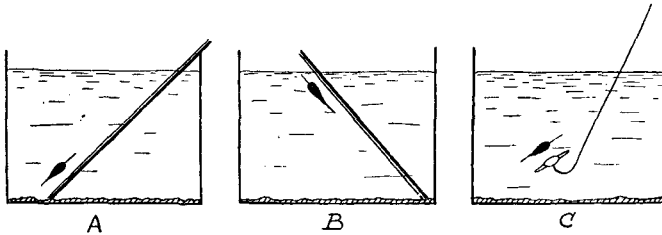


Figure 15. *Betta splendens*. Lateral display of male to reflection in mirror (A and B) and to dummy (C). After Lissman, 1932.

The male newt *Triturus vulgaris* begins its courtship with a visual, sideward display. The newt has to stand in a rather twisted posture to be able to display its lateral surface and yet fix the female with both eyes. This visual display is followed by a tactile stimulus: with a sudden leap (a surprising performance in a newt!) and a strong blow of the tail, the male throws a water current against the female which gives her no little difficulty in holding her ground. This is immediately followed by a third kind of display in which the male probably delivers a chemical stimulus.

A further example is *Anolis* in which the species have a special, conspicuously colored "dewlap" which tends to exaggerate the effect of the lateral compression of the body (Evans, 1938) as shown in Figure 16.

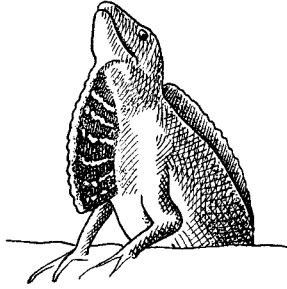


Figure 16. *Anolis carolinense* male. Dewlap display. After Evans, 1938.

Among birds, the lateral display is very common. Numerous instances are found in the Phasianidae, e.g., in the Golden Pheasant, *Chrysolophus pictus* (Figure 17), Amherst's Pheasant, *C. amherstiae*, Bulwer's Pheasant, *Lobiphasis bulweri*, the domestic fowl, and the turkey. But it is also observed, to a lesser degree, in other birds.

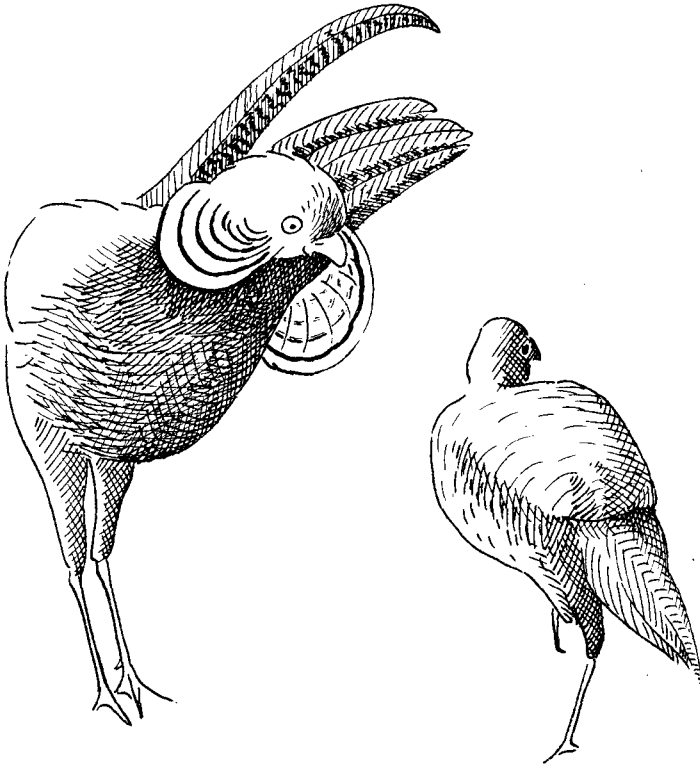


Figure 17. Golden Pheasant. Lateral display of male (left) before female. After Hagenbeck in Heilborn, 1930.

I have seen it in the European Jay, *Garrulus glandarius*, though this species has no feather fans especially developed for the purpose, and it is quite astonishing to see it render itself as flat as a knife.

Apart from the general pattern of lateral display, there are numerous instances of directed display of special parts of the body, some of which show a remarkable and grotesque correlation of movement with structure. Both the African jewel fish (*Hemichromis bimaculatus*) and the South American *Cichlasoma meeki* have a morphological releaser on the gill-cover, consisting of a black patch bordered by a yellowish or greenish golden ring. This structure is used during a frontal threat display which consists, as in so many fish, of erecting the gill-covers. Now in *meeki* the black patch is situated at the ventrocaudal edge of the gill-cover, in *bimaculatus* at the dorsocaudal edge. In conformity with this, *meeki* spreads especially the ventral part of the gill-cover (Figure 18, right), while *bimaculatus* displays its releaser by spreading especially the dorsal part of the gill-cover (Figure 18, left). Both movements are rather specialized forms of gill-cover display.

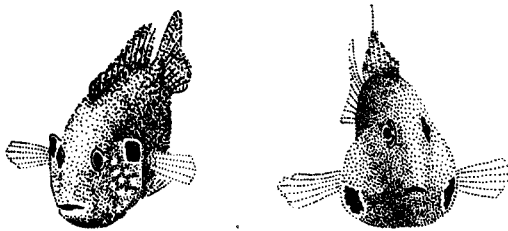


Figure 18. *Hemichromis bimaculatus* (left) and *Cichlasoma meeki* (right). Frontal display. After N. Tinbergen, 1947.

In birds, so many instances of visual releasers are known (see O. and M. Heinroth, 1928; Stresemann, 1927-34; Armstrong, 1942) that I will confine myself to a few rather unconventional types. The male Snow Bunting, *Plectrophenax nivalis*, displays the variegated black and white pattern of the dorsal surface (Figure 19A) and in doing so walks slowly away from the female (N. Tinbergen, 1939a). The threat movement of the Common Crane, *Grus grus*, consists of displaying the occiput, where a red wattle appears (Heinroth, 1928). A male Lapwing, *Vanellus vanellus*, when trying to attract a female to one of his scrapes, displays his under tail coverts, which are a warm chestnut-brown (Figure 19B). When the female moves, the male promptly turns his tail, presenting a full view (Rinkel, 1940). A Flicker, *Colaptes auratus*, also displays its under tail coverts in threat but uses quite a different method: it tilts the tail sideways and for-



Figure 19. *A*, Snow Bunting. Back display. After N. Tinbergen, 1947. *B*, Male Lapwing displaying under tail coverts. After Rinkel, 1940.

ward. The result is a sudden flash of yellow (Noble, 1936). The Red-wing (*Agelaius phoeniceus*) erects its "epaulets" in threat display (Noble and Vogt, 1935), as does also the Tricolored Red-wing, *Agelaius tricolor* (Lack and Emlen, 1939). Chaffinch (*Fringilla coelebs*) males make a similar use of their white epaulets (Lack, 1941).

Erection of crests and other parts of the plumage in birds is, as a rule, confined to conspicuously colored parts, as every bird watcher knows: goldcrests (or kinglets), birds of paradise, pheasants, grebes, ruffs, terns, ducks, etc. Lorenz's study (1941) of the courtship of the Anatinae contains numerous observations of quite unexpected details. For instance, in a special phase of the courtship, males turn the back of the head toward the female. The Pintail, *Anas acuta*, which has a brown lane running between two white stripes, erects the feathers of the brown field. The result is a remarkable strengthening of the contrast (Figure 20). Another movement, performed by nearly all species, serves to display the colored wing-shields and other gaudily colored parts.

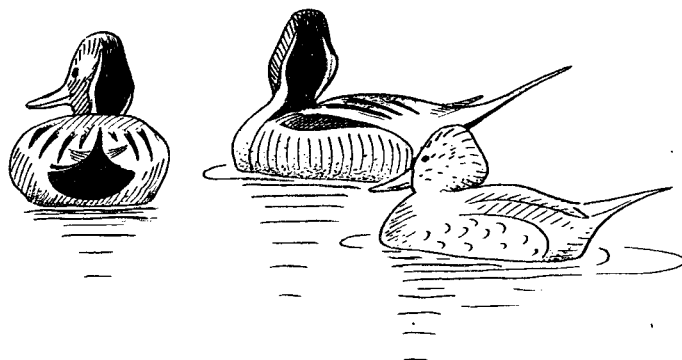


Figure 20. Pintail males displaying neck before female. After Lorenz, 1940 (from motion pictures).

It seems superfluous to enumerate still more cases. Every bird watcher knows instances from his own experience. Yet it would be advisable to publish such facts more often than has been done in the past. A short, accurate description, with a sketch or photograph, not taking, in all, more than one or two pages of an ornithological journal, would be sufficient and would materially help to extend our knowledge.

I am convinced that the correlation of structure and movement will be shown to be much more complex than is known at present. Comparative study would be especially valuable because it helps one to see the significance of a movement merely by stating that it is absent in related forms, coinciding with the absence of a morphological releaser. To cite an instance: one of 13 species of cichlids studied by Dr. and Mrs. Baerends (1948, in press) in the Leiden Zoological Laboratory, *Astronotus ocellatus*, showed a peculiar trembling movement of the tail during courtship. This is the only species out of the 13 that has an "eye" spot at the tail-base. By the trembling ceremony, attention was quite effectively drawn to this releaser. The fact that both trembling ceremony and visual structure were present in this one species and absent in all others strengthened the conclusion that they were correlated.

The best way to get an impression of the significance and importance of visual releasers is to concentrate on a family, or smaller group, of animals to which many species with gaudily colored dresses belong and make a careful comparative study of their behavior. Groups with specialized visual releasers in many differently evolved species are the ducks (of which only the Anatinae have been studied in detail), the birds of paradise, and the pheasants. The peacock, the Argus and Bulwer's Pheasants give us an idea of the host of interesting facts that await discovery in the last group. It is for the same reason that a research program on the cichlid family was started in several laboratories; this family is another instance of a great and varied group of bearers of visual releasers.

In studying such a group, the value of the releaser theory is most clearly demonstrated by the fact that after a short time one is able to predict the nature of the display movement in a newly encountered species after merely viewing its morphological equipment. Thus both Lorenz and I, quite independently, came to the same conclusion when we got our first *Cichlasoma meeki*, viz.: "That fellow must have a tremendous frontal threat display of the operculum." Actually, our letters describing our first thought and how it was proved correct by the fish (Figure 18) crossed in the mail.

Although I have mentioned only a very few of the known facts concerning the correlation between structural and behavioral components of releasers, I will let these suffice. In view of the evidence for the function of visual and other releasers, a rather strong bias would

be required to object to the releaser theory even as a *working hypothesis*. It is my opinion not only that the hypothesis is fully justified but that it has already demonstrated its value as a unifying principle covering a wealth of facts.

PART 2: EXPERIMENTAL METHOD

Experimentation with releasers, as reviewed in Part 1, seems a very simple business indeed. However, this is true only in appearance. The technique is simple enough, but as a method of thinking and planning it has some treacherous pitfalls. It is easy to meddle with animals, to experiment in a vague and random way, but it requires some knowledge of ethology as a whole and some insight into the nature of a given problem to plan really convincing experiments that are relevant to the problem. I will attempt to point out some of the pitfalls to be avoided.

An experiment as such is never "wrong." It is only in connection with the problem and with the conclusion drawn that an experiment may sometimes be called wrong or inadequate. To cite an instance (which naturally takes the form of criticism): when Rand observed that adult Song Sparrows (*Melospiza melodia*) and Catbirds (*Dumetella carolinensis*) carry off feces without waiting for the typical display of the anal feather circling by the young, it is only his conclusion—that the anal circling has no releaser function—which must be called wrong. His experiments are interesting enough and not "wrong" in themselves, but they do not prove what Rand assumes them to prove; they merely show that the adult's reaction can be released by a stimulus situation in which the display of the anal circling is lacking. This does not mean that the anal circling has no releaser function. As I have pointed out in a previous paper (Ter Pelkwijk and Tinbergen, 1937), Leiner's experiments (1929, 1930) in which female sticklebacks were willing to follow males in monochromatic light by no means proved that the nuptial colors of the male have no releasing power but only that the female's responses are not dependent on color alone. As we have seen, other experiments proved the male's red belly to be a very important releaser. Closer consideration of the releaser problem is necessary to understand why a releaser is not always easily detected by experiment.

THE INNATE RELEASING MECHANISM AND RELEASERS

Because the releaser is, in a sense, a reflection of the reactor's releasing mechanism—the "angeborene auslösende Schema" (innate releasing pattern), as it was called by Lorenz—the first thing to do is to examine this mechanism.

One finds the first indication of the existence of something like a "Schema" when an animal appears to be noticeably unselective in its reactions to other animals and to dummies: a stickleback that readily fights any dummy that is red underneath (as every male stickleback in mating condition will do) shows that many "recognition marks" of the opponent male that exist for the human observer are not essential to the stickleback in this situation. In other words, the animal reacts to only a few recognition marks or "sign stimuli," while many other elements of the situation apparently have no influence. (This gives the impression that the animal's perception is "schematic," hence the word "Schema." But I prefer to use the terms "sign stimuli" and "releasing mechanism.") Experiments confirm this conclusion, and it even seems to be a general rule that innate releasing mechanisms are responsive to stimulus situations with only very few sign stimuli.

It is hard for the human observer to realize that an animal often does not use all the sensory signs which its sense organs put at its disposal. Yet it is clearly a fundamental fact of innate behavior in animals. A female stickleback, lured (with visual stimuli) into the nest by the male, will lay eggs only after the male has furnished a prolonged series of tactile stimuli: he repeatedly thrusts his snout against her abdomen, and after some time, this trembling movement induces her to deposit her eggs. Although the female, while in the nest, can see the male throughout this procedure, one can remove the male and replace his activities by producing the "trembling" movement with a glass rod; the female will lay as well after tactile stimulation by the glass rod as after stimulation by the male itself. It is only the tactile stimulus that counts in laying; visual stimuli, while of the utmost importance in other phases of the courtship, are wholly unessential now.

Similar facts have also been recorded in birds. A domestic motherhen will run to the rescue of a chick in distress. This reaction is entirely dependent on the distress call and not on visual stimuli: a struggling chick under a glass dome has not the slightest stimulating influence, but the sound of the distress call from behind a screen will instantly release the mother's reaction (Lorenz, 1935).

Still more astonishing is the fact that even within a single mode of perception (sight, for example), many elements in the situation are ignored. Young thrushes (*Turdus m. merula* and *Turdus e. ericetorum*), which we kept for investigation of their gaping responses, reacted, when still blind, to a slight jarring of the nest. Later, when about 10 days old, they would respond to visual stimuli. These were analyzed with dummies (Tinbergen and Kuenen, 1939). Form or size of the parent dummy did not count at all. Anything from 3 mm. diameter upward would do, provided it was moving. We were surprised, however, to discover that in order to evoke gaping an object had to be

above the horizontal plane through the nestling's eye. The same objects that induced excellent reactions when kept high were ineffective when lowered below eye level. The birds looked at it, thereby proving their eyes could "see" it, but they did not gape. The sense organs "saw" well enough; the bird as a whole did not "see" it. Obviously this is a problem of the nervous system rather than of the sense organs.

This is only one instance among many. Each reaction is susceptible to a rather vague stimulus situation, or a generalized situation, as it is often called. I think it is more accurate to describe it in terms of "releasing mechanism" and "sign stimuli." Each reaction has its own releasing mechanism, responsive only to stimulus situations with few sign-stimuli. Russell (1943) has collected a great number of examples from the literature.

A consequence of this restriction of each reaction to a few sign stimuli is that the releasing mechanisms for the different reactions of one animal may be entirely different from each other, even when the reactions are evoked by the same object. Thus the female stickleback is attracted to the nest by the sight of a red fish, but it is induced to lay eggs by a series of thrusts at the tail base. As a rule, both stimuli are administered by the same male.

Therefore, study of innate releasing mechanisms does not reveal the potentialities of the sense organs. Before I realized this, I had long thought that the grayling butterfly, *Eumenis semele*, was color-blind, simply because it did not respond differently to different colors in the one reaction I happened to study. The males of this species follow passing females in wild pursuit, thus inducing them to go down and watch the male's subsequent courtship. We analyzed the releasing mechanism of the male's first reaction and found that the color of the models we used could be varied at random without changing the male's behavior is not released by a visual stimulus—though the male can fervor. Yet he is far from color-blind. When his reactions to colors are tested during quite another instinctive activity, viz., during his foraging excursions which lead him from flower to flower, he appears to have a great preference for yellow and blue. Red, green, and 30 different shades of gray, which all released his mating flight, never released his foraging activities.

Sticklebacks provide another interesting example. After the female has laid, the male goes through the nest to fertilize the eggs. This behavior: he dashed after paper butterflies of all colors with equal see the fresh eggs clearly enough—but by chemical (and presumably also tactile) stimuli from the eggs: it is sufficient to bring some water in which fresh eggs have been kept for a time into the nest to induce the fertilizing behavior. On the other hand, foraging behavior in sticklebacks can be induced only by visual stimulation; worms

ERRATA

Unfortunately in printing the March 1948 issue of *The Wilson Bulletin* lines 6 and 15 (counting from the bottom of the page) on page 30—both beginning with the word “behavior”—were transposed. Please so mark your copy.

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or *Daphnia* in a glass tube instantly attract them, but meat juice or other extracts that readily activate foraging behavior in many other fish such as the eel (*Anguilla*), for example (see Wunder, 1927), never affect the stickleback.

Von Uexküll's concept (1921) of the *Umwelt*—the [animal's] own world—is based on this fact, viz., that an animal often reacts to only part of the environment as we see it. Analyses of releasing mechanisms enable us to give step by step a precise description of the sign stimuli, which help in building up the animal's "own world." Thus the idea of the *own world*, which was at first rather a vague notion, is substantiated by experiment.

A different method is required for the study of the potentialities of the sense organs. Most reactions, however selective they may originally be in regard to sign stimuli, can be conditioned to respond to any stimulus that can be received by the sense organs. The study of conditioned reactions as indicators of sensory reception has been developed to a high degree of perfection by von Frisch and his collaborators.

The term *das angeborene auslösende Schema*, or innate releasing mechanism, has been abused in several ways, two of which must concern us here. First, it is misleading to speak of the "Schema" of any object in the environment, for instance, a "Schema of the sex partner," for we know that a sex-partner may be to the animal several entirely different things, depending on which instinctive activity brings the animal into contact with the sex-partner. For a female stickleback, the sex-partner "is" a red fish (visual) at one moment, and it "is" something hard in trembling motion (tactile) a mere few seconds later. A "Schema" belongs to a *reaction* of the behaving animal, not to the object in the outer world to which the animal is reacting. It is also for this reason that the term "releasing mechanism" is to be preferred to the word "Schema" with its more or less mystical tinge. It is for the same reason that the word *Kumpan* (companion) as originally used by Lorenz has to be either carried *ad absurdum* or abandoned, for—as Rand (1941:290) quite correctly pointed out—we ought to subdivide the sex companion into numerous sub-companions, such as (in the case of the stickleback) the "visual-courtship-sub-companion," the "tactile-egg-laying-sub-companion," and some five other sub-companions. This procedure is, of course, quite consistent and quite impossible. This was, indeed, clearly recognized by Lorenz himself; in his later papers he has abandoned the concept of "*Kumpan*" and has also accepted the idea that a "releasing Schema" belongs to a reaction, not to an object. However, these are only minor corrections, and it would be unfair to forget that this greater precision and further development in the work has only been possible on the basis of the *Kumpan* paper, which, in spite of its shortcomings ("I don't like

my *Kumpen* paper any more," said Lorenz in 1937), has given a most powerful stimulus to animal ethology. In fact it is one of the classics.

The moral of all this is primarily that the experimenter must see the restrictions of his problem and of the subserving experiments. A releaser never affects the reactor's behavior as a whole, although it may affect an important part of it; a releaser often serves merely to activate one minor element of behavior, and only by studying that susceptible part can we find an answer to the question whether a given structure or movement is in fact a releaser.

REACTION CHAINS

The foregoing considerations deserve special attention when one has to do with a series or chain of successive reactions, each with its own releasing mechanism.

In order not to write exclusively of sticklebacks, though they offer a very convincing example in their chain of courtship activities (N. Tinbergen, 1942), I will relate another instance, discovered in insects. The female of the digger wasp, *Philanthus triangulum*, hunts bees and stores them as food for the larvae. By an experimental analysis of this hunting activity it was found that the wasp searches for bees by flying from plant to plant. Though other tests show that it can smell a bee from at least a meter's distance, no hunting wasp is ever attracted by the odor of a hidden bee, even if it is less than 5 cm. away. Visual stimulation by a moving object of about the size of a bee at once changes the wasp's behavior; it immediately takes a position at about 10 cm. to leeward of the moving object and then hovers like a syrphid fly for 2 to 10 seconds. During these seconds, the wasp "tests" the scent emanating from the bee. Whereas a wasp can easily be induced to hover by all kinds of visual substitutes for a bee (e.g., any other insect of the right size such as a fly or bumble-bee, or even a stick or stone hanging from a moving thread), the substitute must be given the typical scent of a honey-bee to be accepted as prey, that is, to elicit the next link in the behavior chain, namely a flash-like leap toward the prey by which it is seized at once. Sticks that have been given bees' scent by shaking them in a glass tube with freshly killed bees are seized. However, they are not stung; it was shown that the sting is the next link in the chain; it is only delivered after a new sense impression is received, probably from tactile stimuli. Thus the hunting of this wasp consists of a chain of reactions: searching, hovering, leaping, stinging—each of which has its own releasing mechanism. The restriction to the few sign stimuli characteristic of each reaction is not caused by limited capacities of the sense organs, since (for instance) the hovering reaction never responds to olfactory stimuli,

even though a wasp can smell the bee from a great distance—when it loses a bee it has just killed, it finds it again by smell.

The chain character of behavior is responsible for many cases in which a stimulus administered in experiment is capable of eliciting only a fragment of an activity. When, for instance, imitation of the song of a bird does not cause it to actually fight the imitator, it is not because the song has no releasing function. In many cases it will attract the bird at once, but since the visual stimulus from the imitator does not correspond with the visual sign stimuli necessary to evoke the next reaction, viz., the attack, the behavior breaks off. In the English Robin, song attracts a territory-holding male, but the sight of a red-breasted "something" is necessary for the bird to continue its behavior into real attack (Lack, 1943).

CONFIGURATIONAL QUALITY OF SIGN STIMULI

When the separate sign stimuli are studied in detail, it appears that the name "stimuli" can only be applied to them in a rather general meaning, for they are always complicated systems to which the term "Gestalt" may rightly be applied; they are "configurational" stimuli. Some examples may explain this statement. The gaping reaction of the young thrushes mentioned above, when they were in the visual phase, was influenced not only by *releasing* sign stimuli, but also by other stimuli which *directed* the reaction toward the head of the parent bird though they were without influence in releasing the gaping reaction. The head was recognized by a very few sign stimuli analyzed by experiment: the head was to the nestlings a thing higher than the rest of the parent bird (or model); it was a thing nearer to the nestlings than any other part of the model, and it was something protruding from the main outline of the model. The size of the head was unimportant in an absolute sense, but it was very important in relation to the size of the body. A "head" of 1 cm. diameter was more effective than one of 3 cm. when belonging to a "body" of 4 cm. (Figure 21A), but the gaping was directed to the larger head when both heads were mounted on a "body" of 8 cm. and presented to the nestlings (Figure 21B). It is size in relation to size of the body that counts.

Other studies of cases where a head provides the sign stimulus for the release of a reaction lead us to essentially the same conclusion. Portielje (1926) showed that the European Bittern, *Botaurus stellaris*, when cornered by an enemy without possibility of escape, will direct its flash-like, surprising thrusts of the bill toward the head of its enemy. A body without a head does not release the defense reaction, but as soon as a "head" is presented, for instance, by putting a crude cardboard model on the "body," the bird picks at this head. The shapes

of both head and body may vary within very wide limits, but the head must be smaller than the body. Probably there is an optimal relation in size between the two.

The cognition of a "head" has been investigated in still another instance. As mentioned above in the introductory paragraphs, Goethe (1937b), Lorenz (1940), and Krätzig (1940) have tested the innate releasing mechanism of the reaction of several birds, especially gallinaceous birds, to flying birds of prey. In this releasing mechanism, the short neck (i.e., slightly protruding head) plays a decisive part. All bird models, even very crude ones, with short necks elicited escape reactions (of varying intensity and also of different kinds); in some species, the four-week-old cocks assumed an aggressive attitude while the female chicks crouched. Here again, it is not the size or another more or less "absolute" (measurable, quantitative) stimulus that is essential, but the relative size, that is to say, size (length) of neck in relation to size of body.

The innate releasing mechanism of the stickleback's fighting response offers another example. Fighting is maximally elicited by a red male. Experiments with dummies show that the optimal stimulus is not: any red fish, but: any fish that is red *underneath*. Models with a red back instead of a red belly have a much lower releasing value than those with a red belly. This means that not the red as such is a sign stimulus, but a red part of the body in a definite spatial relation to the body as a whole.

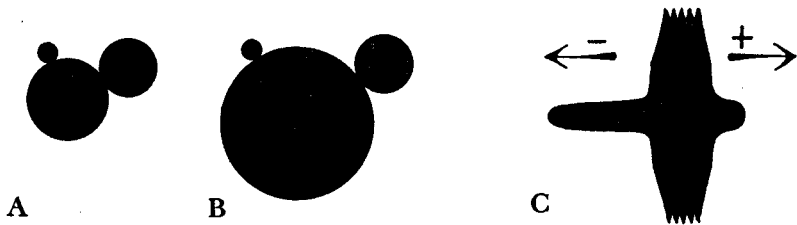


Figure 21. *A* and *B*, Two dummies used for analysis of "head" in directing the gaping responses of young thrushes. After Tinbergen and Kuenen, 1939. *C*, Card-board dummy that releases escape reactions when sailed to the right ("hawk") but is ineffective when sailed to the left ("goose").

Further, all stimuli in which motion plays a part are of a configurational character. The gaping reactions of young thrushes in the visual stage are released by moving objects. Motion toward the animals has an especially strong releasing value. Experiments proved that this type of motion was perceived, not as "growing size," but as true spatial, three-dimensional motion.

We are accustomed to consider configurational stimuli of this kind as relatively simple stimulus situations. By comparison, many other stimulus situations, especially those encountered in training- or conditioning-experiments, are of a much more complex nature. Yet even the relatively simple sign stimuli, when examined closely, are very complicated systems indeed. For instance, a sign stimulus "short neck" indicative of a bird of prey for inexperienced turkey chicks, is valent only in relation to the direction of motion. Lorenz and I made a cardboard model in the shape of Figure 21C. When pulled to the right, the model had a short neck and a long tail ("hawk"); when pulled to the left, it had a long neck and a short tail ("goose"). This model caused escape reactions, such as flight and crouching, only when pulled to the right; merely superficial interest was shown by the chicks when the model sailed in "goose" fashion.

It may be superfluous to stress the fact that these considerations which apply to sign stimuli in general are also relevant to the stimuli produced by releasers. The releaser is a special kind of source of sign stimuli. Probably owing to adaptive evolution, a specialized releaser is, so to say, a materialization of the innate releasing mechanism.

THE STIMULUS SITUATION: HETEROGENEOUS SUMMATION

A reaction of an animal to its environment, either to a "situation," an "object," or an animal, is rarely governed by only one sign stimulus. As a rule, several sign stimuli act together. The courting activities of a female stickleback are reactions not only to the red ventral parts of the male but also to its zigzag dance. A threatening male stickleback has an intimidating influence on its opponent not only through its red color but also through its threatening posture. In birds, color, movement, and voice may often work together. Thus the optimal situation may be a combination of two, three, or more releasers. Recent work shows how several sign stimuli act together to produce a combined effect.

The mating behavior of the grayling butterfly is initiated by a kind of courtship flight: the male follows each passing female. The innate releasing mechanism of this flight is responsive to a combination of sign stimuli, among which type of movement, degree of pigmentation, and distance are the most important (Tinbergen, Meeuse, Boerema, and Varossieau, 1942). The optimal stimulus situation is a dark female fluttering in the typical way of a butterfly, as near to the male as possible. A white model elicits fewer responses than a dark model, a sailing model fewer than a fluttering one, a distant model fewer than one presented near by. A model that was deficient in any one of these respects evoked only relatively few responses. In order to increase the frequency of the responses it was sufficient to "improve" the model by improving *any one* of the deficient stimuli. For instance,

a white, sailing model could be improved just as well by painting it dark as by presenting it in fluttering motion. In general, it was quite indifferent which parts of the situation were presented, as long as "a certain amount" of stimulus was presented.

Exactly the same phenomenon has been described by Seitz (1940) in the cichlid fish *Astatotilapia strigigena*, where the intensity of the reaction appeared to be dependent not on *which* sign stimuli but only on *how many* sign stimuli were presented. This was called the "Reizsummenregel" by Seitz; I will translate this by "rule of heterogeneous summation" to indicate that it is not successive summation of a *repeated* stimulus, but simultaneous summation of *different* stimuli. The importance of this has been stressed by Lorenz (1940).

In general, most responses of the type that are elicited by releasers are not subject to the all-or-none law; on the contrary, they may appear in almost any degree of intensity, depending on the intensity or completeness of the stimulus situation. The experiments summarized above show that incompleteness or low intensity in different sign stimuli does not result in *different types* of deficiency in the reaction, but that the reaction's intensity always decreases in the same way, independently of which part of the stimulus situation is missing. It is as if *a certain quantity* of stimulating "substance" were required. One is tempted to describe this in terms of a reservoir of some substance in which the effects of the several stimuli are thrown together indiscriminately. The contents of this reservoir stimulate the nervous motor center of the reaction in a purely quantitative way, dependent only on the level, not on the composition of the reservoir's contents. Needless to say, this is only an analogy; in reality, nervous centers and impulses are involved.

This discovery is not new. Only the explicit formulation is new. Anybody who is more or less acquainted with animals (including man) has often seen the dependence of the reaction's intensity on a number of different stimuli. Our appetite, for instance, may be slight for many reasons; it can be increased by the sight of food, by an animating companion, by an attractive table, and so on.

The principle of summation of heterogeneous stimuli is important for the correct understanding of our experimental procedure. Most reactions still occur, though at a lower intensity, when one or another of the stimuli is missing in the situation. The consequence is that the mere fact that a reaction occurs in the absence of a certain stimulus does not in the least prove that this stimulus is of no influence.⁴ When

⁴Yet this conclusion is often drawn. Reasoning of this type always reminds me of the case of a Herring Gull with one leg which I observed. This deficient individual lived successfully in the wild for several years. Apparently he could do without the missing leg, but certainly no one would say that Herring Gulls have one superfluous leg or consider nonsensical the conclusion that a leg is a functional organ.

Rand observes that a parent Song Sparrow removes feces from the nest rim without being stimulated by a display of the young's anal feather circlets, he is not entitled to conclude that the feather circlet is of no importance in the reaction. His observation merely shows that the reaction may occur in the absence of such display. This observation alone does not even justify the conclusion that the anal ring is of only minor importance.

In exceptional cases a particular releaser is indeed so all-important as to be the one indispensable factor—the “necessary and sufficient cause”—for a reaction. Lack (1943) found such an exceptional state of affairs in the English Robin. As I mentioned above, the red breast of this bird is such a strong “badge of hostility” that isolated tufts of red feathers, when presented to a territory-holding male, were attacked, whereas a mounted fledgling, which to the human eye was more robin-like than the mere tuft of feathers but had no red breast, was left alone.

A very instructive illustration of heterogeneous summation, exactly comparable with the Rand example, is seen in the contradiction I have already cited between Leiner's conclusion that the stickleback's red belly had no function and Ter Pelkwijk and Tinbergen's experimental proof that the red belly was a very important releaser.

Leiner's experiments demonstrated in a quite convincing way that the female's mating behavior may occur in complete form even when this important releaser is missing (*viz.*, in red light). The principle may be illustrated by the symbols of Figure 22. The column at the left is the optimal stimulus situation, in which the red belly, the zigzag dance, and other external (and internal) factors are all contributing their share. The heavy horizontal line (*th*) indicates the threshold of response, below which the reaction is too low in intensity to reach its goal or even is not forthcoming at all. Leiner's experiments consisted in omitting the red color. The total stimulative value of the other factors combined was still above the threshold. When the internal causes (the “motivation”) are lower (right column), or when the other releasers are not all presented (center column), omission of the red color may result in the lowering of the total stimulative value to below threshold-value. These considerations show that in order to prove the influence of the red color, or, in general, of any other alleged sign stimulus or releaser, one has to apply two methodological principles: First, one must always *compare* the response to Situation A with the response to Situation B. Had Leiner compared the female's behavior in red light with that in sunlight, he might possibly have seen that she was much more willing to act when the male's red releaser was visible than when it was invisible owing to red illumination. However, such a difference in degree is often difficult to observe or,

at least, to describe. Therefore a second measure has to be taken: the intensity of the other stimuli or of the internal motivation has to be lowered in such a way that loss of the one releaser will render the total situation subliminal. The result will be that a model with sign

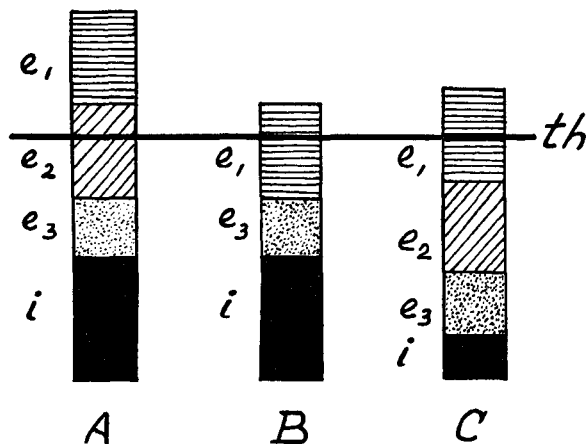


Figure 22. Diagram of responsiveness to sign stimuli. th , threshold of response, i , internal motivation. e_1 , e_2 , e_3 , external stimuli.

stimulus e_1 will evoke the response (Figure 22, center and right), while a model without this stimulus will not. Some trial-and-error experimenting, guided by a kind of intuition which is an indispensable element in the mental outfit of the successful experimenter, will serve to find the right procedure in each case. For instance, one can use models lacking important characters of form or of motion. Often motion is automatically deficient because it cannot easily be imitated with a dummy. (Hence it is often a definite advantage not to work with live animals as "models" but with crude imitations.) Or, because the internal motivation is adding to the influence of the sensory stimuli in the same summative way, it is well to experiment on individuals with more or less standardized, not too high, internal motivation. To take the instance of Leiner's sticklebacks again: it is possible to have a female lay her eggs without any stimulation by a male at all simply by keeping her isolated until spawning occurs as a "Leerlaufreaktion," or spontaneous discharge, for when an instinctive action is not released because of the lack of adequate stimulus, the threshold of stimulus is so markedly lowered that the instinctive action may at last occur without any perceptible stimulus (Lorenz, 1935:162). Hence it is not to be expected that omission of only one stimulus will prevent the female stickleback from spawning. But if one selects only such females as show a certain intermediate intensity of response to

a standard male, one reaches an intensity level of reaction in which presence or absence of one sign stimulus is the controlling factor.

Of course this procedure implies that a sign stimulus detected in this way is not always the only effective sign stimulus, even though the experiment may seem to indicate it. The very nature of this type of experiment, designed to discover a particular sign stimulus, leads to neglect of other possible sign stimuli. Therefore, each experiment of this kind has to be combined with a test in which the more effective of the two models is compared with the optimal situation, viz., the live "actor." As long as a difference in releasing value between the model and live actor exists, it is clear that the model still lacks one or more essential sign stimuli, and to discover exactly what it lacks other experiments will have to be carried out that compare its releasing value with that of a second model differing from it only in respect to one character not yet tested as a sign stimulus.

The reverse conclusion, however (viz., that optimal reaction intensity to a model proves this model to be optimal), is not true. Owing to the fact that internal and external factors (motivation, urge, or drive of varying intensity and sign stimuli, respectively) are cooperating according to the principle of heterogeneous summation, high internal motivation may cause the reactor to respond to all objects offering the minimum adequate external stimulation. The result of such extreme lowering of the reaction's threshold is that the animal reacts indiscriminately to "good" and "bad" dummies. This gives the impression that the animal "does not discriminate" between the dummies. Especially when an animal is dominated by an abnormally strong sex-drive (an unnatural state often encountered in isolated captive animals) such things may happen. Heinroth's observation of a captive Robin (*Erithacus rubecula*) mating with a dead companion and of a young Corn Crane (*Crex crex*), reared in captivity mating with Frau Heinroth's hand (O. and M. Heinroth, vol. 1, p. 13; vol. 3, p. 79), as well as Allen's observation (1934) of Ruffed Grouse (*Bonasa umbellus*) treading a dead grouse or a submissive male, are some of the numerous instances reported in the literature. A dead bird displays a releaser which demonstrates the female's readiness to pair: keeping quiet. The mere fact that a strongly sexually motivated male promptly reacts to the display of this single releaser does not prove that it does not discriminate between a dead animal and a live female. Under "normal" conditions (that is, when motivation is not extremely high), the bird may discriminate very well between a willing female and a corpse.

Further, it is a corollary of this same principle of heterogeneous summation that an object may readily evoke conflicting reactions. During experiments on egg recognition (or in more objective terms:

on the releasing mechanism of incubation responses) in Herring Gulls, it was found that the shape of the egg was important, but the effect of color was negligible, blue, yellow, black, and white eggs having equal releasing value (Tinbergen and Booy, 1937). Red eggs, however, were an exception. All red objects are invariably thrown out of the nest, a yet unexplained fact which has been noticed by several observers. Now it was quite interesting to observe the gull's behavior when an egg of normal size and shape but of an intense red color was offered. The bird repeatedly made incipient movements of sitting down, but again and again it was offended by the red color and vigorously pecked at the (wooden) egg. From my other experiments I knew that the shape was releasing the sitting response, the color the pecking response. If, in the course of this struggle between drives, the sitting drive dominated long enough to allow the bird to sit down, it came to rest, for the color lost its influence and tactile stimuli from the egg now controlled the situation.

Lorenz (1935) mentions similar observations in parent-chick relations in ducks. A female may run to the rescue of a chick of a foreign species as a reaction to the distress call, then may kill it at the sight of the chick's color pattern, which does not fit her innate releasing mechanism since her own species has a different pattern.

In short, we could describe the phenomenon upon which the rule of heterogeneous summation is based by saying that the animal, when it responds to the stimulation of an innate releasing mechanism, does not react to an object, or to a congener, but to a bundle of sign stimuli—a bundle of releasers. As Lorenz has pointed out (1935), the animal in this case does not "see" the congener as a whole; when its several social responses are directed to one and the same individual, it is because this individual carries all the necessary releasers. It is the releaser a bird is reacting to, not the individual that is carrying the releaser. Of course, I am speaking only of the type of behavior that is dependent on releasers, not of conditioned or higher types of behavior.

I have already indicated that not all releasers have the same extreme status as the red breast in Lack's robin. Other characteristics may have an influence, though perhaps a slight one. The degree of dominance may be very different. Again this may be detected by comparing the releasing influence of crude dummies displaying only one releaser with the optimal situation.

The pregnant female stickleback has one powerful releaser, acting on the male: the swollen abdomen. In addition, her special mode of swimming acts as a releaser. In order to compare the value of the swollen abdomen with other possible morphological sign stimuli, the influence of a very crude model with swollen abdomen was compared

with that of a complete (dead) female with a normal abdomen. The first model released courtship reactions of higher intensity than the second one. The swollen abdomen, therefore, had a higher releasing value than all other morphological characters together, but the fact that the second dummy was able to release responses at all showed that it contained some "recognition marks." Lack's experiments, in which he compared the effectiveness of the red breast of the robin with that of a complete bird lacking the red, revealed a much higher value for the releaser.

There can be little doubt that the relative value of the releaser is different in different species, varying from the extreme condition found in the robin to the other extreme, in which a releaser is of only slight importance. While in the former cases it is easy to demonstrate the releaser's function by experiment, there are increasing difficulties in the cases approaching the latter condition. The same difficulties are encountered in those cases where not one, but two, three, or even more releasers are cooperating. It seems to me quite probable that the releasive value of the anal cirlet in nestling song birds is rather slight, because there are two other sign stimuli that cooperate with it, viz., the wiggling movements of the young's abdomen and (according to Rand's experiments) the fecal pellets themselves.

For the same reason, it will not be easy to settle the question whether the "Sperrachen" (colored throat and mouth lining) of passerine nestlings are releasers, because they are supported by gaping movements and by sounds. It will require quite an amount of insight, feeling, and trial-and-error experimenting to settle questions like these. They are a challenge to the ambitious experimenter.

The phenomenon of varying relative importance of releasers among different species and even among different releasers of one species suggests an evolutionary interpretation. In my opinion there can be little doubt that the extreme condition, as found in the robin, where one releaser is so important as to control the releasing mechanism, is the end-result of an evolutionary process directed toward specialization of releasers into very specific, highly "improbable" structures. For more detailed discussions of this problem, see Lorenz (1940) and N. Tinbergen (1940).

INNATE AND CONDITIONED RESPONSES

I have already mentioned that the available evidence strongly suggests that innate releasing mechanisms are always responsive to a combination of only very few sign stimuli. We have reason to believe that this is valid especially for innate, as against conditioned, releasing mechanisms. Seitz's experiments (1940) with *Astatotilapia strigigena* are very instructive in this respect. As mentioned above, a normal

male, reared among other members of its species, responds by fighting to very simple imitations of a male. However, Seitz did not succeed in making any dummy that evoked courting responses in the normal male; it responded only to live females. In a male reared in isolation, courting responses could be evoked by very simple models. The fighting reactions of this male had the same releasive mechanism as those of normal males. Thus the innate releasing mechanism of the courting behavior is originally very simple, but it is changed by conditioning and thereby becomes highly specific or selective, that is to say, it requires stimulation by a very complicated system of many stimuli. The innate releasing mechanism of the fighting remained unaffected by conditioning. Coinciding with this, the male of the species bears releasers which, as a matter of fact, provided the sign stimuli to which the fighting reaction responded, whereas the female does not have any structures that could be classed *a priori* as releasers.

Laboratory experimenters know how difficult it may be to force an animal to react to exactly that stimulus which the experimenter wants to impress upon it. As a result of conditioning, the animal always begins to react to the situation as a whole, including many of even the minutest details, and it is only by continually changing all possible stimuli except the one stimulus wanted that one can get the animal to confine its reactions to this one stimulus.

This all points to the conclusion that the reason the releaser is always a relatively simple thing is that the limitations of the innate releasing mechanism force it to be simple. It will be clear that it is of the highest importance for our insight into these matters not to stop an investigation as soon as the releasing influence of a releaser is demonstrated, but to carry it on by breeding the species, rearing young in isolation, and testing their innate releasing mechanism in exactly the same way as was done with the normal individuals, in order to detect where conditioning steps in.

Of course, these conclusions and considerations are based on relatively scanty evidence, and there are observations that may throw doubt on them. For instance, Kramer (1937), as also Noble (1934), is not sure whether lizards' reactions to the fight-evoking releaser are innate or conditioned.

NATURE OF THE REACTOR'S RESPONSE

So far, our discussion of the experimental method has considered only part of the releaser problem. I have been focussing attention on the problem of the sensory stimulus releasing the reactor's behavior. Something should be said now about another side of our problem, *viz.*, the response of the reactor. This will lead us to a study of other phenomena of great importance for experimental procedure.

Latent responses and repeated stimulation. Every observer knows by experience that an animal does not always and invariably show a prompt response to a releaser. Sometimes the display of a releaser evokes an immediate reaction; at other times the same releaser must be displayed repeatedly before the reactor responds; in other instances, no response is shown at all. As we have seen, these differences in responsiveness are due to fluctuations of the other factors, usually the internal ones.

The cases of a reaction following repeated stimulation are of especial interest to us. The absence of any outward response to the first stimulus might give the impression that the stimulus has no effect at all. However, the very occurrence of responses after several repetitions of the same stimulus clearly proves that there is a certain summation over time, in other words, that the effects of the repeated stimuli have been accumulating within the animal. Though no outward response was observable, there must have been an internal, latent response, resulting with each renewed stimulation in a lowering of the threshold—in an increase in readiness to respond to the next administration of the stimulus.

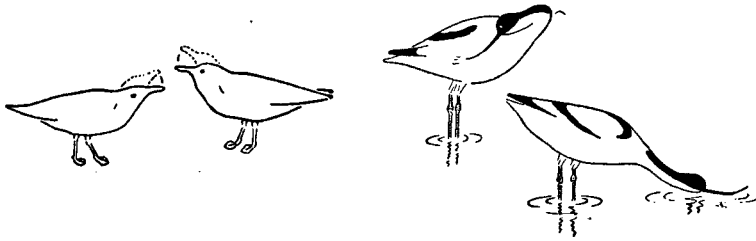


Figure 23. Herring Gulls (left). Begging movements preceding coition. After N. Tinbergen, 1942. Avocets (right). Preening in male preceding coition. After Makkink, 1936.

The tactile stimulus given the female stickleback by the “trembling” of the male is a clear case. In bird courtship, we often observe the same phenomenon; one has only to think of the “begging” movements preceding copulation in Herring Gulls (Figure 23, left; Goethe, 1937a; N. Tinbergen, 1940), the preening movements shown by Avocets (*Recurvirostra avosetta*) in the same situation (Figure 23, right; Makkink, 1936), and many other instances.

This is of importance in two respects. First, it is obvious that one has to be very careful in drawing negative conclusions about the effectiveness of a stimulus when no immediate reaction is observed. Second, it shows that a stimulus may have a more or less lasting after-effect, for without this after-effect no successive summation of stimuli would be possible.

After-effect of stimulation. A few words must be said about this phenomenon of a continuing effect, for it may have a strongly disturbing influence on our experiments. When, for instance, the fighting reactions of a male stickleback are released during an experiment in which a dummy is presented for a certain fixed time, let us say five minutes, the reaction does not stop abruptly with removal of the dummy. It is true that the fish does not actually fight after his "opponent" has disappeared, but for several minutes following the conclusion of the test the threshold of the fighting responses remains lower than usual; in other words, the fighting drive is still activated, and it only gradually dies down to "normal" again. This means that it is necessary to give the animal a rest before a new test is begun in which a second model is presented for comparison of its effect with that of the first model. If we should begin the second test before the after-effect of the first has disappeared, we might get a high intensity of response to a relatively weak model; the weak dummy might, so to speak, profit from the intense effect of the strong model, and we would get a much too favorable impression of the effectiveness of the weak dummy.

Inhibitory interaction among different drives. Closely related to the phenomenon of a drive's after-effect is the fact that activation of one drive has an inhibiting effect on all other drives. A fighting animal is not very susceptible to food-stimuli or to the stimuli that usually evoke escape. This phenomenon can be used in dummy experiments for the purpose of breaking down the after-effects of each test. The easiest way to do this and thus to standardize the tests, is to alternate tests on two different drives, for instance, the mating and the fighting drives. This can be done by presenting models of males and of females in turn. If this method is combined with regular rests between successive tests, the disturbing influence of after-effects can easily be overcome. To prevent loss of time through these forced rests, it always pays to work with a number of individuals at the same time. Each of them gets plenty of rest between successive tests if the experimenter turns from one individual to another in sequence.

Various motor responses correlated with one releaser. A study of, for instance, the alarm call of a Herring Gull shows that the reactor's response is not always one special type of movement. At the sound of the alarm call, uttered by a gull on the discovery of a dog, different individuals behave differently. Some gulls fly up in a panic and begin to call the alarm themselves, or to attack the enemy once they spot him. Other gulls walk from the nest to a look-out post to get a good view of the surroundings. Others merely wake up and stretch their necks. The actual motor response is different in these

various cases, but they all belong to one group—they all form part of the total pattern of alarm and nest-defense behavior. In other words, the function of this releaser is not to release one single reaction but a whole pattern with a special function or purpose: the major instinct of nest-defense. Once this instinct (this “mood”) has been aroused, it is (1) the intensity of response, and (2) additional stimuli, such as actual discovery of a predator, that determine which type of motor reaction will result.

These and many similar facts show that the term *releaser* cannot be used in the narrow sense of a device evoking one special motor response. In many cases, a releaser rather evokes what Heinroth calls a “Stimmung” (mood), a readiness to respond with one group of functionally related motor patterns. This is in accordance with the results of instinct studies in general, which have shown that “a reaction” may be a special motor response in one case, a change in readiness to react with a special motor response in another case, or even a change in readiness to respond with a whole pattern of functionally related movements in many other cases. It is an enormous over-simplification to identify “reaction” with “motor response.” Again, this cannot be elaborated here; for particulars I must refer to my 1942 paper. It must suffice to say that the motor responses of one instinct are not only functionally related but are also dependent on the same causal mechanism, on the same nervous center.

Successive tests and “choice” experiments. In many of the tests described thus far the effects of different dummies have been studied and compared by presenting them in succession. Outsiders watching such work often ask why the two models are not presented simultaneously and the choice of the reactor watched. This question, natural as it seems to be, is based on a wrong assumption, viz., that the reactor will always show a preference for the “strongest” model. This is by no means the case, as a few instances will show.

First, an animal often reacts to the dummy it happens to see first. Slight differences in position between the two dummies presented will influence their relative conspicuousness, and the result is that now one dummy arouses all or most of the reactions, now the other one. In this way, position, or—since “position” is rarely analyzed—“accident,” plays much too large a part in our final statistics, and our result is unreliable or at least confused. This could perhaps be overcome by very careful experimenting, but it would take much more time than the “successive” method would, and gain of time is the only reason for the inclination to prefer “choice” tests.

There is, however, a more fundamental objection to the “choice” method. In an experiment designed to settle the question whether the

so-called scent organs of male grayling butterflies served to stimulate the female's mating responses, we presented a number of females with double the number of males, in half of which we had removed the scent organs. This, therefore, was a "choice" test. The result was not according to our expectations: the females accepted scentless just as frequently as normal males. Close observation of the behavior during the experiments showed that some of the matings with scentless males occurred when a female was surrounded by males of both kinds. Even while a normal male was courting a female, a scentless male would approach her and succeed in attaching its copulatory organs to hers. We suspected that the cooperation of the female in such cases was due to the stimulating effect of the normal male's courtship. We then carried out a series of successive tests in which scentless males and normal males were presented in turn, and found a marked difference in success between them. Although the number of tests was rather small, the obvious conclusion seems to be that the display of the scent organ raises the female's excitability in a general way but does not *direct* her activities to the displaying male. Once she has been excited and her copulatory reactions have been released, she accepts any male, provided he presents the stimuli necessary for the next link in her reaction-chain.

The wing display of a male *Drosophila* seems to have the same kind of general excitatory influence. Sturtevant's results (1915), though perhaps not entirely conclusive, at least point in this direction.

This is not the place to discuss the ethological background of this phenomenon. Referring again to a previous paper where I discussed it at length (Tinbergen, 1942), I must content myself with the statement that there are two types of sign stimuli and, therefore, two types of releasers: those that *direct* the response, and those that merely *release* it without giving spatial guidance. If the latter type is involved, "choice" experiments are of no use, because one dummy may release the response, while another dummy may be "chosen."

As an instance of a simple releasing signal, the alarm call and alarm movements of the Herring Gull may be cited. When a female Herring Gull (with half-grown chicks) that I was observing was disturbed by some careless movements I made in my hide, her alarmed behavior alarmed the chicks too, but since the mother's behavior had no *directive* influence, the chicks did not know where the danger lay, and when the mother's behavior increased in intensity, the chicks actually went to shelter by crouching in my hide.

An instance of a releaser with the double function of releasing and directing the response is the peculiar movement by which the male stickleback indicates the nest's entrance to the female (Figure 24). Turning on its side, the male points its head into the entrance. With

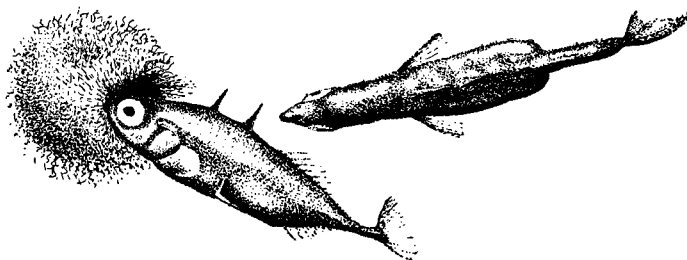


Figure 24. Male stickleback showing nest entrance to female. After Ter Pelkwijk and Tinbergen, 1937.

a dummy played in about the same way, one can get a pregnant female to attempt to "enter" at any place in the aquarium.

It is not necessary to discuss this point further, because I do not want to deny the value of "choice" experiments in all cases. I merely want to point out the fact that it is not a matter of personal preference whether one uses successive tests or "choice" tests; the relative value of the two methods depends on the nature of the releaser to be tested, and a decision on which method should be used can be taken only after trial-and-error attempts in each new case. Needless to say, a systematic study of this problem would be of the greatest value.

SUMMARY

This discussion of the releaser concept has two objects: first, to draw attention to a number of experimental facts proving the releaser function in those cases that have been critically studied with adequate methods; second, to stimulate further research, by pointing out the many requirements to be fulfilled in a really critical procedure, and by showing the incompleteness of the work thus far done.

Part 1 defines the releaser concept and discusses experimental results in the fields of visual releasers (stickleback, robin, Flicker, Shell Parakeet, Herring Gull, lizards, cichlid fish, cuttlefish), of auditory releasers (crickets, birds), of chemical releasers (honey-bee, hyena, butterflies), and of tactile releasers (snails). A selection of observational (non-experimental) evidence on visual releasers is added.

Part 2 presents certain principles which are of importance for planning experiments and for evaluating the results:

Each innate reaction of an animal responds to a limited set of "sign stimuli," which do not influence the behavior as a whole but only special reactions or reaction patterns.

What appears to be "a reaction" is often a chain of reactions, each of which is dependent on its own set of sign stimuli. The function of

a releaser may be confined to any one link of such a chain, as, for example, in the chain of mating reactions of the stickleback.

The "rule of heterogeneous summation," the additive effect of different stimuli, has important implications for experimental practice. Many reactions may occur even in the absence of one of the sign stimuli, provided the motivation, dependent on internal factors, is high enough. Any experiment on the value of releasers, therefore, has to compare the effect of two dummies that differ only in the one releaser to be studied.

The releaser is an adaptation to the innate releasing mechanism, which, for reasons unknown, is dependent on a "simple" stimulus situation. Conditioned behavior responds to a much more complicated stimulus situation.

Many reactions are dependent on repeated stimulation, each stimulus slightly raising the excitatory state, which by accumulation of the effects of repeated stimulation reaches a final state in which the reaction is released.

Many of the so-called reactions released by releasers are not simple "motor responses" but are internal reactions by which the centers of whole patterns or major instincts are activated.

Some releasers have a general excitatory influence and do not direct the reactor's response; in these cases experiments should be of the "successive," not of the "choice," type.

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