

THE STUDY OF INSTINCT

BY

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ACTUAL VERSUS POTENTIAL STIMULI

Sign Stimuli

A mere knowledge of the potential capacities of the sense organs never enables us to point out, in any concrete case, the actual complex of stimuli responsible for the release of a reaction. (From a study of sensory capacity we can infer what changes in the environment can or can *not* be perceived by the animals, but a positive answer about what *does* release the observed reaction is impossible.) This turns upon the peculiar fact that an animal does not react to all the changes in the environment which its sense organs can receive, but only to a small part of them. This is a basic property of instinctive behaviour, the importance of which cannot be stressed too much. For instance, the carnivorous water beetle *Dytiscus marginalis*, which has perfectly developed compound eyes (Fig. 17) and can be trained to respond to visual stimuli, does not react at all to visual stimuli when capturing prey, e.g. a tadpole. A moving prey in a glass tube never releases nor guides any reaction. The

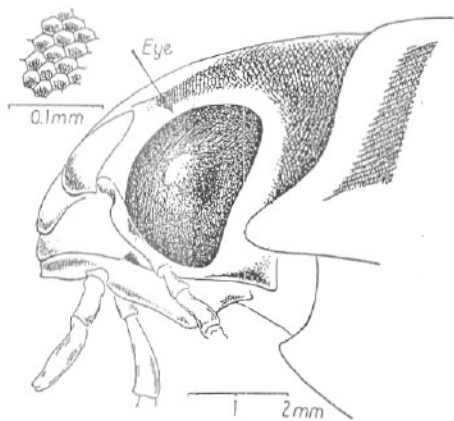


FIG. 17. Head of *Dytiscus marginalis* showing well-developed compound eyes. After Tinbergen, 1947.

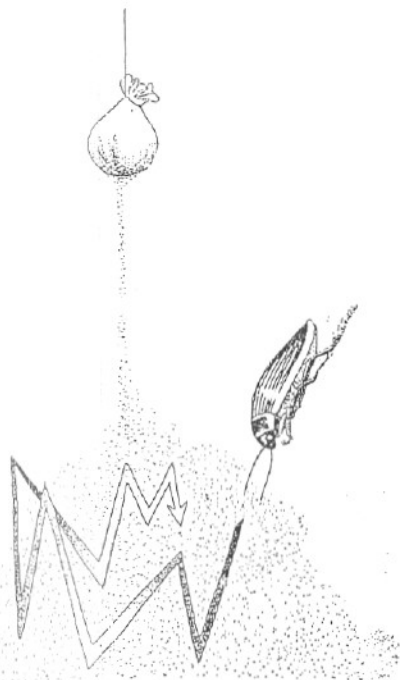


FIG. 18. *Dytiscus* reacting to scent of prey and caught in a 'physiological trap'. After Tinbergen, 1936c.

beetle's feeding response is released by chemical and tactile stimuli exclusively (Tinbergen, 1936c); for instance, a watery meat extract promptly forces it to hunt and to capture every solid object it touches (Fig. 18).

The occurrence of such 'errors' or 'mistakes' is one of the most conspicuous characteristics of innate behaviour. It is caused by the fact that an animal responds 'blindly' to only part of the total environmental situation and neglects other parts, although its sense organs are

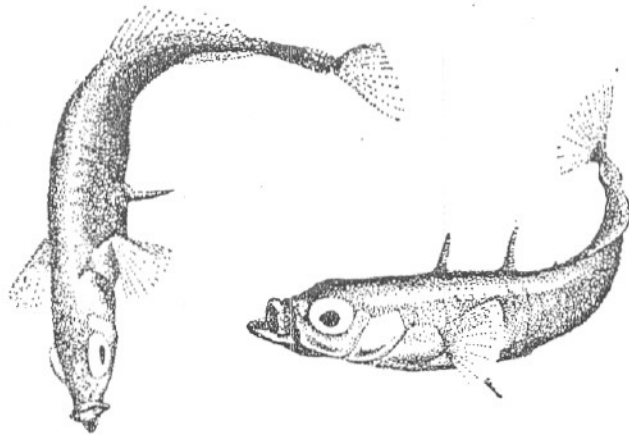


FIG. 19. Two male three-spined sticklebacks fighting. After Ter Pelkwijk and Tinbergen, 1937.

perfectly able to receive them (and probably do receive them), and although they may seem to be no less important, to the human observer, than the stimuli to which it does react. These effective stimuli can easily be found by testing the response to various situations differing in one or another of the possible stimuli. A small number of such experimental studies have been carried out; they have led to important results.

Moreover, even when a sense organ is involved in releasing a reaction, only part of the stimuli that it can receive are actually effective. As a rule, an instinctive reaction responds to only very few stimuli, and the greater part of the environment has little or no influence, even though the animal may have the sensory equipment for receiving numerous details.

For instance, the spring fighting of male sticklebacks (Fig. 19) is especially directed against other male sticklebacks in nuptial markings. As the males differ from other animals, especially in having an intensely red throat and belly, it seems probable that the red colour might be the most important stimulus. This has been tested in the following way.

Models of sticklebacks were presented to a number of males (Fig. 20). Some of the models were very crude imitations of sticklebacks, lacking many of the characteristics of the species or even of fish in general, but possessing a red belly (Series R). Others were accurate imitations of

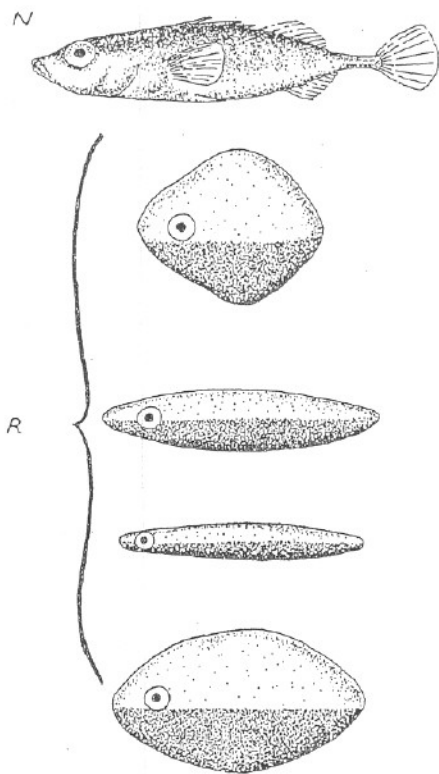


FIG. 20. A stickleback model of series N (above) and four of series R. After Tinbergen, 1948.

sticklebacks, but lacked the red (Series N). The males attacked the first group of models much more vigorously than they did the others. In this experiment the red colour was put into competition against all other morphological characters together. The results prove that the fish reacted essentially to the red and neglected the other characteristics. Yet its eyes are perfectly able to 'see' these other details (Ter Pelkwijk and Tinbergen, 1937).

Much the same condition exists in the English robin. Lack (1943) discovered that a territory-holding male of this species would threaten a mere bundle of red feathers much more readily than a complete

mounted young robin which showed all the characteristics of a robin except the red breast. Again, the red breast is the effective stimulus (Fig. 21).

A somewhat more complicated case is the following. Newly hatched chicks of the herring gull beg for food by pecking at the tip of the parent's bill. The latter regurgitates the food on to the ground, picks up a small morsel and, keeping it between the tips of the beak, presents it to the young (Fig. 2, p. 7). After some incorrect aiming the young

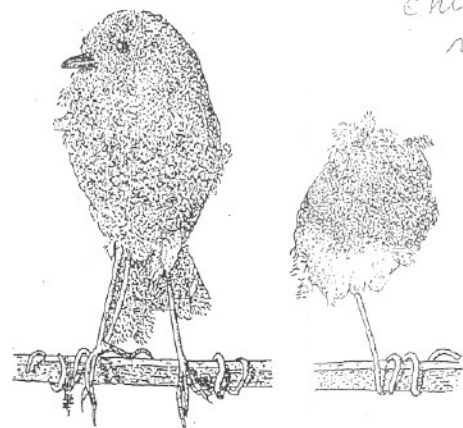


FIG. 21. Two models of European robin. Right: a tuft of red feathers; left: mounted young robin with dull brown breast. After Lack, 1943.

gets hold of the food and swallows it. The bill of the herring gull is yellow, with a red spot at the end of the lower mandible. By comparing the chicks' reactions towards (1) a flat cardboard dummy in natural colours and (2) a similar dummy lacking the red patch, it was found that the red patch was of great importance. Further, a patch of any colour, black, blue, even white, gave the dummy a considerably higher releasing value than the dummy without any patch (Fig. 22). The fact that even a white patch increased the releasing value pointed to the conclusion that contrast between bill and patch played a part; the fact that red had more influence than even black indicated that red as colour had also influence. In order to test the first possibility, the series represented in Fig. 23 was presented. The bills were of a uniform grey of the same brightness in all the dummies; the patches varied from white to black in small steps. The results indicated in Fig. 23 show that contrast was part of the stimulus situation. A comparison of models with varying bill-colour (Fig. 24) shows that (a) red as such is important and (b) yellow has no influence at all. A last series, in which the colour pattern of the

bill was constant but the colour of the head was varied, showed that a model with a white head had no more releasing value than models with black, red, yellow, green, blue, &c., heads. These observations lead to the conclusion that the chick reacts especially to the red patch. This

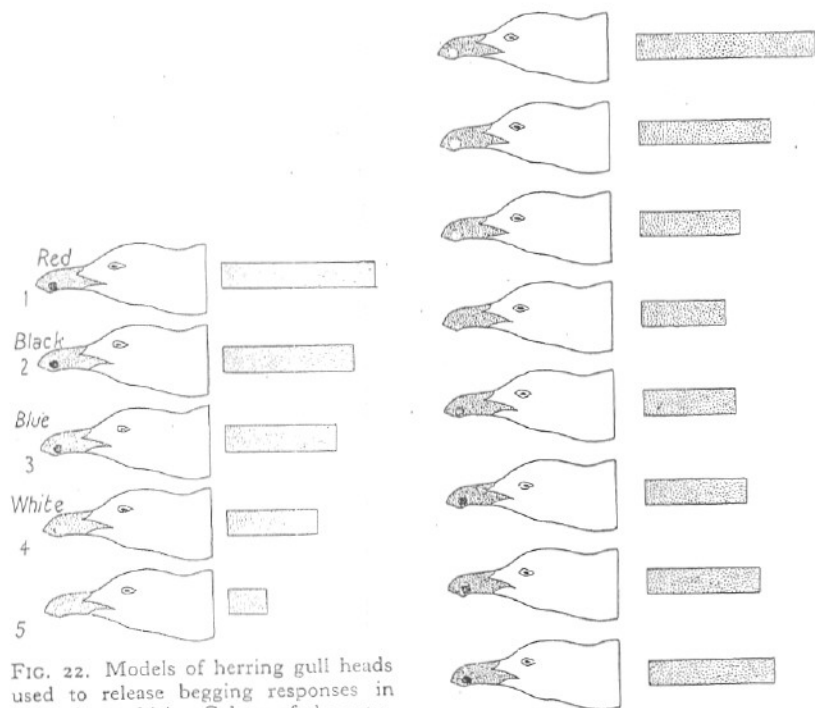


FIG. 22. Models of herring gull heads used to release begging responses in newly born chicks. Colour of the mandible patch varied (1-4) or absent (5). Columns indicate relative frequency of chicks' responses. After Tinbergen, 1949.

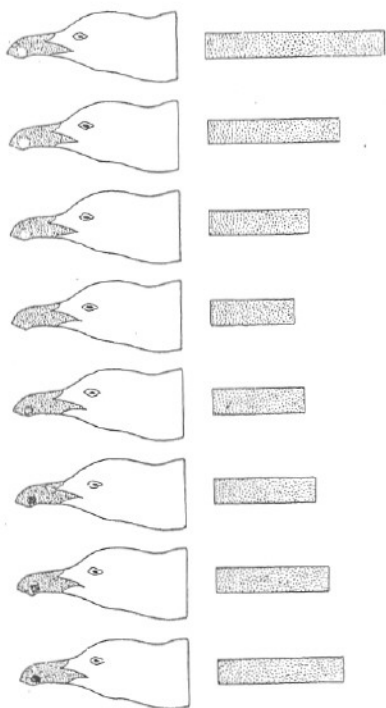


FIG. 23. Releasing value of herring gull models with grey bills with patches of varying shade. After Tinbergen, 1949.

patch works through its colour and through its contrast with the colour of the bill.

No releasing value was found for either colour of the bill or colour of the head (Tinbergen, 1948b, 1949; Tinbergen and Perdeck, 1950).

The reactions of many birds to flying birds of prey are often released by quite harmless birds. The domestic cock gives its alarm call, not only when a sparrow hawk is passing, but also as a reaction to the sudden appearance of a pigeon or a crow. The special type of movement, the sudden appearance, is sufficient to elicit the alarm, although the shape of a pigeon is quite different from that of any bird of prey. In addition, many birds react to the typical shape of a bird of prey in flight. Heinroth and Heinroth (1928) relate how many birds in the Berlin zoo react by

escape to sailing swifts in the first days after the latter's arrival in spring. As the shape of a swift in flight is very similar to that of a bird of prey (Fig. 25)—both have a remarkably short neck—it seems that in this case the special shape accounted for the erroneous reaction. In order to test this hypothesis, several workers have studied the reactions of birds to cardboard models of flying birds (Goethe, 1937; Krätzig, 1940;

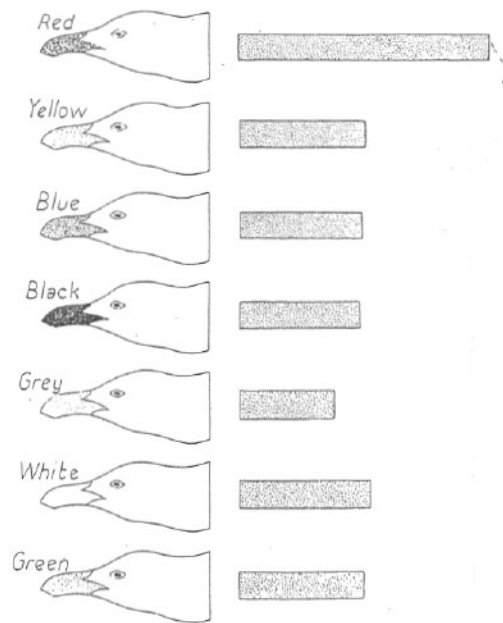


FIG. 24.

FIG. 24. Releasing value of herring gull models with uniform bills of varying colour. After Tinbergen, 1949.



FIG. 25.

FIG. 25. Flying hobby (*Falco subbuteo*) (above) and swift (*Apus apus*) (below).

Lorenz, 1939). These tests all showed that, as long as a model had a short neck, the experimental animals (various species of gallinaceous birds, ducks, and geese) would show alarm. Other characteristics, e.g. shape and size of wings and tail, were rather irrelevant (Fig. 26). This indicates, therefore, that the errors described are due to the birds' reacting to only one out of a number of possible stimuli.

In the visual domain, motion may often be a powerful stimulus. One of the earliest studies of this type concerned the 'recognition' of prey by dragonflies (Tirala, 1923). According to this author, mosquito-hunting species do not react to properties of shape, although their highly developed compound eyes certainly enable them to see even minor differences in shape. They react specially to the type of motion

of flying mosquitoes. Mosquitoes are not hunted when walking on solid ground. Small scraps of paper of varying shape but of approximately the right size promptly release the hunting responses when they are thrown in the air.

These examples concern visual stimuli. Numerous instances are known of the restriction of sign stimuli to other sensory fields.

Striking examples of restriction to chemical stimuli are found in the reactions of the males of certain Noctuid moths to the sexual odours emanated by the females. In *Saturnia pyri*, and also in *Lymantria dispar*, in *Lasiocampa* species, and many other species, males in sexual condition are attracted by virgin females. Fabre was the first to suspect that this must be a reaction to smell. This has since been proven in several cases (see Von Frisch, 1926). The males react so vigorously and so exclusively to the odour that they may try to copulate with any object bearing the female scent and even with the object on which a female has just been sitting.

In other species of Lepidoptera scent plays another part in mating. For instance, in the grayling the male stimulates the female to co-operation in mating by bringing the scent organs of his forewings (Figs. 27 and 28) in touch with the female's chemoreceptors, which are located on the antennae. This display takes place after the sexual pursuit (p. 40), when the female has alighted and the male has taken up a position in front of her. The climax of his elaborate courtship is an elegant bow (Fig. 29) by which the female's antennae are caught between the male's forewings. Males in which the scent organs have been removed have great difficulty in ac-

quiring a mate in spite of intensive courting (Tinbergen, Meeuse, Boerema, and Varossieau, 1942).

Reactions to sound may also be strikingly independent of other possible stimuli. Brückner (1933) studied the social relationships in domestic fowl. He found that a hen coming to the rescue of a chick in

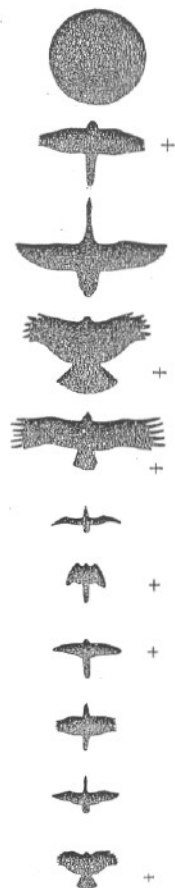


FIG. 26. Bird models used by Lorenz and Tinbergen for testing reactions of various birds to birds of prey. Those marked + released escape responses. After Tinbergen, 1948.

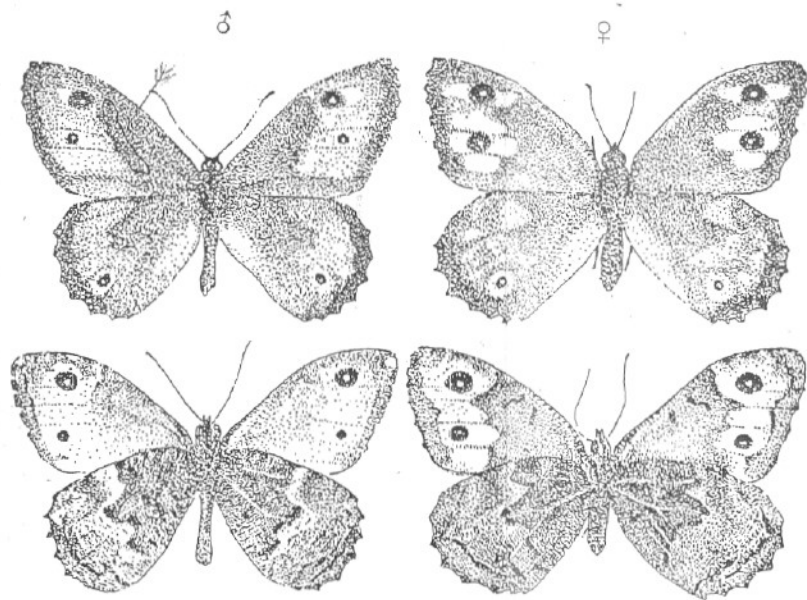


FIG. 27. The grayling. Upper: dorsal side; lower: ventral side. Black line in upper left figure indicates position of scent organ on left wing. After Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

← Courtship of Grayling

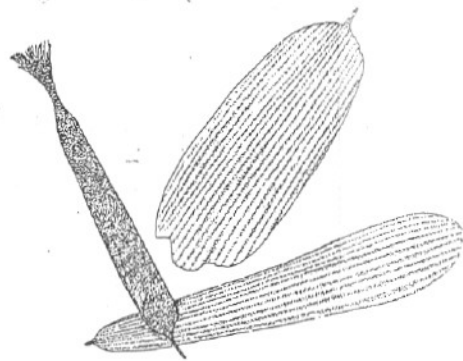


FIG. 28. Two ordinary wing scales and one 'scent scale' of male grayling. After Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

distress is reacting to the distress call, not to the chick's movements. When he fastened a chick to a peg, keeping it out of sight by putting it behind a screen, the mother would come to its rescue when she heard



FIG. 29. Grayling male (right) bowing so that the female's antennae come in contact with the scent organ of the male. After Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

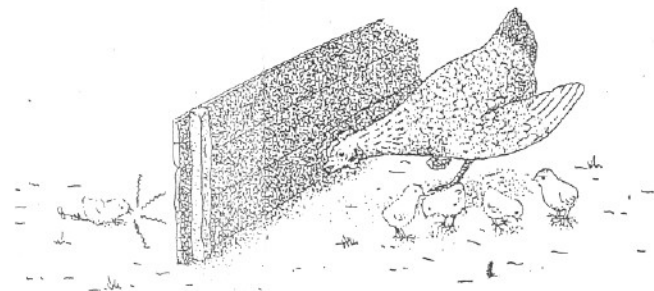


FIG. 30. Brückner's experiments on reaction of domestic fowl to distress call of chick. Above: visual stimulus presented alone; no reaction observed. Below: auditory stimulus presented alone; intensive reaction.

the chick whining. But when the chick was put under a glass dome in full view, so that the mother could see it struggling but could not hear its distress notes, she was entirely indifferent (Fig. 30).

In locusts of the species *Ephippiger ephippiger*, females that are willing to mate wander to the singing males. Whereas they are attracted to invisible singing males from at least 10 yards distance, they ignore silent males even when quite near. Males in sexual condition that were silenced

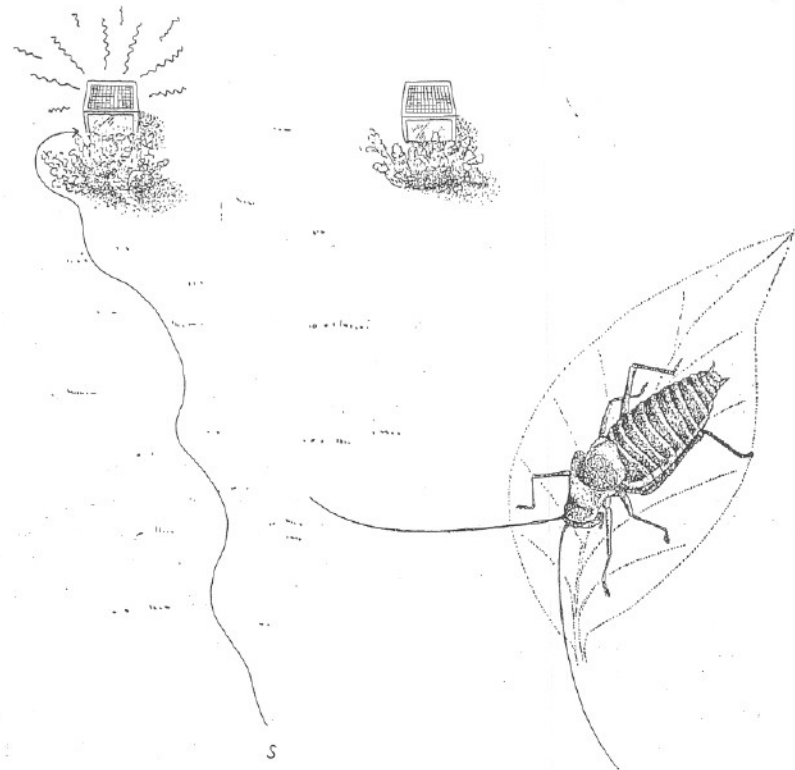


FIG. 31. *Ephippiger ephippiger*. Male (right). Path of female in mating condition towards cage with singing males (left), neglecting cage with silenced males. After Duym and Van Oyen, 1948.

by gluing their wings together, a minor operation, were not able to attract a single female (Duym and Van Oyen, 1948) (Fig. 31).

Touch receptors may also have very specific releasing functions. Fighting in male sticklebacks may consist of their repeatedly biting each other. This response is released by one hitting the other with its snout. It can easily be evoked by imitating this tactile stimulus with a glass rod or any other solid object. Whereas fighting as a whole is dependent on visual stimulation by a male in nuptial markings, the release of this specialized part of the fighting pattern is almost or perhaps entirely independent of visual stimuli.

It is not necessary to carry this review on; facts of a similar nature will be described in several of the subsequent chapters of this book.

Russell (1943), who has published a valuable review of these and similar facts in many different animals, has called these essential stimuli 'sign stimuli'. Later he preferred 'perceptual signs'. For reasons not to be discussed here, I shall use the term 'sign stimuli', although I am quite aware that the term 'stimulus' is open to certain criticisms. As a provisional, descriptive term, however, it will do.

As far as the available facts go, this dependence on only one or a few sign stimuli seems to be characteristic of innate responses.

In every study of reactive behaviour it is essential to be well aware of this difference between what an animal can perceive and what it actually reacts to in a given case. Neglecting this difference may lead to gross misrepresentation.

Thus Allen (1934), in a study of the courtship of the ruffed grouse, found that males in sexual condition copulated not only with females but with males as well, provided they assumed a position more or less resembling the female's normal mating position. (Thus 'a stuffed grouse, a grouse skin or a dead grouse' released the copulatory response in any male.) 'The exact pose was unimportant so long as it was more or less flattened, or at least not mounted in an attitude of display, and the sex of the bird was equally unimportant' (Allen, 1934, p. 192). From these facts Allen drew the conclusion that the ruffed grouse male does not distinguish between sexes. The facts, however, merely show that the copulatory response of the male is released by a stimulus situation in which no morphological sign stimuli play a part. The crouched position of the willing female is the most important sign stimulus. Allen's conclusion, therefore, is too general in two respects: first, males do distinguish between the sexes, but in this reaction they use behaviour characters instead of differences of shape or colour; second, even if they do not react to morphological properties, they may be quite able to see them and hence to distinguish between the sexes. A crouching submissive male or a dead male release the copulatory response merely because the male cannot resist the powerful sign stimulus.

In a similar way, the reactions of insects to the colours of flowers have been misinterpreted. Hive bees (von Frisch, 1914), some flies (*Bombylius*, Knoll, 1921-6), butterflies (Ilse, 1929; Tinbergen *et al.*, 1942), hawk moths (Knoll, 1921-6), and other insects specialized in sucking nectar have been shown to react innately to blue and yellow objects. Although they may react selectively to either blue or yellow, they do not show preference for special hues within the blue-violet-purple group nor within the wide range of orange-yellow-yellowish-green. It has been inferred that they cannot discriminate between

colours within each of these groups, but Lotmar (1933) showed convincingly that hive bees readily distinguished between different hues if specially trained to show differential responses. The recognition of the peculiar nature of sign stimuli as being different from the potential stimuli that can be received by the sense organs prevents confusion of this sort.

The reason why the dependence of innate behaviour on sign stimuli has not yet been generally recognized probably lies in the fact that so many laboratory psychologists have been studying conditioned reactions. Conditioned reactions are, so far as we know, not usually dependent on a limited set of sign stimuli, but on much more complex stimulus situations. I shall return to this problem in Chapter VI.

It is the dependence of innate behaviour on sign stimuli that renders it possible to evoke reactions in an animal by presenting it with dummies. As a matter of fact, when any animal readily responds to a dummy, this is a certain indication that its reaction is dependent on sign stimuli.

As mentioned above, the distinction between *Umwelt*, especially *Merkwelt*, and environment (von Uexküll) was partly based on the fact that different species have different sensory capacities. In this paragraph we have found a further justification of this distinction. The animal's own world is not only dependent on what its sense organs can or cannot receive. Its sensory world is still more restricted; it is composed of sign stimuli, at least as long as we are dealing with innate responses. This implies that the animal's perceptual world is constantly changing and depends on the particular instinctive activity that is brought into play.

The 'Innate Releasing Mechanism'

Up to this point I have been purposely simplifying matters by confining myself to pointing out that the animal does not respond to many characteristics of a situation, and that there are but few essential sign stimuli. I did not try to find out whether the sign stimuli I mentioned were the only effective stimuli. Our next task will now be to find the optimal stimulus situation of a given reaction. Some reactions of the three-spined stickleback may again be taken as examples.

As I showed, the males' fighting response is dependent on the sign-stimulus 'red belly'. The dummy tests described, however, were not adapted to study the influence of the movement, because, in every test, the dummies were either all moved in the same way or kept motionless. Now a male stickleback often moves in a very special way. When encountering another male near the boundary of its territory (which is where most of the fighting takes place) it adopts a posture with the head pointed downward, holding itself in a very peculiar vertical position. Now it can easily be shown that a dummy will evoke a much more

vigorous attack when it is presented in this 'threatening' position than when shown in a normal position (Fig. 32). The fighting response of a male stickleback, therefore, is not only released by a red male, but also by the special movements (posturing) of a male. The response, therefore, is dependent on a combination of these two sign stimuli.

The courting behaviour of a male stickleback before a pregnant

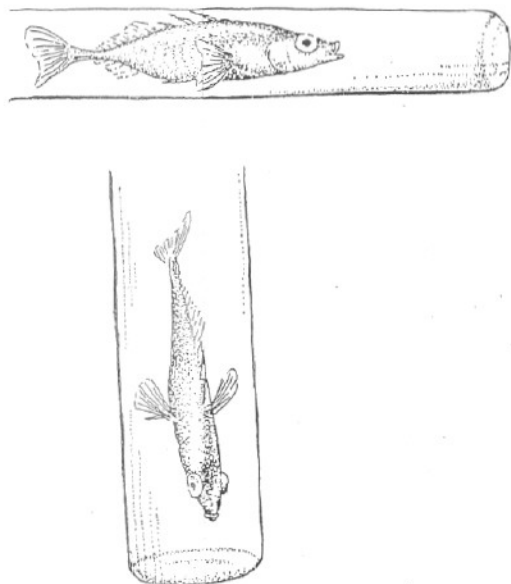


FIG. 32. Male three-spined stickleback prevented from assuming threat posture (above) and threatening (below). After Ter Pelkwijk and Tinbergen, 1937.

female is also dependent on at least two sign stimuli: the swollen abdomen and the special posturing movement of the female. When a crude fish-like model with a swollen abdomen is presented to the male, it will vigorously court this ridiculous dummy, whereas its response to a complete stickleback which has a normal belly is much less intense (Fig. 33). Also, a dummy that is posturing after the manner of a female (Fig. 34) releases the male's courtship much more readily than when it is presented in normal position.

The female's reaction to the courting male is released by two sign stimuli: the red belly and the male's special movements, the 'zigzag dance'.

It is necessary to insert here a few remarks about the technique of these dummy experiments. As will be discussed more fully in a later

chapter, these reactions are not controlled by external stimuli exclusively, but also by the internal reproductive drive. In the autumn or in winter the best dummies will invariably fail to evoke these responses. This is because the drive, or motivation, is too low in intensity. If the drive is of medium intensity a relatively strong stimulus situation will be needed to get a response at all; if the drive is very strong, the slightest stimulation will be followed by an explosive reaction. Under such condi-

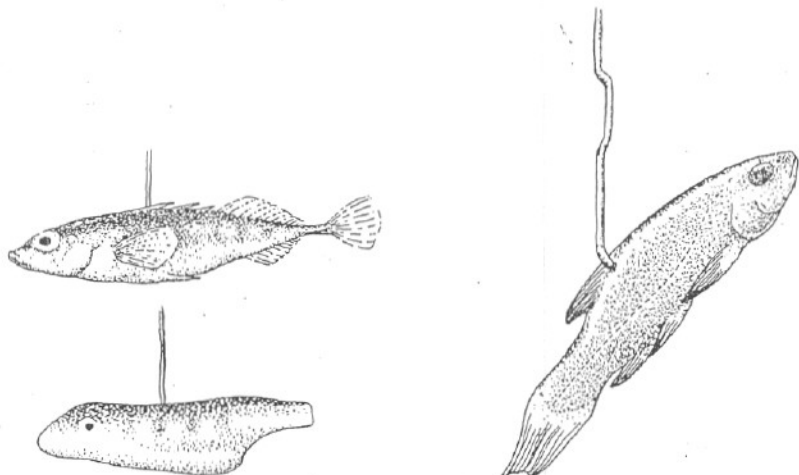


FIG. 33. Two models of female three-spined stickleback. Detailed model with 'neutral' abdomen (above); crude model with swollen abdomen (below). After Tinbergen, 1942.

FIG. 34. Dead tench (*Tinca vulgaris*) of stickleback size presented in attitude of readiness of female three-spined stickleback. After Ter Pelkwijk and Tinbergen, 1937.

tions a female will respond to a dummy that displays only one of the sign stimuli, e.g. the zigzag dance and not the red colour. This explains, for instance, why Leiner (1929, 1930) could get his animals to spawn in monochromatic light of various colours. However, to infer, as Leiner did, that the red colour has no influence in releasing the female's reaction, is a mistake. The monochromatic light test merely shows that red is not altogether indispensable for females with an exceptionally strong drive.

In an experiment of this kind, as in every experiment, it is necessary to compare the reactions to two different situations with each other. These two situations must differ only in the one factor the influence of which is to be studied. In our case we have to compare a dummy displaying the sign stimuli *A* and *B* with a dummy showing only one of them, viz. either *A* or *B*. Now such a test may have results differing with the intensity of the drive. If the drive is weak, both models will fail to

evoke a response. If the drive is strong, both models will give a response; and although the response to $A+B$ may differ in intensity from that to A , the difference is often difficult to detect, because it is only a difference of degree. But when the drive is of medium intensity the animal will show a positive response to $A+B$ and no response at all to A . It is the experimenter's job so to choose his conditions and his animals as to get

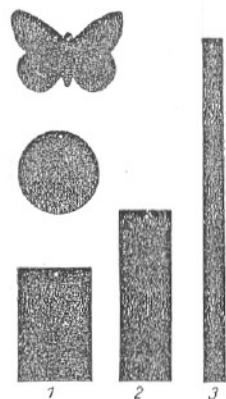


FIG. 35. Grayling models of varying shape. After Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

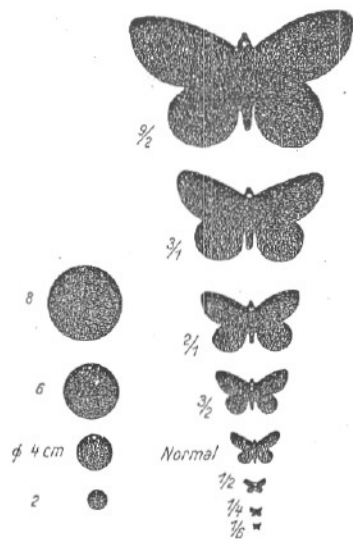


FIG. 36. Grayling models of varying size. After Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

this difference out as clearly as possible. Of course this is not cheating; the difference can be seen under the other conditions, but it is merely less easy to see and above all to describe.

More or less complete studies of all the sign stimuli that affect one single reaction have been carried out in a few cases. One is the mating flight of the male of the grayling (*Eumenis semele*), a satyrid butterfly. The male takes the initiative in mating by pursuing a passing female in flight. A virgin female thus approached alights, and the male performs an elaborate series of instinctive 'ceremonies' which eventually lead to mating. The first reaction, the sexual pursuit, has been studied by means of dummies, in which shape (Fig. 35), size (Fig. 36), colour, light intensity, type of movement (Fig. 37), and distance were varied. The result was that neither colour nor size or shape were of much influence, but that light intensity (darkness), type of movement, and distance had

a profound influence, the 'optimal' female being an object that flies in the typical fluttering way of a butterfly, that is as dark as possible and as near as possible (Tinbergen, Meeuse, Boerema, and Varossieau, 1942).

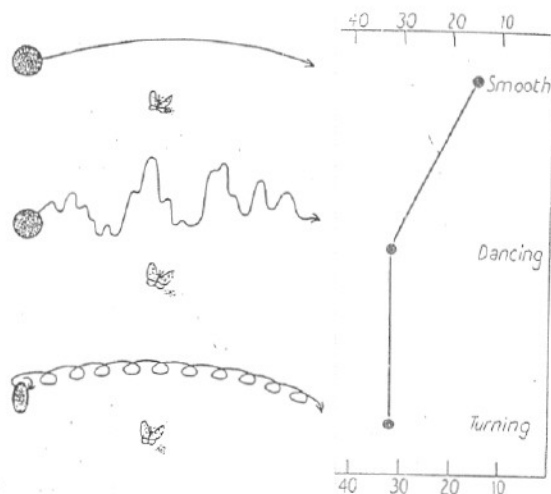


FIG. 37. Influence of type of motion on sexual pursuit of male grayling. Adapted from Tinbergen, Meeuse, Boerema, and Varossieau, 1942.

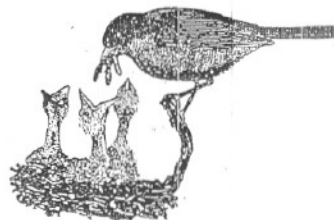


FIG. 38. Gaping reaction of young thrushes. After Tinbergen, 1947b.

The sign stimuli releasing the gaping reaction of young thrushes of about 10 days of age (Fig. 38) are the following: the object (the parent bird) has to move, it may have any size above about 3 mm. in diameter, and it must be above the horizontal plane passing through the nestlings' eyes. Optimal dummies presented below that plane may be seen, as can be judged from eye movements, but they never release the gaping reaction (Tinbergen and Kuenen, 1938).

The strict dependence of an innate reaction on a certain set of sign stimuli leads to the conclusion that there must be a special neuro-sensory mechanism that releases the reaction and is responsible for its

selective susceptibility to such a very special combination of sign stimuli. This mechanism we will call the Innate Releasing Mechanism (IRM), a free translation of the German term *das angeborene auslösende Schema* (Von Uexküll-Lorenz).

As we said before, the fact that so many animals do react to only a few sign stimuli at any one time has the practical implication that, if we know the potential capacities of the sense organs of a given species, this certainly does not mean that we know the external causes of any particular reaction. It does imply, in the second place, that an animal's failure to respond to certain changes in the environment does not prove inability to perceive those changes under any circumstances. It merely proves that they do not influence the IRM of the reaction studied. This is one of the reasons why conditioning is so valuable as a method of studying the sense-organs' capacities.

There is some evidence which tends to show that there is no absolute distinction between effective sign stimuli and the non-effective properties of an object. Lack (1943) found that the posturing of the robin is not exclusively dependent on the sign-stimulus 'red breast', for, rarely, a specimen lacking red on the breast was postured at. Similarly, I found in the three-spined stickleback that dummies lacking red and presented in neutral position would sometimes release attack, though a feeble one. These observations suggest that dependence on a sharply limited number of sign stimuli might represent an extreme case and is, perhaps, a specialization. Another possibility is that conditioning is responsible for the effectiveness of additional stimuli. More experimental studies of IRMs are necessary to elucidate this problem.

Although up till now few IRMs have been studied adequately, what scanty knowledge we have is sufficient to show that in general no two reactions of a species have the same IRM.

As already mentioned, the mating pursuit of the male grayling is released by a stimulus situation in which colour takes no part. The natural conclusion to be drawn from this would seem to be that *Eumenis* is colour-blind. But the observation that *Eumenis* selects blue and yellow flowers to feed on seems to contradict this. When the feeding reactions were analysed in the ordinary way, by presenting the butterflies with paper flowers of standardized coloured and grey papers, *Eumenis* appeared to be able to react quite well to yellow and blue on the basis of a real colour-discrimination (Fig. 39). Here then was a clear-cut case showing that an animal may react to colours in one reaction while not 'distinguishing' between them in another reaction. Of course, this very same state of affairs was the cause of the dispute between von Hess and von Frisch regarding the reactions of the honey bee to colours, which was described above.

Similar results have been obtained with two other species of Lepidoptera. Knoll (1921, 1926) found that the hawk moth *Macroglossa stellatarum* selects yellow and blue objects when hungry, yellowish-green objects when selecting a place to deposit eggs, and dark objects of any colour or grey when selecting a crevice for the purpose of hibernating.

Pieris brassicae selects yellow, blue, and red flowers for feeding, but for oviposition the female selects green objects (Ilse, 1929).

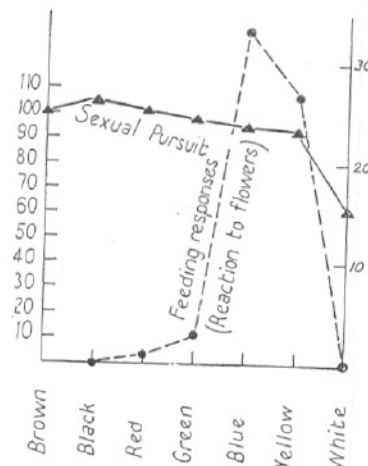


FIG. 39. Reaction of grayling to colour in two different motivational conditions. After Tinbergen, Meese, Boerema, and Varossieau, 1942.

These few instances will suffice to illustrate the general conclusion, viz. that different reactions of the same animal have different releasing mechanisms. This conclusion is still more obvious when one studies different reactions of an animal to the same object. When the female stickleback reacts to a courting male by posturing to him, she responds to his red colour and the special movement of the zigzag dance. But when, within one or two seconds, she enters the nest, her spawning reaction, although equally dependent on stimulation by the male, is released by quite different stimuli. As soon as she enters the nest, the male begins to thrust its snout at her rump with quick, rhythmic movements (Fig. 40). When the male is taken away, the female is absolutely incapable of spawning. But when the experimenter then substitutes a glass rod or any hard object for the male and gives her the same mechanical stimulus, she will respond by spawning. Thus the same object (the male) has to provide the female with entirely different stimuli for the two reactions.

It is not necessary to elaborate this point further. A great number of facts of this kind are given by Russell (1943).

'Supernormal' sign stimuli

The innate releasing mechanism usually seems to correspond more or less with the properties of the environmental object or situation at

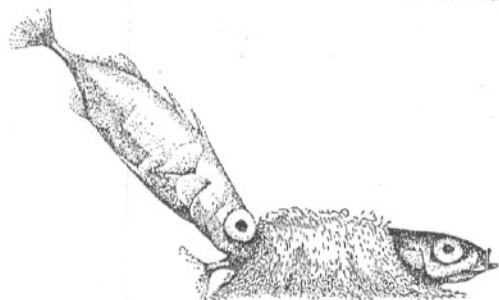


FIG. 40. Male three-spined stickleback stimulating female to spawn by 'quivering'. After Ter Pelkwijk and Tinbergen, 1937.

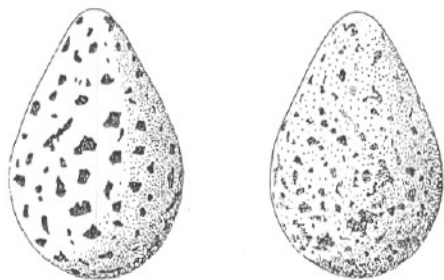


FIG. 41. 'Supernormal' egg (left) preferred by ringed plover (*Charadrius hiaticula*) to normal egg (right). Courtesy of Prof. O. Koehler.

which the reaction is aimed. This is according to expectation, and would even seem to be a truism, for otherwise the reaction would run the risk of being released by the 'wrong' situation and chaos would result.

However, close study of IRMs reveals the remarkable fact that it is sometimes possible to offer stimulus situations that are even more effective than the natural situation. In other words, the natural situation is not always optimal.

This was first discovered by Koehler and Zagarus (1937) in a study of 'egg recognition' (or the external stimuli releasing reactions normally released by the eggs) in the ringed plover. If presented with a normal egg (which is light brownish with darker brown spots) and an egg with a clear white ground and black dots (Fig. 41) the birds preferred the latter type.

In a similar way we found that oystercatchers preferred a clutch of five eggs to the normal clutch of three (Fig. 42). Still more astonishing is the oystercatcher's preference for abnormally large eggs. If presented

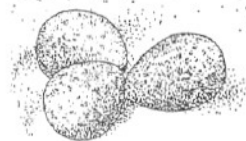
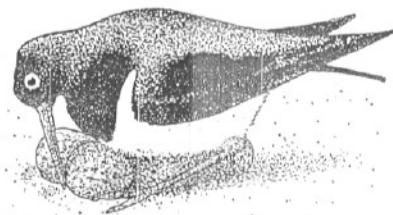


FIG. 42. Oystercatcher (*Haematopus ostralegus*) incubating 'supernormal' clutch of five eggs in preference to natural clutch of three.



FIG. 43. Oystercatcher reacting to giant egg in preference to normal egg (foreground) and herring gull's egg (left). After a photograph in Tinbergen, 1948.

with an egg of normal oystercatcher size, one of herring gull's size, and one double the (linear) size of a herring gull's egg, the majority of choices fall upon the largest egg (Fig. 43).

Another instance is the male grayling's sexual pursuit flight. As was related above, dummies of females of different colours had about the same releasing value. There is, however, a slight difference. The darker

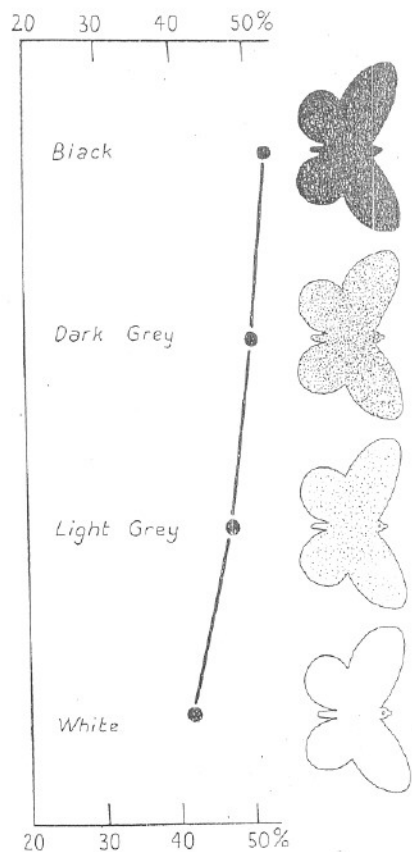


FIG. 44. Effectiveness of grayling models of various shades of grey. Changed after Tinbergen, Mecuse, Boerema, and Varossieau, 1942.

colours get more responses than the lighter ones. If models of different shades, varying from white to black, are presented, the darker shades get progressively more responses. A black model even evokes more reactions than a model in natural colours (Figs. 39, 44). Moreover, models of much greater size than normal get more responses than models of normal size (Fig. 45).

The full significance of the phenomenon of 'supernormal' sign stimuli is not yet clear. A closer study might well be worth while.

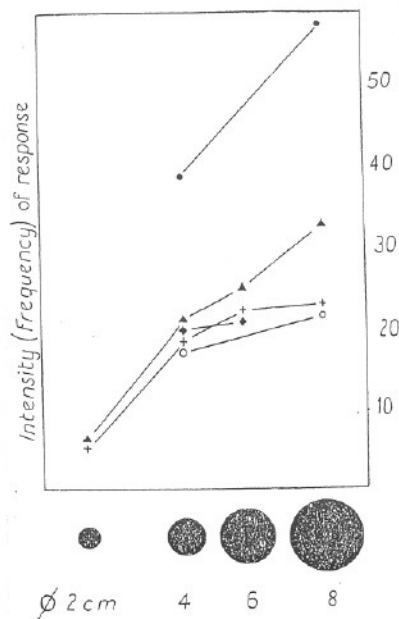


FIG. 45. Releasing value of circular models of varying size as presented to male grayling. After Tinbergen, Mecuse, Boerema, and Varossieau, 1942.

Reaction chains

Consistent study of the dependence of behaviour on sensory stimuli has further revealed the fact that many reactions, even relatively short and simple ones, are in reality a chain of separate reactions each of which is dependent on a special set of sign stimuli. Usually the first indication one gets of the chain character of a response is a sudden break during its progress. Such an abrupt break can be prevented by presenting a new stimulus situation of the special kind required at the right instant. The reactions of foraging honey bees to flowers, for instance, begin with a response to a visual stimulus in which colour plays an important part. Yellow and blue paper models of flowers especially attract bees from a considerable distance. However, a bee rarely alights on these models; at a distance of about 1 cm. it will hesitate and then lose interest. But if an odour of the right kind is added to the model, the next link in the chain is released: the bee settles down on the model and searches for nectar. In the complete response, this second reaction has to be followed by a third reaction, the insertion of the mouth parts into the flower and the consequent reaction of actually sucking nectar. These reactions depend on visual, tactile, and chemical stimuli, the exact part played by each of which has not been studied. What fragmentary information we have, however, shows that we have to do with a relatively long chain of reactions (von Frisch, 1927).

The hunting behaviour of the bee-hunting digger wasp *Philanthus triangulum* gives us another example (Fig. 46). A hunting female of this species flies from flower to flower in search of a bee. In this phase she is entirely indifferent to the scent of bees: a concealed bee, or even a score of them put out of sight into an open tube so that the odour escaping from it is clearly discernible even for the human nose, fails to attract her attention. Any visual stimulus supplied by a moving object of approximately the right size, whether it be a small fly, a large bumble bee, or a honey bee, releases the first reaction. The wasp at once turns her head to the quarry and takes a position at about 10-15 cm. to leeward of it, hovering in the air like a syrphid fly. Experiments with dummies show that from now on the wasp is very susceptible to bee-scent. Dummies that do not have bee-odour are at once abandoned, but those dummies that have the right scent release the second reaction of the chain. This second reaction is a flash-like leap to seize the bee. The third reaction, the actual delivery of the sting, cannot be released by these simple dummies and is dependent on new stimuli, probably of a tactile nature (Tinbergen, 1935).

One of the most complete analyses of chain reactions of this type has been carried out with the mating behaviour of the three-spined stickle-

48 BEHAVIOUR AS A REACTION TO EXTERNAL STIMULI

back (Fig. 47). Fig. 48 summarizes the results. Each reaction of either male or female is released by the preceding reaction of the partner. Each arrow represents a causal relation that by means of dummy tests has actually been proved to exist. The male's first reaction, the zigzag dance, is dependent on a visual stimulus from the female, in which, as already mentioned, the sign stimuli 'swollen abdomen' and the special

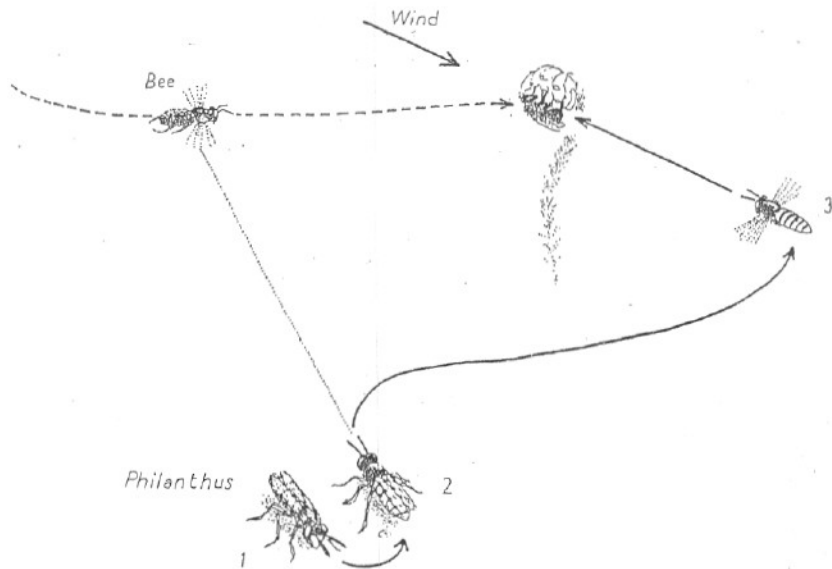


FIG. 46. Sequence of hunting behaviour of *Philanthus triangulum*. After Tinbergen, 1935.

movement play a part. The female reacts to the red colour of the male and to his zigzag dance by swimming right towards him. This movement induces the male to turn round and to swim rapidly to the nest. This, in turn, entices the female to follow him; thereby stimulating the male to point its head into the entrance. His behaviour now releases the female's next reaction: she enters the nest. As described above, this again releases the quivering reaction in the male which induces spawning. The presence of fresh eggs in the nest makes the male fertilize them.

Most of the links in these two reaction chains are dependent on visual sign stimuli, which are different for each of the links. The spawning depends on tactile stimuli. The male's ejaculation of sperm depends on a situation in which chemical and presumably tactile stimuli play a part (Ter Pelkewijk and Tinbergen, 1937; Tinbergen, 1942).

No doubt much the same state of affairs exists in most mating

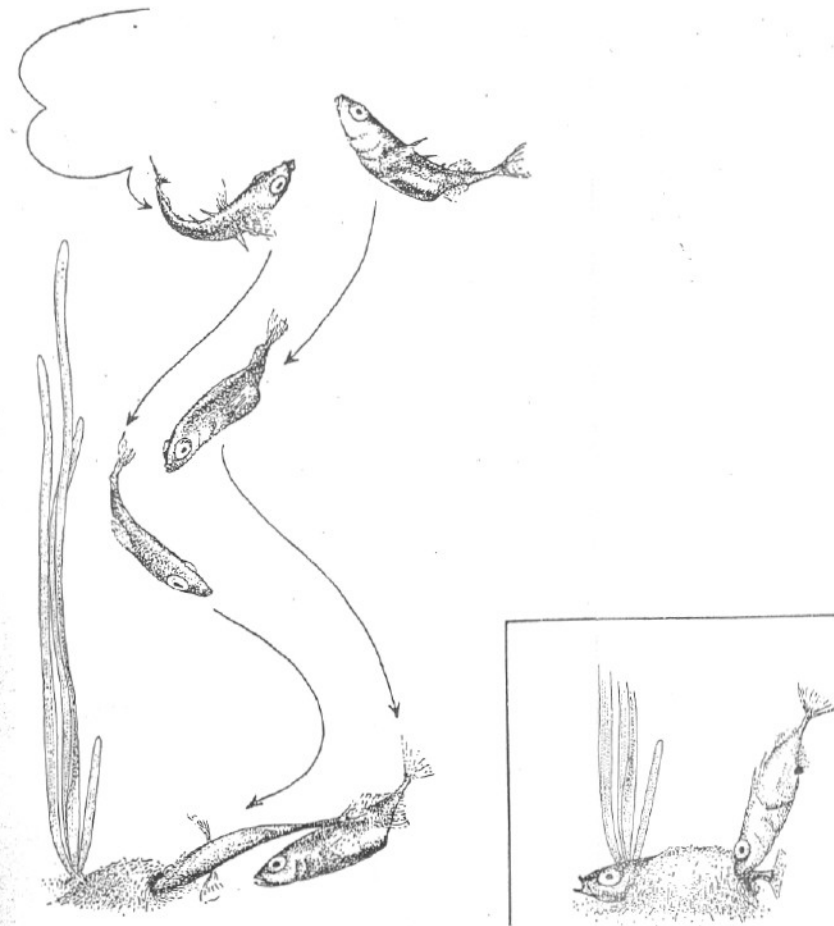


FIG. 47. The mating behaviour of the three-spined stickleback.

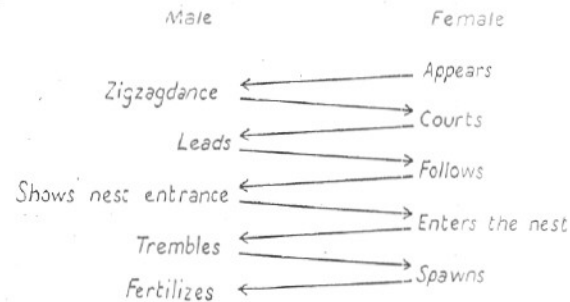


FIG. 48. Schematic representation of the relations between male and female three-spined stickleback. After Tinbergen, 1942.

behaviour. The long and complicated mating behaviour of the snail *Helix pomatia* L. (Fig. 49), reaching a climax in the release of the love-shaft by which the partners mutually stimulate each other to perform the final act, has been shown by Szymanski (1913) to be a reaction chain. By imitating the tactile stimuli delivered by the movements of one of the partners he could get the other partner to go through the entire series of reactions. The case is different from that of the stickleback in



FIG. 49. Mating *Helix pomatia* (left); love-shaft enlarged (right).
After Meisenheimer, 1921.

that *Helix* is hermaphrodite, and the behaviour of the two partners is identical.

Ambivalent Behaviour

The fact that each reaction has its own releasing mechanism may lead to ambivalent behaviour when two sign stimuli belonging to different reactions are present at the same time.

In the breeding season a herring gull reacts to every red object in the nest by carrying it away, a reaction noticed by several observers, though its function is not entirely clear. The reaction of sitting down on the nest to incubate is released by sign stimuli from the eggs. The most important sign stimulus is a visual one. The shape is essential: any object of approximately the size of an egg and having a rounded form is accepted. Now when the gull is given a bright red dummy of egg shape, it will alternately show the two different reactions in incipient form: first it may peck at the egg and try to get it out of the nest, in the next instant it may raise its ventral feathers and settle down on the egg. The two sign stimuli 'something red in the nest' and 'egg-shaped object in the nest', respectively, were, as it were, struggling for priority, each activating a different action.

Innate Behaviour in Mammals

The work done with mammals, especially the rat, has been reviewed by Lashley (1938). His conclusions, though agreeing with the views set forth in this book in most essentials, differ in one important aspect. Contrary to our conclusion that an instinctive reaction is dependent on a limited number of sign stimuli, Lashley concludes that 'the accumulated observations suggest that the instinctive behaviour is dependent upon a complex of stimuli' (1938, p. 454), and that 'the stimulus is not a characteristic colour or odour, but seems to be a pattern, having the same characteristics of organization which we have found in studies of visual discrimination of objects' (p. 455).

In my opinion the available facts do not yet allow us to see whether this difference of opinion is due to a real difference in the behaviour; it seems quite probable that mammals are different from lower vertebrates and invertebrates. However, part of the discrepancy is certainly due to the fact that in the work reviewed by Lashley the chain character of the reactions was not sufficiently realized and investigated. If, for instance, we should study the mating behaviour of the male stickleback as a whole, we should find that many properties of shape, motion, colour, and even tactile and chemical properties of the female play a part in releasing the whole reaction. Analysis of the reaction, however, showed that mating, in this case, is a chain of separate reactions each of which is dependent on only a minor part of this complex of stimuli. Thus Lashley's conclusion is absolutely valid for the mating response as a whole, but it may be untrue of each of the separate elements of the chain.

It is certainly necessary to attempt a much more detailed analysis of 'mating behaviour', 'maternal behaviour', &c., in the rat before it will be possible to draw a conclusion about the nature of external releasing stimuli.

In other respects, too, students of innate behaviour have so far given insufficient attention to mammals. Yet the study of mammalian behaviour, differing as it does from the simpler type found in, for example, birds and fish, would be a test of the general applicability of our conclusions. Of course, it is also indispensable for a better understanding of human behaviour. The highly interesting study by Schenkel (1947) on the behaviour of the wolf demonstrates the possibilities of the ethological approach.

Innate or conditioned?

So far no mention has been made of the problem of determining which of the reactions discussed were innate and which were not. It is often impossible to judge this from observation of the adult animal. For instance, in all the species where the parents take care of the young, the

behaviour of the latter may be conditioned by the adults in a number of ways. But an individual may also learn from experiences with other parts of the environment, such as food or predators. As we shall see in Chapter VI, learnt behaviour is by no means rare in the majority of species.

The only way to find out what behaviour is innate and what is acquired during individual life is to raise individuals in isolation, to observe the development of their behaviour, and to study the influence of different environments upon it. Various aspects of learning by individual experience will be discussed in Chapter VI. Here, however, something must be said about the criteria that allow us to recognize innate behaviour.

First, we must distinguish between the motor element of a response and its releasing mechanism. When the motor responses in the experimental individuals raised in isolation are identical with those of normal controls, this does not necessarily mean that the releasing mechanism is the same. For instance, gulls and terns (like many other birds) feed their young; gulls by regurgitating and presenting small bits to their young, terns by presenting a freshly captured prey in the tip of the bill. These responses are innate. But their IRMs are changed by experience. During the first few days the parent birds are willing to feed any young of their own species, provided they are of the same age as their own young, but after several more days they have learned to know their young individually and respond to them alone; strangers are driven away (Tinbergen, 1936b; Watson, 1908; Watson and Lashley, 1915).

Whereas it is easy to see whether an individual raised in isolation shows the same motor responses as normal controls, it requires experimental study, and hence much time, to see whether the IRMs are the same in both. Thus it is only natural that we should know many cases of innate motor responses but only few of innate releasing mechanisms. Our knowledge of innate behaviour has been greatly widened by Heinroth, who has raised practically all the European bird species in isolation and studied their behaviour (see, especially, Heinroth and Heinroth, 1928). Lorenz has carried his work on and has extended it greatly (see Lorenz, 1931, 1935, 1941).

In older text-books another method for recognizing innate behaviour is often mentioned. If, it is said, the behaviour in all members of a species is alike, one can be pretty sure that it is innate. This, however, is a mistake. In numerous cases the external conditions under which the young grow up are in many respects exactly the same for all. In some species of songbirds, for instance, the nightingale, the song is individually learnt. As the young learn it from individuals of the same species, all of which have about the same song, every juvenile male individual learns the song of the species. Not only in cases like this, when the motor

response is changed, but also in cases of change of an IRM by conditioning, the learning conditions may be the same for all individuals. As was stated first by Noble and Curtis (1939) and was corroborated by Baerends and Baerends (1950), some cichlid fish learn to confine their parental activities to young of their own species during the first time they breed. If a young pair are given eggs of another species in exchange for their own first brood, they will accept them and raise the young

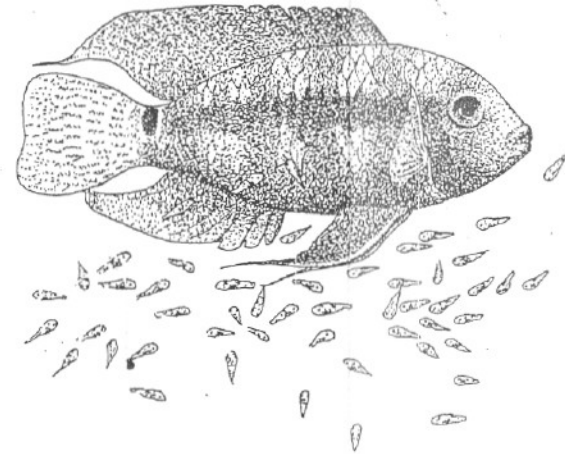


FIG. 50. Cichlid fish with young.

(Fig. 50). From then on they will never again raise young of their own species; they kill their own young as soon as they hatch. Normal experienced pairs will accept eggs of other species but they kill the young. This shows that, under normal conditions, these fish get conditioned to young of their own species when they breed for the first time. Here again, the fact that under natural conditions all individuals behave alike does not justify us in concluding that the behaviour is innate.

On the other hand, if it is observed that a certain response is not present in the young animal, this does not mean that it is acquired during individual life. First, a reaction may be innate and yet not appear before the animal is adult. The most extreme instances of such a state are the reproductive behaviour patterns. But, second, the gradual appearance of an activity during a slow, long period of development does not necessarily point to learning. The gradual improvement in the flying movements of birds, for instance, is only in part due to the acquisition of skill by practising. For the greater part it is the expression of a growth process, as will be discussed in Chapter VI.

In spite of all these pitfalls it is quite often possible to infer that an activity is innate without doing special experiments. As regards the change of IRMs by conditioning, there are a great number of species where the possibility does not present itself during normal life. For instance, how does a young cuckoo recognize and select a mate of its own kind? It has never seen a cuckoo before. And how could a male stickleback be conditioned to select only pregnant females of its own kind? From the moment of hatching it has only associated with young of its own age and with its father, and after it became independent it has only seen individuals in neutral condition, either males or non-pregnant females.

As regards the motor responses, there are even more species where learning by imitation is out of the question because they never get a chance to watch the performance of the response. Most insects, for instance, never have any contact with their parents' generation. Thus the complicated digging movements of a sphegid wasp can never be learned from other individuals.

Thus it is understandable that, on the whole, enough knowledge has been gathered to have a rough idea of what is innate and what is not. Reconsidering the examples given in the preceding paragraphs, it can be taken as certain that the behaviour of these sorts is innate: the reaction of birds to birds of prey, of the male three-spined stickleback to the female and vice versa, of the male robin to other robins, of *Eumenis* males to females, of insects to flowers, of a gull to eggs, &c.

What is 'a Reaction'?

So far we have concentrated our attention on the external causes releasing behaviour; we have called every movement released by an external stimulus 'a reaction' or 'a response'. It would be well to consider another element of a response, viz. the motor element, before continuing our study of the releasing agents.

In many cases the result of a stimulus is a very simple motor response. When we twitch the toe of a frog it simply withdraws the foot. When we touch the antenna of a locust it turns the antenna away. But when a dog walks through a herring gull colony in June, the gulls will utter their alarm call and the half-grown young react to this call by running to their shelters—each chick having a special hiding-place which it has learnt to use—and crouching. This is a more complex reaction, though still a relatively simple one. When 'unemployed' honey bees, waiting in the hive for a messenger, are at last activated by one performing the 'honey dance' (Fig. 51), the stimulus delivered by the dancer bee stimulates them to leave the hive. They fly in a definite direction over a definite distance (both communicated to them by the dancer) and begin

to search for flowers, selecting only those that emanate the scent carried by the messenger. They suck honey, and after having made a 'locality study', they fly home. In this latter case the stimulus given by the messenger releases a complicated behaviour pattern (von Frisch, 1923, 1946).

These few examples may suffice to show that the concept 'response' or 'reaction' covers a wide variety of motor responses of very different degrees of complexity. Although it is quite justifiable to treat them as units as long as one is only concerned with the external releasing factors,

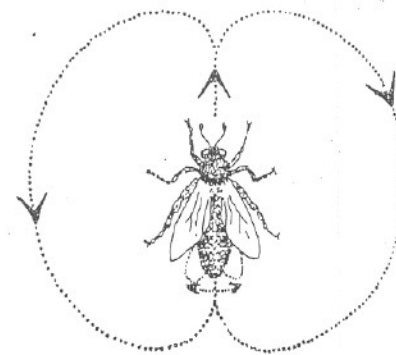


FIG. 51. The honey bee's dance. After von Frisch, 1946.

we should constantly bear in mind the fact that each of these 'units' is a more or less complex system, awaiting analysis. This analysis has already made some progress; it will be dealt with in Chapters IV and V.

Social Releasers

As we have already seen, many innate responses are dependent on stimuli given by other individuals of the same species. Because the study of these responses is of great importance for animal sociology, several have been investigated. The results confirm in a striking way the conclusion we have already drawn; many of these responses are dependent on the reaction of an innate releasing mechanism to a limited set of sign stimuli. Several instances mentioned in the paragraphs on sign stimuli and innate releasing mechanisms were concerned with such social responses.

The fact that these social responses provide the most striking examples of innate releasing mechanisms is not accidental. As we shall see later, the social relationships of many animals are based upon the functioning of structural or behavioural elements releasing specific responses in fellow members of the same species. These releasing features, whether