

The Learning of Detours by Wrasse (*Ctenolabrus rupestris* L.).

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With 13 Figures in the Text.

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PREFATORY.

THERE is probably no branch of biological research which can continue indefinitely without finding itself compelled to take account of the specific behaviour, if not actually the psychology, of the organisms with which it deals. This necessity has already been noticeable even in those departments of study in which attention is concentrated on the more abstract features of organisms, and in which individuals are regarded, as far as it can possibly be managed, as units of a standard type, acted on by independent external forces. No better illustration can be found than the attempts at relating the phenomena of organic structure to the causal agency of natural selection. If further light is to be thrown on this fundamental problem, no subjects are more suitable for the purpose than sexual selection and mimicry. But in both these fields of investigation progress is arrested until considerably more is known of the

behaviour of the animals concerned—in the former, of the actual effect which display of sexual structures exerts on choice of mates, or stimulation of coition; in the latter, the whole problem depends on the extent to which the mimetic characters can serve to impose on the sensory discrimination of predators. Lloyd Morgan (1900, p. 311) was one of the first to appreciate how the situation was developing. "Many interesting problems," he wrote, "which are keenly discussed by evolutionists in the light of natural selection presuppose conscious situations which are more or less tacitly taken for granted." Of course, stress need not be laid on the expression "conscious": it is sufficient for the point at issue to put "discrimination responses" in place of "conscious situations."

If behaviour cannot be ignored in the morphological sphere, still less is this possible in the ecological, when problems concerning the distribution of populations, and of relations of individuals to their physical and biotic surroundings, are encountered.

There are two rather different ways in which behaviour characteristics come increasingly to force themselves on the attention of ecologists.

(i) The fixed and regular aspects of behaviour of which account has to be taken, or which at least have to be assumed or are presupposed, may take on an intricate and specific form requiring elucidation by special study. As a clear illustration from animal ecology, one may cite the significance of the factor of "habitat selection" in interpreting the causes of distribution of breeding birds in an area of mixed habitats, as recently shown by Lack (1933). In marine biology similar cases come to notice. The vertical distribution of populations of plankton organisms is evidently to a large extent dependent on the specific behaviour reactions of the animals to the illumination of the water, or other factors in their environment. The availability of food for, e.g. bottom-living fishes, or shore birds, seems to depend more than at first might be expected on the special methods (due to specific feeding reactions) the animals employ to obtain it; so that the *setting* of the food organisms has to be taken into account, in addition to their mere *presence*. To quote one other familiar example—the breeding migrations of many fish are unquestionably regulated by special instinctive responses, and until something more is known about these the whole study concerned with the factors which affect the movements of populations of these species can scarcely progress far.

(ii) Secondly, it may come about that it is insufficient to regard only the fixed and regular aspects of behaviour, but that account has to be taken of the fact that the behaviour of both individuals and communities is modifiable, and, within limits, capable of adaptive, or even progressive, change. It seems that most ecological problems which have to take concern of special features of behaviour are destined to come up against the complicating factor of the *modifiability* of behaviour. Even in the

case of the vertical distribution of plankton the effects of physiological adaptation to optical stimulation have to be taken into account, significant shifts in the level of maximum concentration being attributable to this factor (F. S. Russell, 1931, pp. 400-405). In vertebrates this aspect can probably never be ignored for long. The return migration of fish to their breeding grounds, in so far as it is dependent on reactions to environmental stimuli, appears to involve reactions conditioned by the past reactions of the fish. At least there is evidence that this is so in the case of the Pacific Salmon (Rich and Holmes, 1928).

Again, the diets of shore and estuarine birds, some of which can utilize a considerable variety of food organisms, may vary according to the birds' acquired habits. It is a familiar fact that birds may ignore an unfamiliar source of food until discovering it by chance, when subsequently they may take heavy toll of it. This may happen, in the case of shore birds, to an extent sufficient to affect appreciably the mortality of shore invertebrates, and so once again the modifiable aspect of behaviour (of predators) has to be reckoned with, in the study of such a comparatively abstract property (of the food organisms) as the rate of mortality.

Another illustration which has recently come to notice shows the intricate relation between ecology and animal behaviour. The distribution of the Great Grey Seal (*Halichoerus grypus*) population in the South-Western area of England is intimately related to the presence of suitable breeding quarters (Steven, 1936). But whereas in the Scillies the seals lay their pups on open beaches, on the mainland of Cornwall they breed entirely in the interior of caves. Whatever has been the cause of this choice (and it probably resides in the attacks on the stock made in the past by man), it is evident that an acquired habit, or behaviour modification, has to be reckoned with. Since the areas which provide suitable breeding caves are severely limited, and the effect of this limitation is reflected on the distribution of the seal population—for instance, causing an almost complete absence on the south coast—the distribution, therefore, is directly affected by this acquired habit of the Cornwall seals.

These examples may serve to indicate how ecological investigations which primarily deal with the most general aspects of some animal population come to be concerned, firstly, with special features of the animal's behaviour, and, secondly, with the *modifiability of that behaviour*. The second aspect opens up an interesting field for investigation, and it is taken as a starting-point for a line of research of which the present paper is offered as a first contribution.

Viewed on a broad scale, all biological study is seen to have its origin in the observations made on organisms in their environmental setting and in the problems thereby raised. It is not complete until the results of the train of research so instigated are directed back to the observations

which provided the starting-point. Unless its direction is adequately orientated with respect to this main circuit, laboratory research is apt to narrow in scope, to settle in water-tight compartments, to become too unnecessarily abstract. We have seen that the problem of the modifiability of behaviour is raised in purely ecological studies, which circumstance at once draws it out from its recess among subjects of predominantly academic interest and brings it within the province of action of the marine zoologist. If any justification is required for research on the subject of the modifiability of behaviour, it is the above consideration on which main emphasis is to be laid. At the same time the claims are not to be overlooked of the intrinsic interest of the subject itself; of its bearing on academic problems such as the evolution of intelligence; of its relation to the subject of development and maturation; of the contribution it can make to the interpretation of learning, and the contacts thus established with general biological theory; and, lastly, of the problems it raises, and should assist in solving, with regard to methods and technique—as yet imperfectly developed—appropriate in the investigation of behaviour.

DETOUR EXPERIMENTS WITH TELEOST FISH.

With a view to making some contribution to the study of the modifiability of behaviour in Teleost fish, it was decided to utilize the method known as "detour" training as a basis for experimental work. The value of this method has been pointed out by E. S. Russell (1931) who, applying a technique made familiar by Köhler in his classical work on chimpanzees, undertook experiments with the freshwater stickleback (*Gasterosteus*). The capacity of the fish was tested for reaching a food object by a roundabout path. The food, presented inside a glass pot, was easily visible through the glass, but could only be reached if the fish made a detour round through the opening of the pot. At the start the fish attempt to reach the food directly, and may spend a long time swimming at the pot before eventually finding the opening by chance; but after continued repetition they come to acquire the habit of swimming straight to the opening. In the same way they come to adopt an efficient method of escaping from the pot, an action which at first presents difficulties.

We have evidently here to deal with a behaviour modification of an adaptive type which may be placed in the category of "learning," if this term is used in a fairly general sense. The animal "learns" to develop a response which enables it to overcome an obstruction in its path to a food-object, which functions as the immediate "goal" of its activities. The acquired efficient response has to grow out of several discrete movements, which are at first given independently of each other.

The main problem is to discover how this change in behaviour, this development of a more efficient response, is to be interpreted: what, in fact, are the necessary conditions for its occurrence, and how it is related to the fish's neural organization. The state of the theory of learning in general is such that there is no ready interpretation of the phenomenon. The "learning" of detours is actually a simple form of maze-learning, and presents many features in common with that shown in "puzzle-box" situations, in which the learned response involves the performance of certain movements in a correct order. It is noteworthy that neither in maze-learning, nor in other kinds of problem-solving, does present knowledge extend far enough to make possible an adequate interpretation of the learning process. On the one hand straightforward accounts in physiological terms of a strictly mechanistic type cannot absorb all the facts; on the other hand a theory, such as that of the "gestalt," which majestically ranges over the facts, travels too far beyond those at present available, and, further, is too comprehensive even to have acquired a precise formulation.

The difficulty is augmented by the fact that most of our existing information on problem-learning is derived from higher vertebrates which, it might be said, exhibit the phenomenon in too complex a form. We require to know more of the behaviour of vertebrates lower in the scale which are capable only of the elementary types of problem-learning. With such animals—and here it is that Teleost fish come in—simple situations can be presented which allow of adequate experimental control.

Russell's experiments were carried far enough to give some suggestive indications (1931, p. 408). He established the fact that the fish are normally able to learn simple detours; that the correct solution was first found by chance, and that at first the activity of the fish is undirected, at least in respect to the obstruction; that change in behaviour occurs with repetition of the trials, marked by a change from undirected to directed activity, and by a sudden fall in the learning curve; and that, associated with the acquirement of the efficient response, the pot appears to acquire some sort of significance from the aspect of the fish, as though some change in sensory organization had occurred.

But the question still remains—how did the performance of the correct movements, at first brought about accidentally, become "stamped in"? The suggestion is implied that it comes about as a result of change of sensory organization, of which the fish's reactions to the pot itself give evidence. The fish comes to sense a certain relation between objects in its surroundings, and adjusts its movements accordingly. This is in harmony with the "gestalt" viewpoint. But there is no claim that the experiments are adequate to serve the difficult function of demonstrating

the validity of this interpretation. Nevertheless, the results can perhaps be said to be suggestive; and it should be realised that if this interpretation of detour learning can, by further experiment, be shown to hold, a considerable step forward will have been made in the study of the sensory capacities of lower vertebrates.

The experiments described below aimed at procuring detailed observations on the fish over the whole course of training, in order to find what relations could be established between the final learned response and the various behaviour reactions given in earlier stages. For instance, it was important to enquire how far successful *methods* of making the detour, perhaps at first arrived at fortuitously, determined the method by which the learned response was performed. Again, were there, it was asked, any features of behaviour in earlier trials which determined whether a learned response would be established or not? The simplest type of detour was chosen and a record kept of all movements of the fish against a time scale throughout the trial. The records were subsequently subjected to analysis, and, where possible, quantitative data were abstracted. The main features which emerged are discussed in the second half of this paper, after the experiments have been described. It may be noted that the procedure adopted in this investigation resembles somewhat that of the field naturalist, who first sets out to record as minutely and impartially as possible the behaviour, whatever it may be, shown by an animal under observation, and subsequently works out the most important features of the mass of details as a whole; rather than that of the experimentalist, tackling a clear-cut problem, who arranges his experimental conditions so that a definite answer is given one way or the other. In elaboration of these experiments it should be possible to harmonize the best of both methods.

METHODS.

General procedure. The fish used in these experiments were small, immature specimens of the Rock Wrasse (*Ctenolabrus rupestris* L.), from 5 to 7 cm. in length. This species readily adapts itself to captivity and lives well in tanks of restricted size. It soon gets over the effects of any shock that may be induced by capture in a net or disturbance of its tank. Altogether the species proves an excellent experimental animal.

For the whole of the time during which it was subjected to experiment, each fish was kept isolated in a rectangular glass dish (size either $42 \times 24 \times 12$ cm. or $36 \times 28 \times 15$ cm., internal dimensions). Preliminary experiments were made on three fish (A, B, and C) in the early part of 1934, in two dishes set up inside a larger tank (in the main laboratory) screened from excessive light. The remaining nine fish (D1 to 9) investigated together in the later months of that year were kept in a darkened room.

the dishes ($36 \times 28 \times 15$) lying in a row on a long table, screened from each other with strips of cardboard. The dishes were provided with air circulation.

The fish, in each case, was allowed to get thoroughly accustomed to its surroundings, and to take food off a piece of thin wire. After being placed in the experimental dish it was never fed in any other manner. Prior to the feeding an electric light of moderate intensity was switched on. In the main experiment the lighting of the room served as a signal—and probably actually acquired this association—that feeding was about to take place. It was found that the fish very soon came readily to associate the wire with food and gave positive reactions to the observer when he approached the dish. They followed movements of the hand when this was passed over the tank, and also were closely attracted to the pipette used from time to time for picking up debris accumulated in the dish. Any shock reactions given at first soon disappeared, and they soon became indifferent to such extraneous stimuli as may have reached them (e.g. vibration from footsteps in neighbouring passages). These facts are emphasized to show that feeding responses, at least, were free from inhibitions which might have interfered with the experiments.

After an adequate period had been allowed the fish for settling down, experimental feedings were started. The fish now never fed except in a situation in which it had to surmount a certain obstruction: it now always had to take an indirect route to reach the food. Whatever type of obstruction was used the procedure at each feeding followed along the same lines. The fish was enticed to a particular corner of the dish, and at the same time the obstruction (in most cases the arrangement of glass plates described below) was carefully lowered into the tank. The food, still presented at the end of a thin wire, was then transferred to an appropriate position, and left hanging in the water on its wire support. The fish was able to detect the food by sight, but was in such a position that it could not directly reach it. Actually, it had either to enter a pot or pass round a glass plate. A stopwatch was set going as soon as the fish began to swim towards the food, and a record of the observed movements of the fish was taken. The observer's head and shoulders were in the fish's range of view, but it was found that the fish was too absorbed in its attempts at reaching the food to be affected even by quite considerable movements on the part of the observer. For precautionary measures, however, the observer kept still all through the trial, as nearly as possible in the same relative position with respect to the dish. As soon as the food was taken, the obstruction was removed, and the fish once more left in a clear tank. Two such feedings, on an average, were given to each fish in one day. After a time it was possible to reduce the amount of food given at

each trial to a very small quantity, so that as many as five feedings could be given in one day before the food ceased to attract.

The food, for the most part, consisted of the muscle of freshly killed prawns. This was now and again varied with small pieces of squid.

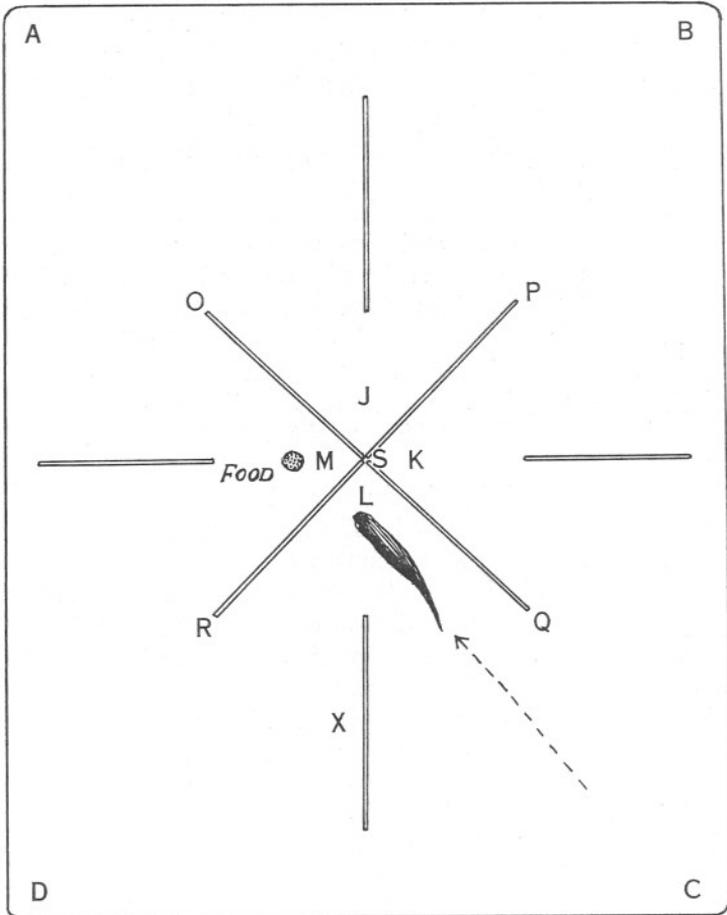


FIG. 1.—Diagram of the arrangement of glass plates used in training the fish. See text, p. 505. $\times \frac{1}{3}$.

A, B, C, D marks the inner edge of the glass dish. J, K, L, M, S, and X are positions to which special reference is made in the accounts of the experiments. O, P, Q and R mark the positions of the edges of the four central radiating glass plates.

Apparatus. The only special apparatus that requires description is that employed to furnish the fish with a detour path. In the majority of experiments here described it consisted of a special arrangement of glass

plates (the glass 2 mm. thick) set in a pattern shown in Fig. 1. These plates were held in a wooden frame made to fit over the top of the dish (Fig. 2). At each feeding the loaded frame was lowered into the dish, the glass plates then forming a sort of maze restricting the directions in which the fish could freely move. In Fig. 1 a number of positions in the horizontal plane are marked by letters, and it will be convenient to use this lettering for describing positions in the dish. The plates OS, PS, QS, and RS were each 8.6 cm. wide. The side plates were fixed so as just to protrude into the square O, P, Q, R.

With this apparatus both the position of the food and the starting position of the fish could be varied in different ways. The symmetrical

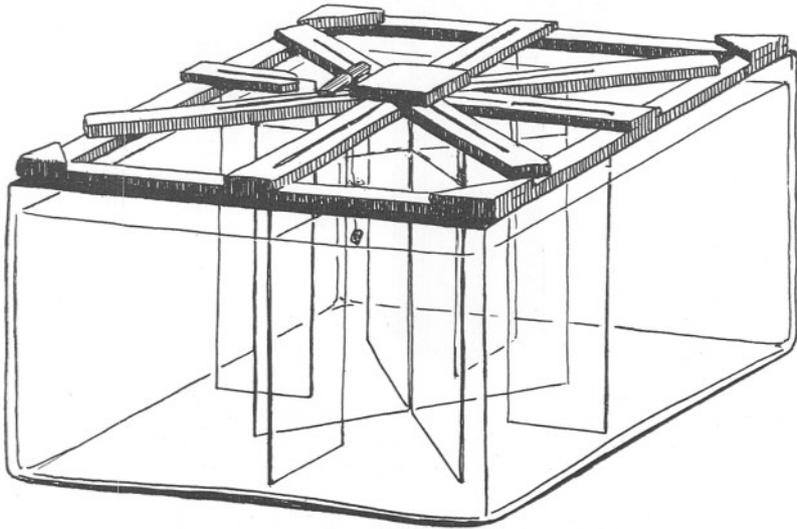


FIG. 2.—Optical view of glass dish with the wooden frame, holding the glass plates, in position. See text, above.

arrangement of the plates also permitted an easy exchange from right to left, such as is required in testing transfer of learning. In practice, the food (except in the case of fish B) was always placed during training at the position M, and the fish started from the neighbourhood of C. The fish thus had to circumvent the edge R; and in doing this had to make a detour of some 6.5 cm. If the glass plate had a clear surface, or even if its edges were marked with a black line, this simple detour was quite enough to test the fish's capacities to its limits. The other portions of the "maze" served their purpose during tests on fish which had learnt to make a detour of the plate R S.

The wire supporting the food was lightly held on a piece of wood resting on the frame in the position shown in Fig. 2. A loop was made in the

wire in such a way that the wire fell naturally into a vertical position when placed on the support.

Another piece of apparatus used consisted of a glass tube fixed horizontally on a weighted upright support (Fig. 3). The tube, 10.2 cm. in length, and of 3 cm. internal diameter, had an opening on the side placed uppermost, near the closed end. Through this opening the food, suspended on a wire, was lowered, and thus came to rest inside the tube 8.5 cm. from

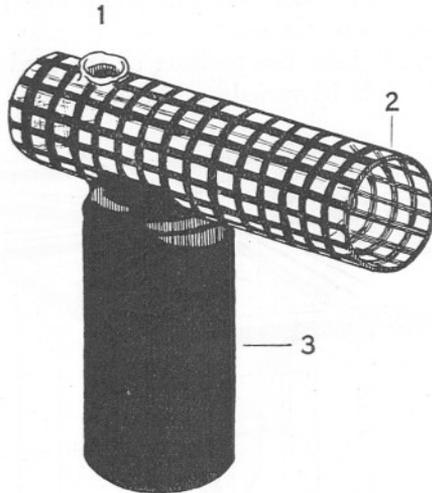


FIG. 3.—Sketch showing the tube, painted with black meshwork, presented to fish D9. See text. $\times \frac{2}{3}$.

1. Hole through which food wire was inserted.
2. Mouth of tube. 3. Weighted support.

its open end. The support was painted black and the glass tube covered by a heavy black meshwork, roughly painted on. The extent of the tube was thus made visibly conspicuous, though the food could still be seen through the meshes. The fish could not reach the food except by passing through the open end of the tube.

DESCRIPTION OF EXPERIMENTS.

I. DETOURS NECESSITATING ENTRY INTO A GLASS RECEPTACLE.

E. S. Russell (*loc. cit.*) has adequately demonstrated that fishes are capable of learning to find their way into a pot, either of clear or somewhat opaque glass, whereas their first reactions lead them to attempt to reach the food directly.

An important characteristic of this type of detour experiment is that the obstruction is more or less easily visible and the indirect route can be

in some sense "surveyed" by an animal with adequate powers of vision. The possibility is offered that the pot or tube may become viewed as an object, and both the food and the way of access to it sensed in relation to the object as a whole. This evidently happens in the case of higher mammals, and may well happen to a greater or lesser extent in that of teleost fish. Russell found that the fish, after training had progressed, came to give special reactions to the pot itself, as though it had acquired a new significance in their world. This at least indicates that the fish were capable of sensing the pot as an object.

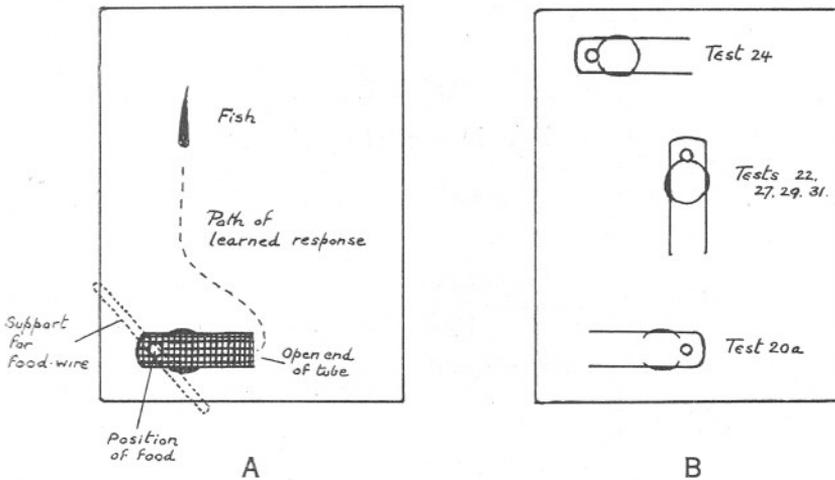


FIG. 4.—Diagrams of conditions presented to fish D9. $\times \frac{1}{8}$.

A. General conditions under which training took place. B. Three alternative positions of the tube given in the tests indicated.

Since the wrasse proved capable of learning a more difficult type of detour, more suitable for procuring the type of data required, it was not considered necessary to repeat the pot experiments. One fish, however, was given the meshed tube described on page 506 (Fig. 3). The tube with its black support could not have failed to provide a conspicuous object, and the meshwork marked the glass obstruction in a conspicuous manner.

Fish D9.

Length: $5\frac{1}{2}$ cm.

After 8 days in the dish the fish had settled down and took food readily off the wire. The pot was then introduced (Nov. 23): the fish showed "apprehension" and could not be enticed closer than to 5 cm. of the new object. The pot was removed and replaced the next day. Two feedings were then given (Nov. 24) as close to the pot as the fish would approach, now about 3 cm. The pot was now left in the dish until Nov. 26, when feedings were given both over it and close by its side. The inhibitory influence of the pot was now disappearing. The pot was then left in the dish, and next day it was possible to give the first trial feeding, the pot now having no inhibitory influence at all. Thus the latter was overcome in four days.

For the first day (Nov. 27), when three experimental feedings were given, the pot was

left in the dish, but subsequently it was removed after each trial. It was always placed in the same position in the dish near corner D, in the position shown in Fig. 4a.

The fish was attracted to the far side of the tank. The baited wire was then lowered into the hole on the upper side of the tube, and hooked over a wooden support resting on the corner angle of the dish (Fig. 4a). The stop-watch was set going as the fish passed the middle of the dish in the direction of the food.

A modification, however, of this procedure had to be introduced after a dozen trials. The pot, by then, had become such an attraction in itself that the fish now often entered it before there was time to introduce the food at all. So the food was now placed *inside* the tube before the latter was lowered into the tank. It now lay on the bottom of the tube near its closed end, and, incidentally, was now in a more inconspicuous position.

The duration of the trials are given in Table I. These figures serve to indicate the rapidity with which the fish came to develop an efficient performance.

TABLE I.
FISH D9. DURATION OF TRIALS.

Date.	Serial No.	Duration of trial.	Remarks.	Date.	Serial No.	Duration of trial.
Nov. 27	1	7' 18"		Dec. 7	19	0' 11"*
..	2	3' 04"		..	20	0' 14"*
..	3	5' 43"		..	21	0' 16"*
28	4	2' 25"	Entered tube a second time.	..	22	(Test)
..	5	2' 18"	Investigated opening before	10	23	0' 14"*
29	6	1' 59"	[food introduced.	..	24	(Test)
..	7	0' 49"		..	25	0' 14"*
..	8	(4' 51")	Not adequately attracted	..	26	0' 08"
30	9	0' 26"	[by food.	..	27	(Test)
Dec. 1	10	3' 05"		12	28	0' 09"*
3	11	0' 36"		..	29	(Test)
..	12	1' 29"		..	30	0' 19"*
4	13	0' 32"*	Food now introduced with pot.	..	31	(Test)
5	14	0' 11"*	Efficiency now attained.	13	32	0' 09"*
..	15	0' 27"*		..	33	0' 17"
..	16	0' 13"*		..	34	0' 09"*
6	17	0' 10"*		..	35	0' 14"
..	18	0' 12"*				

Any doubts as to whether the pattern on the tube prevented vision of the food inside were quickly dispelled during the first trial. For two periods, each of about $\frac{3}{4}$ minute, the fish made persistent attempts at reaching the food object through spaces between the meshes. It worked actively all round the closed end of the tube. It even snapped at the glass from below. Its behaviour was perhaps remarkable when it is remembered that only two days previously it was still nervous of approaching the pot.

More than seven minutes passed before the fish eventually reached the food in this first trial. After some fruitless efforts at reaching the food directly, it spent some time swimming irregularly around the pot, with occasional excursions into other parts of the dish. But it was a long time before the fish came right opposite the opening of the tube; for the latter

* Food already inside the tube, lying on the bottom, when the tube was lowered into the tank. All trials after 13, except 18, 26, 33, and 35.

lay rather high in the water and the fish tended to swim at a lower level. It was not until 7' 13" that the fish's movements brought it immediately abreast of the opening, and that for the first time could it have had an open view of the food. It would not have been surprising if the fish had now displayed hesitancy. Viewed from the opening, the food had a bizarre visual background of radiating and intersecting black streaks, which may well have obscured the outlines of the food object in the fish's visual field, even if the pattern did not itself exert an inhibitory effect. The fact is, however, that *the fish swam straight into the tube and snapped at the food without the least hesitation.*

The next few trials were performed in a similar manner, the fish swimming into the tube the first time it happened to come opposite the opening. It never again took so long as on the first occasion, and would doubtless have given still better results if it had not shown a tendency to swim round underneath the opening.

There were early signs that the fish was beginning to acquire some familiarity with the apparatus in which it was fed. After trial 4 it swam into the opening a second time. At the beginning of 5 it swam up to the mouth and looked inside, before the food was introduced. Again, at the beginning of 6, it swam up to the opening and inserted its head into the tube. But in both these trials, once the food had been introduced, the fish still persisted for some while in its attempts at reaching the food directly, and took over two minutes to make the detour.

In trial 7 for the first time the fish reached the food in less than a minute. Trial 8 is unsatisfactory, as previous to it the fish had been accidentally disturbed, and when the trial was given it did not appear to be at all strongly attracted to the food. It was still probably in a certain state of inhibition. The length of duration of 10 is to be attributed to disturbing influences. There was some delay in presenting the food, and during this interval the fish swam into the empty pot at least twice on its own "initiative." There was also a second observer present. Apart from these two trials, a reasonably steady improvement in efficiency of performance may be seen.

An important factor in the increase of efficiency was a reduction in the time spent in attempts at reaching the food direct. This suddenly fell to 5" in trial 9, and, though the next three trials gave 1' 30", 20", and 36" respectively, it suddenly became negligible from 13 onwards. From this point the fish no longer spent any time in attempting to reach the food direct through the glass.

Trial 13 marks a point of rather sudden improvement. After this trial an efficient response can be said to have become established. From 14 onwards the fish rarely even swam to the closed end of the tube where the food lay: as it passed towards the tube, at a distance of about

10 cm., it diverted its course somewhat to the left to bring it to the open end.

It is to be noted that this main step in the progress of learning also coincides with a modification in the experimental conditions referred to above—from 13 onwards the food was inside the tube when the latter was placed in the dish. It is possible that this change exerted an effect on the course of learning; but if it did so, the effect was a favourable one. It is noteworthy that the main difference involved was that the food was made *less* conspicuous—probably invisible except at close quarters—and so may not have held the same attraction as before. It is therefore possible that there was less to distract the fish from its growing tendency to move to the open end of the tube, but if this were so, the fact is certainly noteworthy. If not, then the sudden improvement has to be regarded as an independent feature of the learning process (e.g. as in fish D5, pp. 528, 550).

When the original conditions were repeated (trials 18, 20, etc.) there was no difference in the fish's performance from that in other trials.

During the efficient period (14 onwards) the fish, as has been stated, rarely even visited the closed end of the tube. In the best performances it swam straight to the opening, and in, without hesitation. But it still on occasions swam round the pot once or twice, having missed the opening first time.

Certain tests with the pot placed in different positions were made. The positions are shown in Fig. 4. Thus in trial 20*a* the pot was turned round so that its opening faced corner D. The fish took its usual course, swimming straight to the left-hand end (left, that is, from the position of the fish) and made persistent efforts to get into the tube at this point. The trial was abandoned at 1' 30". Trial 24 provided a mirror image of the normal situation. The fish again tried the left-hand side first, but this time did not persist in attacking the end: it swam to and fro and reached the food in 37". Both these tests indicate that the fish had acquired the habit of *moving to the left-hand side of the tube*, whatever its position, rather than to distinguish the open long arm of the tube from the short closed arm.

Four tests were made with the pot standing in the middle of the dish, the opening facing towards the observer. The fish was started on the left-hand side. In the first two (22, 27) the fish swam round and round the tube and did not enter it even when coming abreast of the opening. Both tests were abandoned, after 3' 30" and 2' 15" respectively. However, both 29 and 31 were solved readily (10" and 30"). It is possible that the different relation to the electric light, and so a difference in the illumination of the interior of the tube, was responsible for the failure of the first two tests. One can at least conclude that the position of the tube relative

to its background and to the angle of approach of the fish was still of importance.

These details of the performances of fish D9 are given to illustrate the type of result obtained with wrasse when the arrangements seem to supply optimum conditions for learning. The obstruction is easily seen, while at the same time the food remains visible ; there is only one indirect route, which can probably be readily surveyed by an animal with adequate powers of vision ; the task of discovery of the indirect route is well suited to the natural exploratory behaviour of wrasse. It emerges, however, that this type of detour problem is not well suited to the sort of analysis we wish to undertake. The fact that there is really only one method of solving the problem is a severe limitation, and the efficient response is arrived at too rapidly to allow of comparisons between its separate components.

II. DETOURS NECESSITATING PASSAGE ROUND PARTITIONS OF GLASS.

With the apparatus described on page 504 it was possible to try out a detour of another type—one in which the obstruction is invisible or only figures very obscurely in the fish's visual field. Other varieties of glass plates can always readily be substituted, such as ones with their surface marked in some way so as to render it conspicuous to the fish. The apparatus also allows of other modifications of experimental procedure and is thus conveniently adaptable.

The results of the preliminary experiments, with fishes A and B, showed that wrasse are capable of learning to get round a plain glass obstruction effectively, although an efficient response is acquired with difficulty and precariously maintained. Fish A was presented with the problem subsequently given to other fish, of group D, but since other conditions differed somewhat, caution must be used in making detailed comparisons between the performances of A and other fish.

The experiments on fishes D1 to 8 were carried out simultaneously under comparable conditions. D2, 3, 4, and 5 were given an obstruction of plain glass, as in the case of A. With D1 and 6 the plate was edged with a black strip, 5 mm. in width. D7 and 8 were presented with a glass plate of similar dimensions, but with its surface marked with a meshwork of scratched lines. The lines on this plate were ruled at 5 mm. intervals, with the aid of a glass-cutter. Though made as firm as possible, and very noticeable in the air, they did not show up very conspicuously under water.

In all these cases, during training, the food was presented at M (Fig. 1), and the fish started from corner c.* A detour of 6.5 cm. to the left had to be made.

* Except fish B.

Fish A.

Length 6.5 cm.

Jan. 4, placed in experimental dish standing in an empty tank in the main laboratory, under conditions referred to on page 502. For 12 days fed with *Mytilus* and pieces of Polychaete worm off the end of a wire, until it had become thoroughly habituated to this method of feeding and its conditions in general.

Jan. 16, first experimental feeding. Jan. 16–Feb. 10, 67 experimental feedings given. Feb. 10–14, interval during which fish was moved from the tank and water renewed. Feb. 14–March 3, 67 experimental feedings given. March 4–19, interval during which dishes were disturbed. March 20–22, 11 further experimental feedings.

Trained to plain glass obstruction, detour 6.5 cm.

The experiments on this fish constituted the main part of the preliminary investigations, carried out between January and March, 1934. For the first fortnight there was no indication that the fish was acquiring any increased efficiency in its performance, but eventually it developed a stable learned response, working leftward along the glass until reaching the edge.

The general course of learning is shown graphically in Fig. 5, in which a curve is given representing the duration of successive trials. As is usual with these "learning curves," its course is very irregular until the learned response is stabilized, when it remains at a uniform low level. The averages of groups of five successive normal trials are as follows (trials which are called "tests," in which the conditions are altered in some particular respect are not included in these figures):

Date.	Serial No. of trials.	Average duration.	Date.	Serial No. of trials.	Average duration.
Jan. 16–18	A 1–5	7' 52"	Feb. 14–16	B 1–5	2' 03"
18–22	6–10	5' 38"	17–19	6–10	1' 17"
22–23	11–15	2' 26"	19–20	11–15	0' 38"
24–25	16–20	5' 03"	20–21	16–20	0' 14"
25–29	21–25	6' 16"	23–24	24–28	0' 16"
30–31	26–30	1' 36"	24–25	29–33	0' 11"
Jan. 31–Feb. 1	31–35	1' 29"	26–28	34, 43, 44, 48, 49	0' 11"
Feb. 1–2	36–40	1' 09"	March 1	50, 53, 55, 57, 58	0' 12"
2–3	41–45	0' 32"	2–5	59, 62, 64, 65, 66	0' 12"
3–5	46–50	0' 37"	March 20–21	C 1–5	1' 02"
5–6	51–55	0' 31"	21–22	6–10	0' 12"
7–8	56–60	0' 48"*			
8–9	61–65	0' 18"			

First series (trials *AI* to *67*). In the early trials the fish found considerable difficulty in reaching the food, and the average duration of the first 24 trials was higher than in any other fish. To start with, there was a conspicuous contrast between two alternating phases of behaviour: the movements were partly directed towards the food, resulting in the fish keeping close to the glass; partly random with respect to the food, resulting in the fish swimming away to various parts of the tank. These two phases alternated continuously; the attraction of the food always returned when it had been lost temporarily. But it was only the first 7 trials that were characterized by this behaviour. After that the fish

* Includes one "bad" performance of 2' 27".

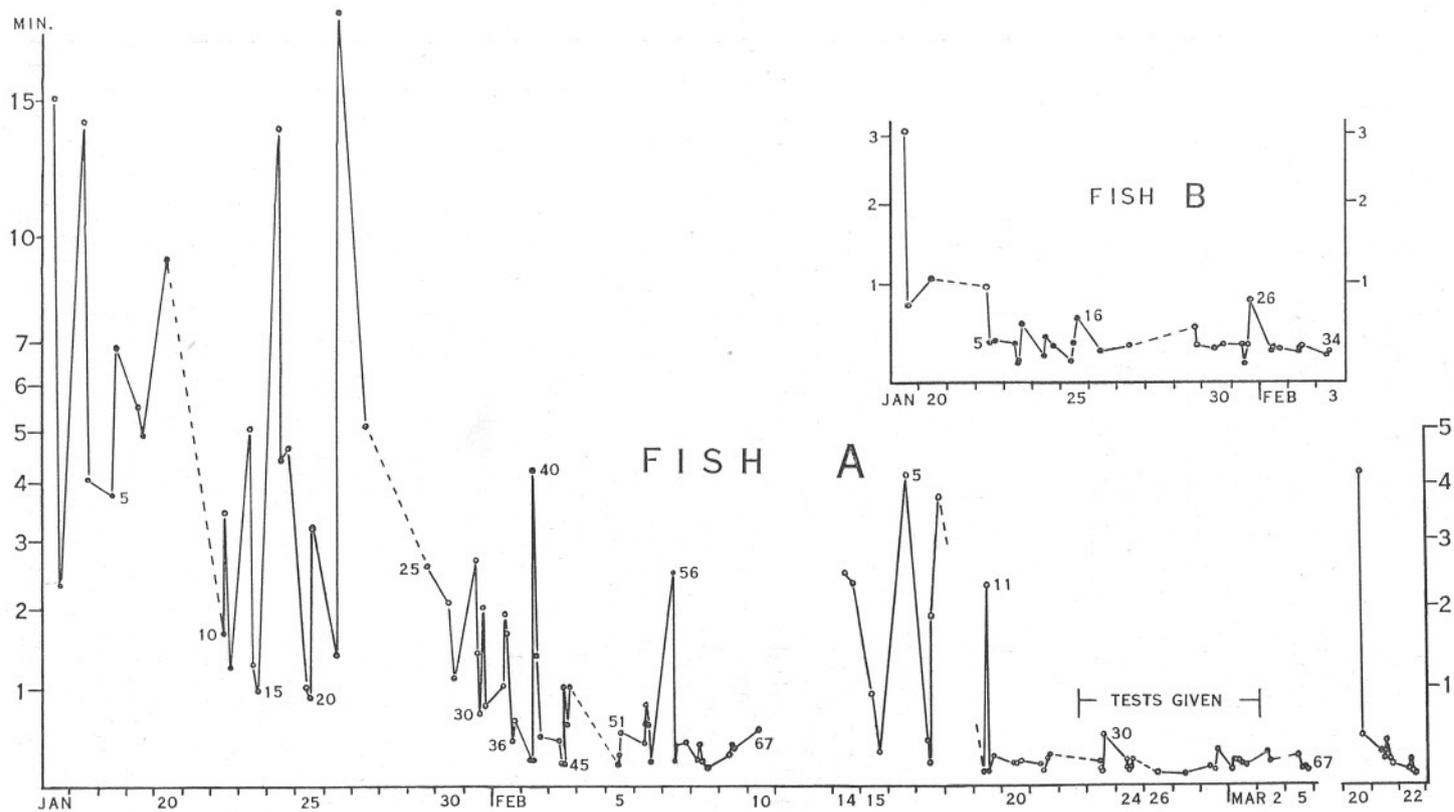


FIG. 5.—Learning graphs of fishes A and B. The duration of each normal trial feeding is plotted on a logarithmic time scale, and lines drawn between successive points. The line is broken when an interval includes one whole day on which no feedings were given. Serial numbers of the trials are placed at intervals along the graph.

was, on the whole, remarkably persistent in attacking the glass, even though the trial lasted several minutes. This was the first noticeable change in the fish's behaviour.

Another 18 trials passed without any further indication of improvement in efficiency. The average duration still showed no sign of decreasing. Trial 23 lasted over 19 minutes, during which time the fish gave no signs of having acquired anything, except the loss of the tendency to swim right away to other parts of the tank. It is all the more remarkable, therefore, that shortly after this a definite improvement became apparent. The curve (Fig. 5) shows a decided fall in its mean level at the point marked by trials 25 and 26.

Analysis of the results shows that at this point two changes in the behaviour occurred simultaneously which together made for a marked improvement in efficiency. (1) At this point there was the first real drop in the time spent at the start of the trial in attempting to reach the food directly. Previously these times had fluctuated a good deal and were sometimes very long. For trials 19 to 23 they still maintained the high average of 2' 20"; but in the period 24 to 29 they had dropped to 1' 05". (2) At this point the fish for the first time displayed a tendency to bear steadily leftwards down the glass, and this tendency was maintained.

The next "improvement" came at 36. The fish from this point onwards firstly, often moved straight down the glass leftwards as soon as it had started moving left, and, secondly, succeeded in passing the edge *at the first attempt* four times out of five. With respect to the latter feature no further improvement was shown.

Further stages in the acquirement of a more efficient response were as follows. By 45 the leftward movement had come to be almost invariably a sideways movement along the glass, wheeling movements round the edge having become virtually eliminated (see below). At 55 the tendency to move straight down the glass as at the first leftward movement was almost established, and at this point the second marked drop occurred in the time spent in attempts to reach the food directly.

The learned response involved a swimming leftward along the glass in a more or less continuous movement until the edge was reached, the fish "feeling" its way round by making constant contact with the surface. In this movement the fish was orientated either at right angles to the glass, or, more usually, making an angle of 45°, having turned half-left. In either case the food was in the range of vision of the right eye. With regard to the process by which this response was established, one point deserves comment. During the first 25 trials, when the fish only succeeded in getting round the edge by lucky random movements, two methods of accomplishing the feat were equally frequent. Either (*a*) random working over the surface happened to bring the fish to the edge and so sometimes

on and round, or (b) it happened to swim to the left and got round in a wide sweep. At 26, as has been seen, there was a sudden tendency shown to work down the glass in a continuous movement; that is to say, an efficient response began to develop out of method (a). Method (a) may be said to have started to acquire significance. But at the same time method (b) had been learnt in some measure, the fish sometimes turning sharply to the left and a further sharp right wheel bringing it round the edge. For a time, then, there was an antagonism between two methods. Eventually the response developed from (a) predominated—as in all other fish subsequently trained under the same conditions—and by 44 method (b) was practically eliminated. This antagonism no doubt hampered and delayed the smooth course of learning. It is possible, however, that the successful accomplishment of the trial through method (b) may have been partly responsible, through a “transfer of learning,” for an improvement in method (a) shown at 36, after which the fish normally got round at the first movement down the glass, having learnt to swim left for an appreciably long stretch.

A further complication occurred with respect to method (a), the movement along the surface of the glass. This was normally accomplished by the fish keeping more or less at right-angles to the glass, or turned half-left, the food being viewed through the right eye. But the first attempts in reaching the food after the first leftward movement were often made at an angle of 45° to the glass, the fish orientated *half-right* and the food in the field of *both eyes*. A certain antagonism between these two positions had therefore to be overcome. This was more clearly shown in fish B (p. 519).

In view of these complications, it is not surprising that the process of learning was long and not by any means straightforward. The action was learnt in a precarious way. Nevertheless the results obtained from other fish show that an efficient performance can be established before there is any stabilization of the actual movements performed or in the orientation adopted, and demonstrate that variation in the methods of making the detour *need* not set up antagonisms which impair the acquisition of a learned response.

Second series (trials B1 to 67). After an interval of four days, during which the fish was subjected to disturbance, trials were renewed. The fish proved to have lost a good deal of ground, but it was not long before it regained the efficiency acquired during the first series of trials.

The tendency to move leftwards was retained from previous training, but at first the fish was inclined to travel only for a short distance down the glass. A change came at 5, from which trial onwards it always carried on so as at least to come close to the left-hand edge. A further rather sudden change came at 10, after which the fish only rarely failed to pass

round the edge in its first leftward movement. After 10 there is only very slight general improvement in the action of moving leftwards.

Another retention from previous training relates to the time spent at the glass opposite the food before the first leftward movement. This period was short from the start of the second series, but there was a sudden and quite marked improvement after 9. The average duration from trials 5 to 9 was 11", while for subsequent groups of 5 trials the values were as follows: 7", 6", 7", 5", 5", 5", 4", 3". The change at 10 coincided with the improvement noted above with respect to the continuity of the leftward movement.

When the learned response had been thoroughly established, some experiments were made to test the extent of organization of the action. The experimental conditions were modified in certain respects, and the effect on the fish's behaviour observed. These "tests" are described below.

Third series (trials CI to II). After an interval of 15 days from the completion of the second series, trials were renewed on March 20 to 22. The first took over 4 minutes; but after this trial the fish rapidly improved. Trials 2 to 6 averaged 0' 21", and 7 to 11 averaged 0' 10".

Tests in which sight of food was interrupted. In trials B35 and 36 a prism was placed against the back of the glass, near the edge, in such a manner that, as the fish passed leftwards, the sight of the food was cut off without the intervention of an obvious partition. In the first trial the fish hesitated twice at the edge of the prism, but went round successfully the third time. In the second trial it went straight round first time. Thus it appeared that, for perfect performance of the detour response, the food need not be visible all the time.

In trial 38 a piece of mirror was placed at right angles to the glass, again cutting off the view of the food, and, instead, presenting the fish with a reflection of itself. The fish solved the trial perfectly successfully at first leftward movement. Similarly when the test was repeated (39). In the next trial, however, it stopped in front of the mirror and behaved as if its reflection had been detected. Trial 41 was once more performed efficiently; and trial 42, by contrast, resembled 40, the fish reacting energetically to its reflection.

These few trials showed definitely (1) that the fish was sensitive to its mirror reflection, and may be induced to react to it. But (2) in spite of this fact, the learned action may proceed normally, as in 38, 39, and 41, although the vision of the food object is replaced by the mirror reflection. The impetus of the learned action is evidently strong enough to overcome the attraction of the mirror reflection. These tests, then, serve to show that it is not merely inessential that the food be in sight all the time, but the action has strong enough impetus to progress in spite of distractions.

Tests in which the detour was extended. In these tests the fish had to pass two partitions instead of one. It was started from κ, instead of from L. The results are given below. In all eight trials the fish reached the food by working to the left. It thus passed first from κ to L, and then had to perform the normal course to which it had been trained, from L round to the food.

Average of previous 9 normal trials (L to food): $10\frac{1}{2}$ secs.

<i>Trial No.</i>	K to L.	L to food.	Total duration (secs.).
45	8	14	22
46	92	28	120
47	264	15	279
51	12	8	20
52	11	10	21
54	8	11	19
60	16	7	23
61*	(24)	(12)	(24)

It will be noted that the fish gave an excellent performance on the very first test, and with the outstanding exceptions of the second and third tests, showed that the conditions presented no special difficulty. The passage from κ to L was made in the same manner as the learned response from L to food, and was performed as rapidly. The lapse in trials 46 and 47 involved a temporary inability to pass from κ to L, and it is interesting to note that just previously the fish had been given a long unsuccessful trial from J, following which a temporary instability in its response appears to have resulted. It is, however, the efficient performance of six out of eight tests that is significant, and serves to show how a learned detour response can serve to facilitate greatly the response to a detour of greater complexity.

These tests gave a hint that the fish had acquired a tendency to move to the left rather than towards the right when meeting an obstruction, for when at κ it worked toward Q rather than P. Two tests in which the fish was started from J gave further evidence of this. From this position it could reach the food either by passing one partition to the right, or three partitions to the left. One of these tests (45a) was unsuccessful. The fish did not reach the edge o at all, and the trial was eventually abandoned. The other (61) was performed successfully in 2' 31", the fish *working round to the left*, and eventually reaching the food by the most roundabout route. The fish had evidently acquired such a strong tendency to move leftwards that it was unable readily to adapt its movements to conditions representing the mirror image of those to which it had been trained.

* Part of longer trial.

Fish B.

Length 7 cm.

Jan. 2, placed in experimental dish in an empty tank in the main laboratory, under conditions referred to on page 502. For a fortnight fed with *Mytilus* and pieces of *Polychaete* worm off the end of a wire, until it had become thoroughly habituated to this method of feeding. It took food somewhat more readily than fish A, which was investigated at the same time.

Jan. 17-18, first trials with the glass partitions, which however proved unsuccessful, the fish showing increasing "panic" on repeated contacts with the glass.

Jan. 19-Feb. 8, 48 experimental feedings.

Trained to plain glass obstruction, with short detour of 4.1 cm. Later transferred to detour of 6.5 cm., as presented to most of the other fish.

The fish proved more energetic than A, and at first was much disturbed on making contact with glass partitions. It was trained to a very simple detour. A plate of 8.3 cm. width was interposed between it and the food, the course on either side of it being left free. It had thus to pass sideways 4.1 cm. either to the right or the left.

The learning curve is given in Fig. 5. The averages of groups of five successive trials are as follows :

<i>Serial No.</i> <i>of trials.</i>	<i>Average</i> <i>duration.</i>	<i>Serial No.</i> <i>of trials.</i>	<i>Average</i> <i>duration.</i>
1-5	1' 15"	21-25	0' 18"
6-10	0' 20"	26-30	0' 25"
11-15	0' 19"	31-34	0' 15"
16-20	0' 25"		

After only 5 trials a level of efficiency was reached, and no further improvement was shown. A constant method of solving the trial was adopted. The fish first spent a little time in attempting to reach the food directly. It then began to bear to the right, all the time keeping orientated towards the food. It continued steady rightward movement until reaching the right-hand edge of the glass, passing which it swam straight forward to the food. Except for one of the earliest trials, it always made the short detour in this manner. The variations in the durations of the trials were largely due to variation in the time spent before bearing to the right. Once it had started sideways movement it almost invariably continued until the edge was reached.

The constancy of the level of efficiency after trial 4 is noteworthy. Though there was room for improvement, none was shown after this trial.

After 34 trials, the fish was given a longer detour, of the same type as that to which other fish were trained from the start. The only difference lay in the fact that it had to move round by the right instead of the left. (Food presented at κ , fish started from near corner D.) After 14 trials had been given the fish began to grow lethargic and training had to be discontinued. Nevertheless some significant results were obtained.

The average duration of groups of successive 5 trials was as follows :

1-5	0' 46"
6-10	0' 36"
11-15	0' 52"

The effect of the previous training was at once apparent. No random movements were made from the glass; there was strong tendency to move down the glass to the right, the fish keeping orientated towards the food; and the first three trials were performed by the method previously learned. At the same time, however, the fish showed some hesitation in moving continuously down the increased length of glass. There seemed to be a limit to the distance it would readily withdraw from the food. This hesitation did not decrease: rather it led to new reactions which upset the stability of the response.

From the fourth trial onwards it began to make turns towards the right, and to work down the glass at different angles. In some trials it reverted to the original behaviour, but these were rather less efficiently performed than others. Probably on account of a certain confusion in behaviour thus introduced, the duration of the trials, after first declining somewhat, became distinctly longer than when the fish was first presented with the 6.5 cm. detour.

Fish D2.

Length: 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28-Oct. 11, seven feedings given. Oct. 12, frame with glass plates tested in the tank; fish took food readily just after in spite of the disturbance. Oct. 13-Nov. 13, 45 experimental feedings.

Plain glass obstruction; detour of 6.5 cm.

The curve for the duration of trials is shown in Fig. 6. The average duration for successive groups of five trials is as follows :

<i>Serial No.</i>	<i>Average duration.</i>	<i>Serial No.</i>	<i>Average duration.</i>
1-5	2' 18"	26-30	1' 14"
6-10	2' 19"	31-35	1' 0"
11-15	6' 36"	36-40	2' 51"
16-20	3' 44"	41-45	2' 30"
21-25	2' 22"		

The experiments on this fish were abandoned, when, after 45 trials, it seemed farther off establishing a learned response than at the start.

This fish was decidedly "nervous" in the early stages, and tended to give shock reactions to the glass partitions in a manner not observed in other individuals. For some time it was only possible to give one trial a day. This effect, however, had worn off by trial 10, and the fish's behaviour was thence normal.

For the first few trials the fish showed a strong tendency to move to other parts of the dish, though it repeatedly returned towards the food. From trial 4 onwards, however, this tendency was only shown in a modified form or appeared only after the trial had lasted a considerable time. From this point the fish worked steadily, often actively at the glass, and was unusually persistent in its attacks on it.

With regard to the failure to establish an efficient response, certain features are worthy of notice. The earlier trials were mostly solved by

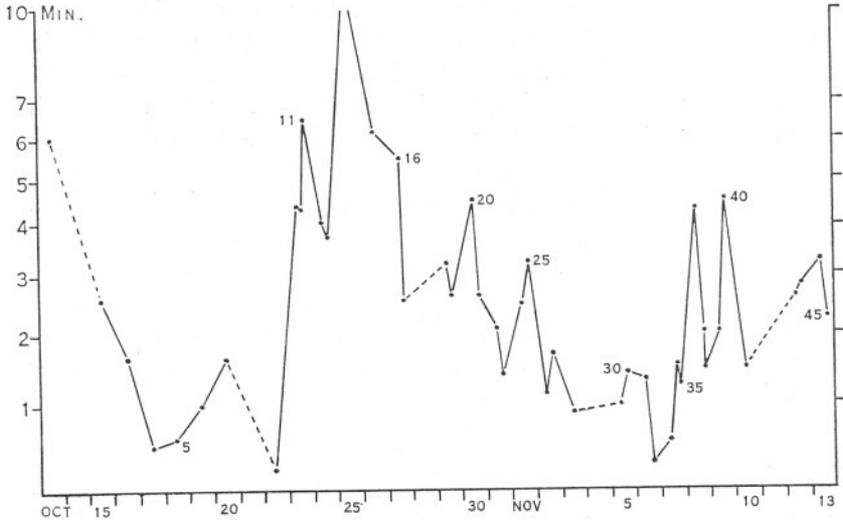


FIG. 6.—Graph of duration of trials of fish D2. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

the fish giving a left-turn, swimming left, and right-wheeling round the edge. The left-turn movement was thus apt to lead directly to a solution. During trials 3 to 12, 10 such left-turn moves were made, and no less than 6 were effective in this way. Yet this movement suddenly dropped out at this point. The same thing happened in the case of other fish which did eventually acquire an efficient response and is commented on at a later stage.

For a period, between trials 25 and 35, some improved efficiency was shown. Though, in the main, there was gradual improvement from 14 onwards, trials 17 and 26 mark two stages in which there was comparatively sudden change. The first point marks the complete disappearance of all random movements away from the glass, and at the same time the frequency of leftward movements along the glass (after the first) increased. The second marks quite a sudden permanent reduction in time spent in attempts to reach the food directly, another sudden increase

in frequency of leftward movements, and withdrawing movements from the glass (which had been a conspicuous feature of some earlier trials) quite suddenly disappeared.

The improvement was not maintained and a marked "lapse" occurred after 35. The trials now show an increase in time spent in attempts to reach food directly, before any leftward movement, a decrease both in frequency of leftward movements (after the first) and in their efficiency. There was also a return of withdrawing movements from the glass. It is interesting to note that the decrease in efficiency of leftward movements set in while their frequency was still increasing (trial 29); the lapse was thus to some extent forecast.

The performances during the last 10 trials, though comparable in duration with those of the earlier, differ in some other respects. Notably, there was no return to making random movements away from the glass, or to making left-turns. If the fish had "learnt" nothing else, it had acquired the habit of working persistently at the glass. Its responses to the situation, though relatively ineffective, had become more stabilized.

Fish D3.

Length: 5½ cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given. Oct. 13–Dec. 13, 83 experimental feedings.

Trained to plain glass obstruction; detour of 6.5 cm.

The curve for the duration of trials is given in Fig. 7. It will be seen that after trial 10 the curve sinks to a low level from which it sharply rises at intervals, representing intermittent inefficient performances. After 42, inefficient performances become more frequent, until at 51 a bad spell sets in during which the durations of the trials are even greater than at the start of the experiment. Towards the end efficiency is increasing considerably, and the fish is well on the way to establishing an effective response when the trials are eventually abandoned.

From 16 to 42 there was a spell over which the times averaged 12", if three intermittent "bad" trials, which stand out in marked contrast to the others, be omitted. During this period, then, the fish had produced an efficient response, on which, however, it appears to have had a precarious hold. The explanation of this, as well as some understanding of the bad lapse that set in, is forthcoming when the observations on the fish's behaviour are examined.

A peculiarity of the behaviour was the exceptional activity shown at the start of the trial. The fish set at the glass with a burst of energy, which, however, waned after half a minute or so. Unless it had passed the edge in this opening period of activity, the fish settled down to steadier, but still persistent, attempts to reach the food through the glass.

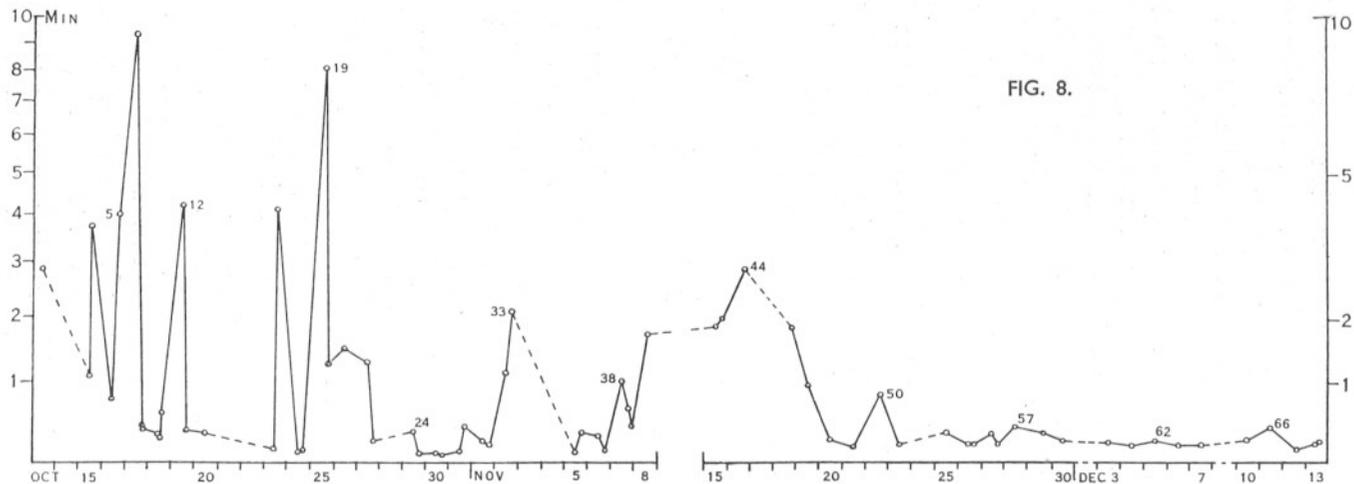
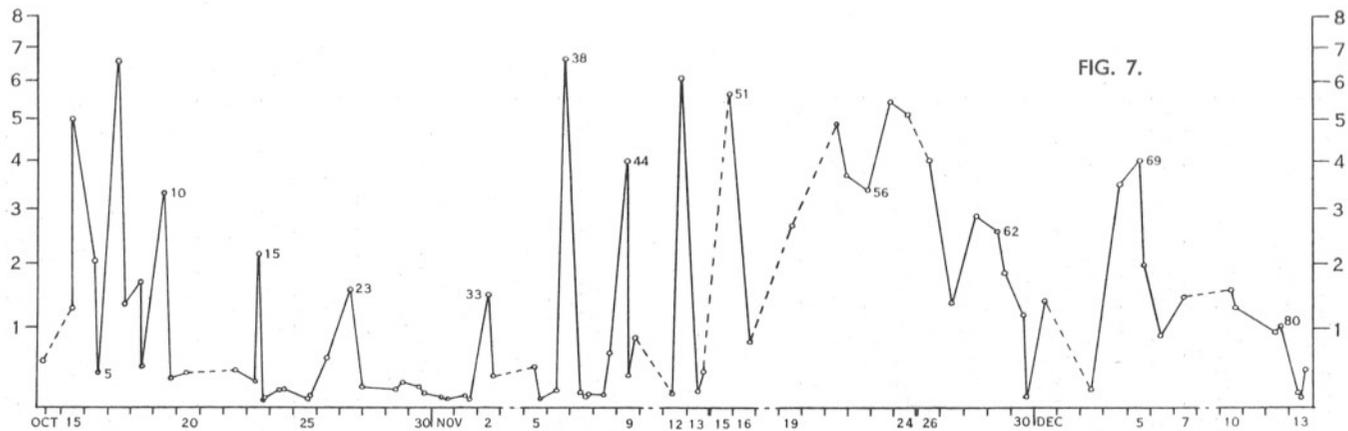


FIG. 7 (above).—Graph of duration of trials of fish D3.

FIG. 8 (below).—Graph of duration of trials of fish D4.

(A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

Another peculiarity was that the fish never made random movements away from the glass to other parts of the tank. It held persistently to its attempts at passing the glass obstruction. During the opening period of activity it was, from the start, inclined to work leftwards along the glass keeping orientated towards the food (as with fish B, p. 518). When less active it was less inclined to bear leftwards. The success of the trial, therefore, depended a good deal on the success of the efforts of the first half-minute. Several of the fish in early trials spent some time in attempting to pass straight to the food before bearing to one side. In the case of D3 the duration of this period was at a minimum level as early as the 4th trial.

The features of the behaviour shown in early trials might well have been expected to work together towards a rapid acquisition of an efficient response. And to a large extent this proved to be so. The one drawback, which was never adequately overcome, was the decrease in activity after the first half-minute. If the trial lasted beyond this period it was likely to be prolonged considerably. The conspicuous intermittent "bad" performances were due to this cause.

Compared with that of other fish, the behaviour was remarkably uniform and invariable. Also there was a decided indication of a cycle of responses repeated in each trial, if prolonged. The more energetic opening "attacks" on the glass at the start led the fish to bear left in a very short time and to bear left far enough to get near or reach the edge round which it had to pass. Working up and down the glass it was liable frequently to reach the edge during the opening period. All the time the fish kept approximately orientated in the direction of the food. As activity decreased the extent of glass traversed also decreased, and the fish settled to a quieter "attack" on the glass in the middle region of the plate. The occasions on which it came as far left as the edge now became less frequent, and the chances of achieving a solution decreased considerably. It was not, as a rule, until the trial had lasted some while that any other movements were given. These consisted in sharp turns either to the right or the left. It is noteworthy that all the first 6 trials were solved as a result of a complete or partial left-turn. But the success of the left-turn movement, as in the case of other fish, did not lead to the establishing of this method of solution. After trial 6 the left-turns were almost entirely of a partial kind, and they soon became merged in the general leftward movement along the glass. As to right-turns, the fish had a spell of these in trials 3 and 6, but only very occasionally in other trials.

The short durations of 9, 11-14, and 16 onwards were the result of the edge being passed during the more active spell. The fish, however, took some time to acquire the habit of reaching the edge, and passing it, in one continuous movement.

The bad lapse which set in between 40 and 50 was associated with an entirely new feature which appeared for the first time in 48. In that trial the fish began repeatedly to withdraw straight back from the glass. This movement was quite a "useless" one and tended to check leftward movement. It figured largely in trial 51 and from 53 onwards, when it was regularly given after the first half- or three-quarter minute. In 54, for example, the fish spent over 4 minutes continuously moving backwards and forwards in the middle region of the glass without once getting near the edge.

It might at first sight be supposed that the development of this useless habit was responsible for the lapse. But it is probably more true to say that it developed as a *result* of the lapse, being a symptom rather than a cause. Trial 44 can be said to mark the beginning of the lapse: the fish took 4 minutes to reach the food, but during the time did not give the withdrawal movement at all. The inefficiency of the performance resided in the fact that the fish showed disinclination to move leftwards, and, when it did so, to move far enough.

The improvement towards the end of the series was marked by a reduction in the time spent in making withdrawal movements, and the increased tendency to make half-left turns towards the edge R. Most of the later trials were solved by the latter movement.

Four tests were given with the squared glass substituted for the plain glass (see p. 561).

Fish D4.

Length: 4 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28–Oct. 12, seven feedings given, food taken with exceptional eagerness. Oct. 13–Dec. 13, 69 experimental feedings.

Trained to plain glass obstruction; detour of 6.5 cm.

The curve for the duration of trials is given in Fig. 8. The averages for successive groups of five trials are as follows:

<i>Serial No.</i>	Average duration.	<i>Serial No.</i>	Average duration.
1–5	2' 35"	36–40	0' 29"
6–10	2' 07"	(Interval)	
11–15	1' 08"	42–45	1' 53"
16–20	2' 44"	47–52*	0' 22"
21–25	0' 42"	53–57	0' 17"
26–30	0' 11"	58–62	0' 15"
31–35	0' 46"	63–67	0' 15"

In spite of the fact that several good performances were given during the first 20 trials, and that trials 25 to 28 were performed exceptionally well, it was a considerable time before a consistent response was established.

* Trial 48, on consideration, omitted. Fish sluggish, behaviour abnormal.

The fish worked at the glass energetically, and was apt to make sudden darts. Its movements were rather variable. In early trials it sometimes turned left and swam into the region of corner D, and on five occasions reached the food by swimming up from this corner. It also showed a tendency to make right turns, which sometimes took it into the region of corner C, and in four trials it moved from there into K.

The movements which took the fish round the edge R to the food varied considerably. Sometimes the fish kept orientated towards the food, withdrawing along the glass surface obliquely leftward; sometimes it turned partially to the left, keeping the food within range of vision of its right eye; sometimes it turned left and wheeled round the edge. And there were modifications of these three main methods. It is noteworthy that, after 12, the third movement proved an effective method of solving the problem. Yet for a long time it was only occasionally attempted.

In spite of the variable quality of its reactions to the obstruction, the fish, after 23, gave a series of performances in which its methods were consistent (the first of those enumerated above). At first, too, it seemed to have established a consistently *efficient* response, but lapses set in. By Nov. 7-8 the fish appeared definitely to be in sub-normal health, and after 41, the series of experimental feedings was interrupted. Trials were suspended until Nov. 15, during which period the fish was fed normally in an ordinary manner, off the wire.

When trials were resumed (42) the fish had recovered normal activity. Trials 42 and 43 were solved in just under two minutes, both by the third method. The fish, then, had lost the previously established tendency to make the detour by method 1. But, at the same time, it had retained certain features from its previous training. (i) It had come to move leftwards almost immediately, never spending more than 8 seconds in attacking the glass in the original position; and (ii) it had come to keep up a persistent attack on the glass not making any movements away to other parts of the tank.

As indicated by the figures for the duration of the trials, a sudden change came at 47, which marked the beginning of a series of efficient performances. A learned response can now be said to have been established: the sudden improvement is noteworthy. It is also of interest to note that the variable quality of the fish's responses, which had reappeared after 43, persisted for some time after efficiency was established. The method of solution was not stabilized until efficiency had been attained. The significance of this feature is discussed on page 551. Towards the end the left-turn-and-right-wheel movement tended to predominate.

Fish D5.

Length: 5 cm.

Sept. 25, transferred to experimental dish. Sept. 27, P.M., took food well. Sept. 28-Oct. 13, eight feedings given. Oct. 15-Dec. 13, 102 experimental feedings.

Trained to plain glass obstruction: detour of 6.5 cm.

The curve for the duration of trials is given in Fig. 9. The averages for successive groups of five trials during training are as follows:

<i>Serial No.</i>	Average duration.	<i>Serial No.</i>	Average duration.
1-5	11' 36"	21-25	0' 36"
6-10	5' 51"	26-30	0' 13"
11-15	3' 18"	31-35	0' 14"
16-20	0' 48"	36-39	0' 12"

Before the 40th trial an efficient learned response was securely established, and after this various tests were performed on the fish. In spite of apparently hopeless efforts in early trials, this fish emerged as the most proficient performer of those trained to the plain glass obstruction.

The earlier performances were outstandingly "bad." The fish was excessively disposed to wander over various parts of the tank, particularly in the right-hand part, and only eventually reached the food when it happened to move round near it. After twelve trials had been given it seemed no nearer a learned solution of the detour than at the start, and appeared to be a hopeless case. Yet by the 18th trial it was well on its way to acquiring an efficient response, which was established from 24 onwards. An improvement came with comparative suddenness, following on a remarkable change in the fish's behaviour. The change may be said to have dated from the end of 13.

The manner of the fish in early trials contrasted sharply with that of fish D4. Its movements were characteristically leisurely and it was not subject to more violent bursts of activity. In contrast with fish D1 (p. 531), however, it had little tendency to persist in working against the obstruction, but constantly reacted by turning and swimming away from the glass to some other part of the tank. However frequently it might return in the direction of the food, this lack of persistence remained. The solutions of the early trials were more conspicuously fortuitous than in the case of any other fish. Of the first twelve, five involved swimming up from corner D, in three the fish swam in an arc between R and D from the front of the tank, and in three an approach was made from corner A. Only in two (5 and 9) did the fish keep at all close to the glass in moving leftwards round the obstruction, in both of them turning left and wheeling round to the right. No habit was developing which could provide a basis for a learned response.

Trial 13 progressed on the same lines as the previous inefficient trials. The fish had had three short spells at the glass, when random movements brought it into the right side, and thence to the back part of the tank.

It moved round again to corner c, and, 2' 15" from the start of the trial, moved up to the food in the original position. It then behaved in a changed manner: it bore leftwards, keeping close to the glass, continued till the edge was reached, and passed the edge at 2' 25", snapping at the food immediately after. It had never made the detour in this manner before.

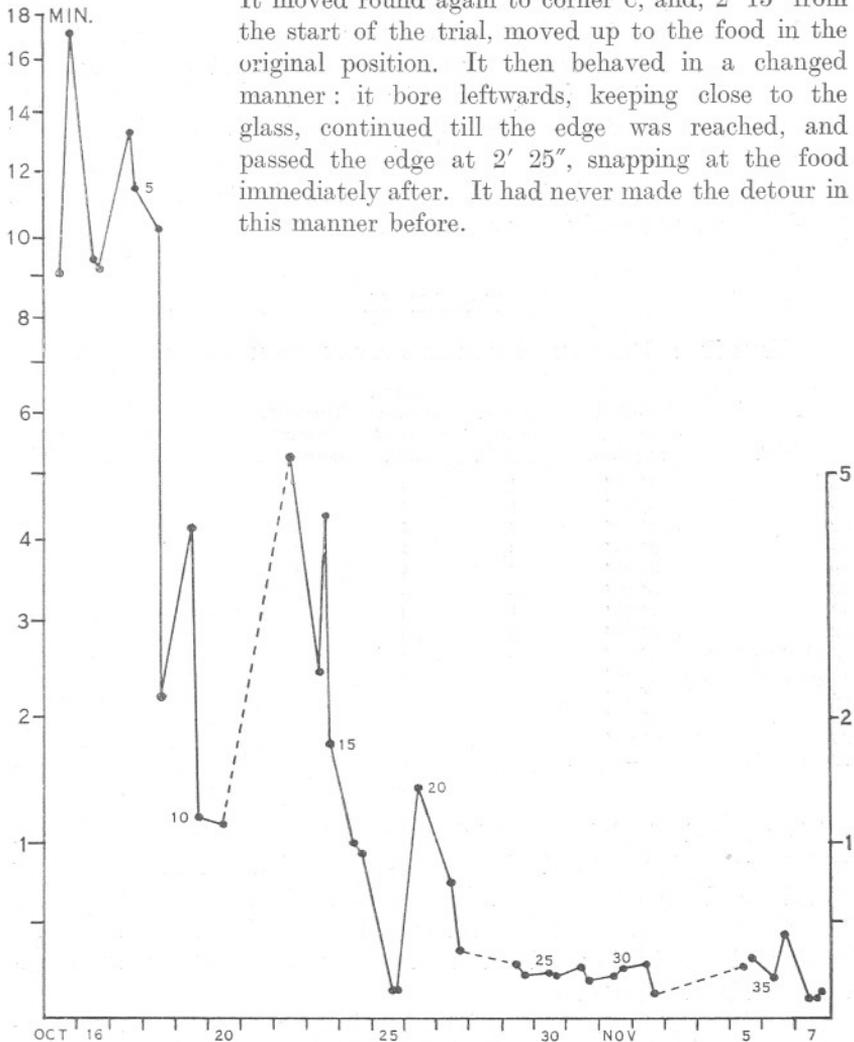


FIG. 9.—Graph of duration of trials of fish D5 during training. (A broken line is drawn over intervals which are greater than one whole day. Serial numbers of trials are placed at intervals along the graph.)

The type of behaviour shown at the end of 13 persisted in all subsequent trials. Though 14 was not solved until over 4 minutes, the whole of the period was occupied with leftward movements along the glass. Though

the fish had still to learn to work more continuously leftwards and to desist from minor withdrawing movements, the contrast between this performance and preceding trials was most striking. And the changed behaviour was permanent. Persistent working over the middle and leftward side of the glass almost completely replaced other movements. The reaction of turning sharply to right or left and swimming away from the glass suddenly and completely dropped out. The data given in Table II illustrate this feature. Moreover, turning movements of any sort were only very rarely given. Only two full left-turns were noted in the whole series of trials from 14 to 39, and no right-turns at all. Even half-left turns were only very occasional.

TABLE II.

FISH D5: RANDOM MOVEMENTS AWAY FROM OBSTRUCTION.

<i>Trial.</i>	Period spent at glass.	Turns L. toward corner D.	Turns L. toward front of tank.	Turns R. toward corner C.	Remarks.
5 *	1' 47"	1	—	4	
6	8' 10"	1	7	7	
7	c. 7' 00"	7	7	4	
8	2' 05"	3	4	2	
9	4' 05"	3	4	3	
10	0' 30"	—	—	2	
11	1' 05"	1	3	—	One withdrawal.
12	c. 4' 00"	2	5	3	
13 (first period)	0' 42"	—	2	1	
13 (second period)	0' 10"	—	—	—	
14	4' 20"	—	—	—	Several withdrawals.
15	1' 44"	—	—	—	" "
16	0' 58"	—	—	—	
17 onwards	—	—	—	—	No withdrawals after 21.

The method of solving the trial achieved for the first time at the end of 13, by working leftwards close to the obstruction and finding the way round the edge R, characterized all subsequent trials. It has to be noted, however, that the actual movements which took the fish round the edge still varied considerably, and continued to vary after efficiency in performance had been acquired.

After the change of behaviour, it was not long before a marked improvement in the efficiency of the fish's performance became noticeable. Trials 18 and 19 both were solved in less than 10 seconds. After 21, trials were consistently good. The steady improvement is indicated by the figures given in Table III. It will be noted that leftward movements increased both in frequency and in efficiency.

TABLE III.

IMPROVEMENT IN PERFORMANCE OF FISH D5.

Trial Serial No.	Total duration.	Leftward movements per min.			Ratio unsuccessful : successful— (ii) over (iii).
		(i) Total per min.	(ii) Un- successful.	(iii) Successful.	
14	4' 21"	1.6	1.4	0.2	6
15 to 20	5' 13"	3.3	2.1	1.1	1.8
21 to 39	4' 18"	7.2	2.8	4.4	0.6
Period of Maximum efficiency. Normal trials, between 80 and 101	1' 36"	11	2	9	0.2

Tests.

Food presented on the right. From 40 onwards certain tests were performed on the fish which were intended to throw light on the nature of the learned response. One series of ten, carried out at regular intervals between 40 and 58, consisted in presenting the fish with, so to speak, a mirror-image of the conditions to which it had been trained. The food was presented at κ , and the fish had to move to the right round edge q . The results are summarised in Table IV.

TABLE IV.

FISH D5: TESTS IN WHICH FOOD WAS PRESENTED ON THE RIGHT OF THE DISH.

Test Serial No.	Trial Serial No.	Duration		Remarks.
		Test.	Normal trial.	
A 1	40, 41	13' 00"+	0' 10"	
2	42, 43	0' 26"	[2' 43"]	
3	44, 45	0' 22"	0' 28"	
4	{ 46	0' 10"	0' 12"	
5	{ 47, 48	1' 02"		
6	49, 50	0' 31"	1' 02"	
7	51, 52	1' 53"	1' 36"	Very marked tendency to withdraw
8	53, 54	10' 00"+	0' 17"	[appears.
9	55, 56	14' 00"+	2' 25"	Again marked tendency to withdraw.
10	57, 58	4' 15"	0' 25"	" " " "

The times marked with a plus sign indicate that the trial was abandoned before the fish reached the food.

In all cases the test trial was given first, followed by a normal one. An unfortunate result of the tests was that the normal performances were somewhat upset, one conspicuous bad habit developed in the former—that of withdrawing repeatedly from the glass—being transferred to the latter.

Nevertheless one or two definite points emerge. In the first place, the performances of the tests are seen to fall sharply into groups. (1) The fish proved quite incapable of giving adequate rightward movements, and the behaviour in the tests differed conspicuously from that in the normal

control : these tests include 1, 8, 9, and 10. (2) There was no significant difference in the performance on the two sides, and the learned behaviour can be said to be completely transferred : viz. trials 2 to 7. The fish thus exhibited two quite distinct behaviour patterns under the new conditions.

Secondly, the fact that the fish was capable of exhibiting transfer of learning without having to learn the new detour anew is worthy of notice. Tests 2, 3, and 4 were all performed as efficiently as could have been expected were transfer of learning a reality. Also it may be noted that the first test was all but solved in an extremely short time, the fish just failing to pass the edge at 5" (after which it never moved to the right again).

A "bad" habit, involving the useless movement of withdrawing repeatedly from the glass for a short distance, appeared first in tests 1 and 7 and was again shown in the normal trial which followed the latter. The movement became conspicuous in trials which followed, and a series of normal trials had to be given to train it out. After 67 normal efficiency was re-established. Evidently, then, the tests set up a certain instability in the fish's behaviour.

Fish started from other parts of dish. Between 74 and 102 the tests consisted in starting the fish from some part on the right-hand side of the tank, the food placed in the normal position. The fish thus had to make a longer detour, and two courses were opened to it, either round to the right and up to food passing edge 0, or round to the left. It was found that the fish sometimes took one route, and sometimes the other. The main feature shown was that the passage round to the right took, on the average, a longer time, and evidently presented greater difficulties, than that to the left. This is seen from the figures given below, derived from combining all the tests, and averaging the times spent in reaching the food from three starting-points. A large difference is seen between the rightward and leftward courses. Evidently, then, the learned response had established a facility for leftward movement.

TABLE V.

FISH D5 : COMBINED RESULTS FROM TESTS IN WHICH THE
DETOUR WAS EXTENDED.

The figures denote average of time taken to reach food from the
positions indicated.

From position	BF	EB	
	2' 22" ———→	1' 41"	Rightward movement.
	0' 46" ———→	0' 31" ———→	0' 09" Leftward movement.
From position	BF	FC	GC

The end part of the rightward course, round the edge o, resembled a mirror-image of the normal conditions (passage from GC). It is therefore comparable to the conditions presented in the first series of tests, in which the fish had to make a passage round q. It may be noted that the fish's behaviour in the first two trials (73 and 79), in which it had to find its way round o, compared with its behaviour in the former tests. On the first occasion it failed to get round o at all, showing no inclination to bear to the right. The second showed complete transfer, the performance being accomplished efficiently in 10 seconds.

The interpretation of the process of learning exhibited by the fish is further considered in the discussion (pp. 549-552).

Fish D1.

Length: 5½ cm.

Sept. 25, transferred to experimental dish; P.M., took food. Sept. 27-Oct. 11, seven feedings given; soon came to take food readily. Oct. 12, frame tested in dish; disturbance sets up fright reactions in the fish, which would not take food immediately after; but fish took food readily two minutes later. Oct. 13-19, seven feedings. Oct. 20-Dec. 7, 61 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black strip, ½ cm. wide. Detour 6.5 cm.

The curve for the duration of trials is shown in Fig. 10. The average duration for successive groups of five trials is as follows:

<i>Serial No.</i>	<i>Average duration.</i>	<i>Serial No.</i>	<i>Average duration.</i>
1-5	1' 07"	26-30	0' 48"
6-10	3' 33"	31-35	1' 05"
11-15	4' 19"	36-40	2' 26"
16-20	0' 55"	41-45	2' 21"
21-25	2' 28"		

The fish was characteristically a steady worker, moving slowly and deliberately. It never exhibited any marked bursts of activity. From the start it showed a tendency to work persistently at the glass, and never moved off to the right-hand side of the tank.

The only movement it made away from the glass involved a full left-turn and passage to corner D or to the front of the tank. During the earliest trials, twice did the fish swim up to the food from corner D, and on three occasions a full left-turn followed by a right-wheel took the fish round the edge R. But after the 6th trial the left-turn movement suddenly dropped out of the fish's repertoire and was only given on one other occasion during the next 36 trials.

As the above figures indicate, the fish failed to establish a learned response. There were two periods in which improvement appeared to be coming, but the promise was not fulfilled. And this in spite of the fact that the fish's behaviour was perhaps more stereotyped than in any other

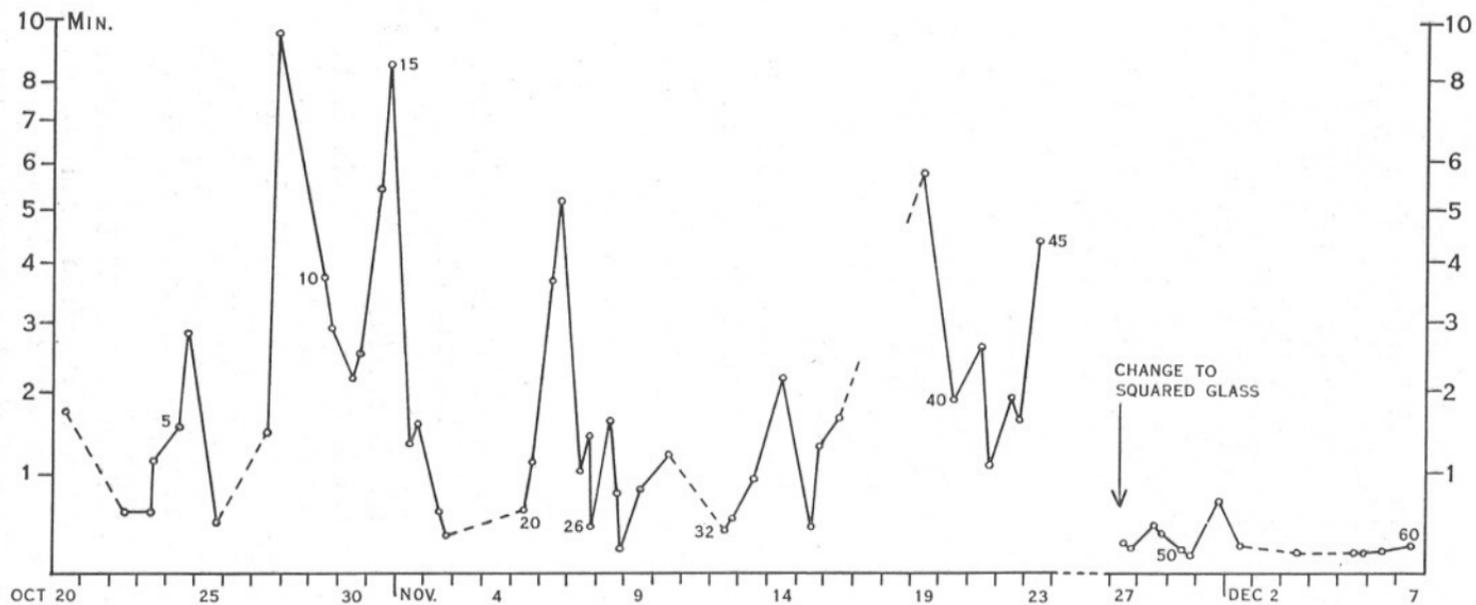


FIG. 10.—Graph of duration of trials of fish D1. Note the sudden change to an efficient performance when squared glass was substituted for plain glass (see p. 561). Two normal trials given the latter period were abandoned unfinished at 3 minutes.

fish. With the exception of the left-turn movements mentioned above, it kept remarkably uniform throughout. The fish settled into a habit of reacting to the obstruction in a certain manner which eventually led to its passing the edge. Yet the performances did not consistently improve.

Some tests were performed on this fish in which the plain glass was replaced by another on which a meshwork of fine lines had been scratched (p. 511). The results were striking, the fish giving a series of perfect performances, showing that something had been learned during the first 45 trials. These results are dealt with on pp. 560-561.

This fish gave no evidence that the black edge of the glass had any effect in facilitating the passage round the detour. Neither were any special reactions given to the band, nor was the fish induced to perform movements different from those given by other fish against plain unbordered glass.

Fish D6.

Sept. 25, transferred to experimental dish: P.M., took food with gentle coaxing. Sept. 27-Oct. 18, 13 feedings given. Oct. 19-Dec. 13, 75 experimental feedings.

Trained to plain glass obstruction, with glass bordered on top, bottom, and at left edge with a black stripe, $\frac{1}{4}$ cm. wide. Detour 6.5 cm.

The curve for the duration of trials is shown in Fig. 11. The average duration for successive groups of five trials is as follows :

<i>Serial No.</i>	<i>Average duration.</i>	<i>Serial No.</i>	<i>Average duration.</i>
1-5	1' 34"	41-45	1' 04"
6-10	4' 12"	46-50	1' 05"
11-15	5' 18"	51-55	0' 45"
16-20	4' 58"	56-60	0' 44"
21-25	3' 28"	61-65	0' 40"
26-30	1' 06"	66-70	0' 42"
31-35	0' 58"	71-75	0' 54"
36-40	1' 08"		

The durations thus settle down to a uniform average level of about $\frac{3}{4}$ minute. This comparatively high value is due to the fact that the fish learned the alternative circuitous path to the food, moving to the right and passing three partitions (Fig. 1, partitions Q, P, and O). D6 was the only fish to give this curious result.

It is of special interest to examine the early behaviour to discover the steps which led to the acquisition of the response. Careful analysis of the movements made by the fish during early trials has shown certain features which can only be summarized here.

(i) From the start the fish had a tendency to react to the glass by making sharp turns to the right or left. The first four trials were solved as a result of a left turn ; in two cases the fish wheeled widely round the edge, in two it swam into corner D and up to the food from that point.

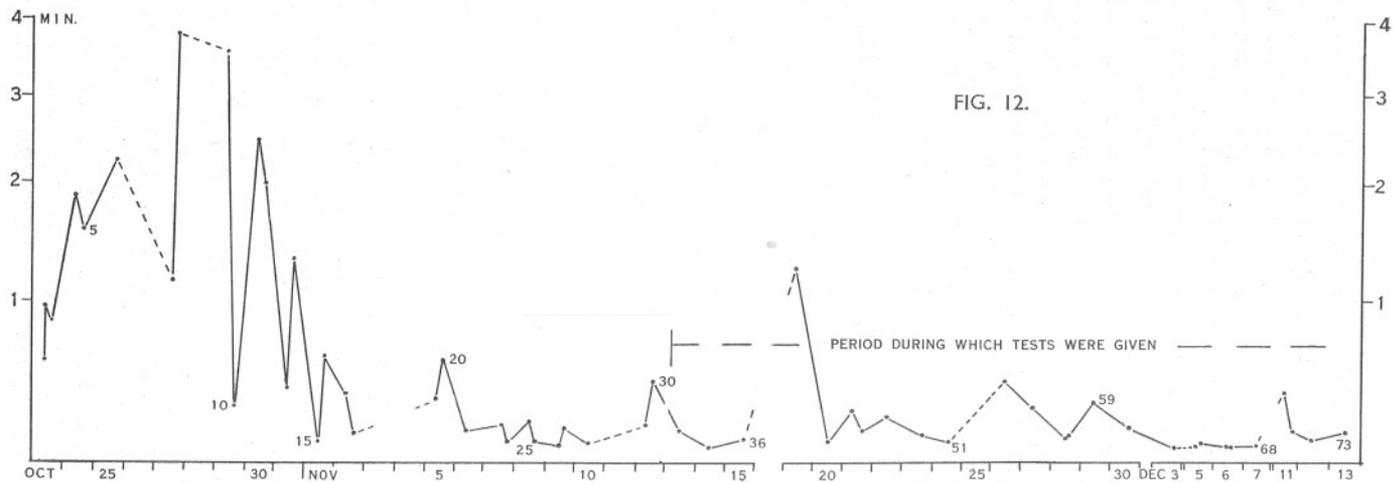
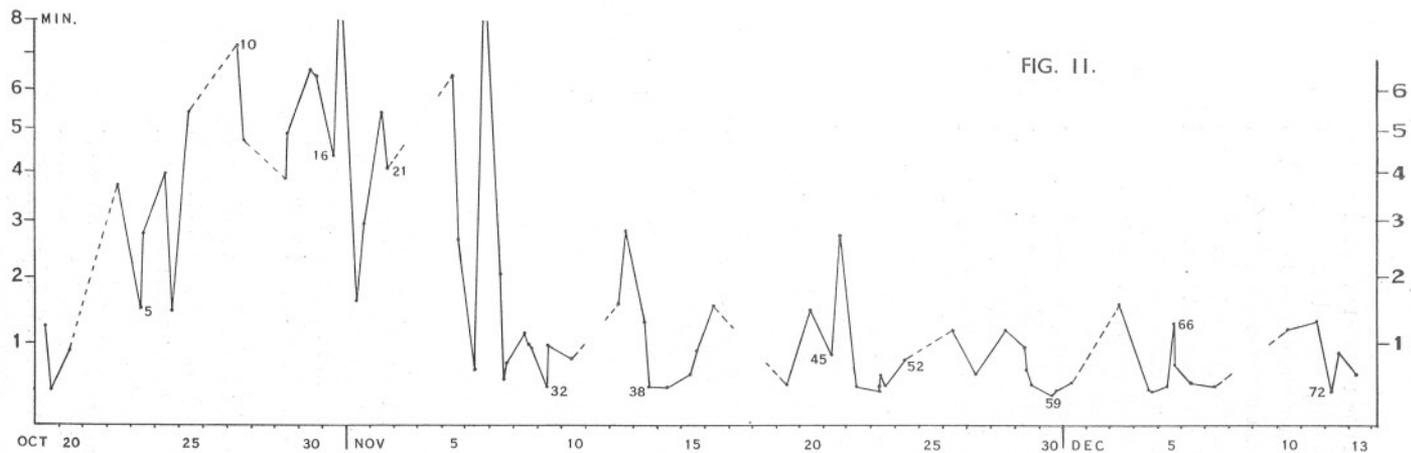


FIG. 11 (above).—Graph of duration of trials of fish D6, which acquired the habit of making the detour by the roundabout route.

FIG. 12 (below).—Graph of duration of trials of fish D7. From Nov. 13 onwards various tests were regularly given: only the normal control trials are given in the graph.

(ii) A new feature of behaviour appeared in trial 4: the fish began repeatedly to withdraw from the glass along the line of its approach (i.e. back in the direction of corner c). This trait persisted and came to be an outstanding peculiarity of the behaviour of this fish, normally characterizing the opening period of almost all trials from 4 onwards.

(iii) Left-turn movements, occasionally given in early trials, were very successful in leading to a solution. Yet they became less and less frequent, and virtually disappeared after trial 13. Several other fish showed this feature. Right-turn movements were more frequently given than left turns, and their frequency, if anything, increased. This feature was not shown by any other fish. It is evidently connected with the fact that the right-turn movement became associated with the withdrawing movement mentioned above.

(iv) Almost as soon as the withdrawing movement appeared, right-turn movements became associated with them. The effect was that the fish now frequently turned past edge q into the region κ . Other fish in early trials occasionally found their way into this compartment, but none so persistently as D6. From this position the fish almost always passed farther to the right, round into region j. Here it once again found only a single partition between itself and the food, and further movement to the right usually took it round the edge o. From trial 5 onwards the fish normally reached the food from this side of the tank.

(v) Finally, the fish showed exceptional disinclination to bear leftwards along the glass partition in its first assaults. This movement in fact was only given on three occasions during the first 10 trials (as contrasted with some 40 full turns). On first making contact with the glass opposite the food, the fish began withdrawing movements almost at once, and soon found its way into compartment κ .

The tendency, then, to withdraw and bear right (in spite of the success of left-turns in the earliest trials) resulted in the fish working round the tank to the right and approaching the food from the direction of A. Trials 5, 6, 8, 9, 11, and 13 were solved in this manner. Moreover, from this point onwards this course was invariably taken, and came to be followed with increasing efficiency.

It was some time, however, before any real improvement could be noticed. The time taken to reach compartment κ varied from 5" to over 4 minutes, and frequently the fish moved back round q. Occasionally, too, it would pass back into κ after reaching j. The time spent in circumventing edge o varied from 31" to 3' 39". Eventually, a rather noticeable improvement came suddenly at 23. From this trial onwards the course was followed continuously: only on one occasion (25) did the fish move back from region κ . The passage from q to p was now performed with very little hesitation, the time taken not exceeding 13", and falling to an average

level of 10", gradually decreasing to 6". The time spent in making the passage round o for a period of 20 trials did not exceed 35", with a minimum of 9". Efficient performances of total duration between 25" and 40" became increasingly frequent.*

As time went on the fish became increasingly adept at threading its way round the glass obstructions, until it was not far short of acquiring a complete co-ordinated response. It is probable that, with repetition, co-ordination of successive motor responses was occurring to some extent. Just before trial 46, during a delay in the presentation of the food, the fish was observed to swim round the whole course in about half a minute, though there was no food present. At trial 56, and again on the last day that experimental feedings were given, the fish swam the whole course on its own initiative in the minimum time of 25".

Certain tests with this fish deserve notice. In the first place it was found that the black border on the glass plate SR could be removed without the least effect on the reactions of the fish. From trial 50 onwards plain glass was always used. In view of comparable evidence from fish D1 (p. 533), it may be inferred that the existence of this band does not aid the fish in perceiving the glass plate as an object.

Secondly, valuable evidence was obtained that the passage round the glass maze to the right was not dependent on influences external to the dish—for instance, such impressions of objects beyond the maze as may have figured in the fish's visual field. In trial 59 the frame was reversed, the fish started from A, and the food presented at K. The relations of the fish and food to the maze were thus unaltered, but the fish had to swim away from the light and towards the observer. The fish gave an exceptionally efficient performance, reaching the food in 22". The same conditions were repeated next trial (60) and again the fish traversed the route with little hesitation, reaching the food in 25". Further, it was found that, in normal trials, the position of the light could be varied without any effect on the fish's response. Evidently then, the fish's movements were made relative to the food and frame and were independent of features external to it.

With this fish, learning as it did a comparatively long detour, unusual opportunities were afforded for examining the learning of different parts of the route. If backward association occurred (see p. 553) it might be expected that the last part (passage round o) would be acquired first, and

* Viz. :

<i>Serial No. of trials.</i>	Number of efficient performances.	<i>Serial No. of trials.</i>	Number of efficient performances.
21-30	2	51-60	6
31-40	4	61-70	6
41-50	4		

the efficient performance of movement into κ acquired last, only after the passage round p and o had become a fully co-ordinated movement. Analysis of the records shows no indication of any feature of this sort.

The route is conveniently divided into three sections. (1) Start of trial to passage round q ; (2) passage round q to passage round p ; (3) passage round p to passage round o . All through, the second section was more quickly and efficiently traversed than either of the others. The average times (in secs.) for successive five trials after 25 were 10, 9, 8, 6, 8, 9, 6, 6, 7, with no abnormally long times to overweight the average value. The corresponding times for the passage from p to o (3) were 64, 27, 21, 33, 27, 21, 20, 22, and 34. It appeared evident that the closer proximity of the food when the fish reached position r acted as a hindrance to the efficient passage round o . Again, though both for a time varied considerably from one trial to another, the duration of the final passage from p to o was all along somewhat greater on the average than that from the start to q (section 1). The final section of the detour therefore presented greater difficulties than any other. And though the efficiency of performance of the different parts increased in rather too fluctuating a manner to show any definite precedence for any one, it can at least be said that the latter section was certainly not learned in advance of the rest.

Fish D7.

Oct. 10, transferred to experimental dish from another similar dish. Oct. 13–Oct. 22, 7 feedings given. Oct. 23–Dec. 13, 73 experimental feedings.

Trained to glass marked with meshwork of fine lines (p. 511). Detour 6.5 cm.

The curve for the duration of trials is shown in Fig. 12. The average duration of successive groups of 5 trials during uninterrupted training is as follows :

<i>Serial No.</i>	<i>Average duration.</i>	<i>Serial No.</i>	<i>Average duration.</i>
1–5	1' 10"	16–20	0' 25"
6–10	2' 13"	21–25	0' 10"
11–15	1' 17"	26–30	0' 12"

This fish proved a good subject. It worked actively and persistently, was not easily distracted, and was not given to making erratic movements. It seldom made any movements away from the glass to other parts of the tank, and on the rare occasions when it did so, it soon returned to the glass.

During the first three trials the only reactions given after continued failure to reach the food direct were full turns to the right or left. Each of these trials was solved in under a minute as a result of the first full left turn.

A complete change of behaviour was shown in the next four trials,

which were less successfully performed : the fish now worked close to the surface of the glass, and showed but little tendency to turn to the side. It eventually worked its way round the edge *r*. During these trials the first indication was obtained that the fish detected the lines on the glass, for its passage down the glass was jerky, and it appeared definitely to move from one square to another.

In the trials that followed there reappeared a tendency to give full turns, predominantly to the left. Between trials 10 and 20 a steady improvement took place, and 21 marks the onset of a spell of uniformly efficient performances.

The period of improvement was marked by an increase in both frequency and efficiency of left-turns, right-turns and other movements dropping out. The method by which the fish passed round the obstruction was constant from 9 onwards : it turned full-left, swam left, and wheeled to the right round the edge. This response became established.

There are two noteworthy features in connexion with this learned response. Firstly, the response is one which *other fish, trained to the plain glass, proved incapable of establishing*, although all performed several early trials successfully by this manoeuvre (see p. 548). Secondly, the fish soon came to give the left-turn movement on its first passage up to the food before first coming in contact with the obstruction. This never occurred in the case of fish trained to plain glass. The fish turned left regularly on reaching a point 2 to 3 cm. distant from the glass ; and this may be taken as a good indication that it detected the pattern of lines at this point. No doubt the pattern also served as a guide to the edge of the glass, and enabled the fish to wheel right at the correct moment. At any rate, the contrast between the behaviour of this fish (together with D8, p. 539) and that of other fish is a striking fact.

Tests in which food was presented at κ. Between 31 and 52, eight tests were performed in which the conditions presented a mirror-image of those to which the fish had been trained (as with D5, p. 526).

TABLE VI.

TESTS WITH FISH D7.

Food presented at K, fish started from D.			Plain glass.		
Nos. of trials.	Duration.		Nos. of trials.	Duration.	
	Test.	Normal.		Test.	Normal.
31, 32	0' 26"	0' 10"	45, 46	1' 34"	0' 15"
33, 34	0' 25"	0' 05"	47, 48, 49	0' 09", 0' 18"	0' 09"
35, 36	0' 08"	0' 08"	50, 51	1' 31"	0' 07"
37, 38	1' 44"	1' 15"	54, 55	0' 20"	0' 18"
39, 40	0' 06"	0' 07"	56, 57	0' 34"	0' 07"
41, 42	1' 40"	0' 16"	60, 61	0' 09"	0' 10"
43, 44	0' 05"	0' 10"	64, 65	0' 24"	0' 08"
52, 53	0' 16"	0' 25"	67, 68	0' 21"	0' 06"
			72, 73	0' 18"	0' 10"

The performances of the fish were, on the whole, essentially comparable with the normal tests performed immediately after, and indicate an almost complete "transfer of learning."

Tests in which plain glass was substituted for squared glass (Table VI). Ten of these tests were given between 45 and 72. The durations of performances varied somewhat, but were on the average considerably higher than the normal control tests. Only two were performed as efficiently as the normal. It is evident that the fish found the conditions more difficult; yet the performances are clearly much better than if the fish had had no previous training. The level of the first five trials is somewhere about that of the 12th in the main series: there is, then, some sort of "transfer."

As regards the method of solving these tests, it is of interest to observe the difference made by the absence of the scratched lines. Whereas in the normal trials the fish now invariably turned left before reaching the glass, in the tests it always swam straight into the glass. It then spent a longer or shorter time working close up against the glass, sometimes delaying considerably before bearing leftward. Sooner or later, however, the fish would suddenly turn left and continue, wheeling round the edge. The variations in the times of the tests depended mainly on how long it took the fish to make a full left-turn.

It is of further interest to note that the method of solution of the tests with plain glass was (a) identical with the method learned during training to the squared glass, although (b) the method was never regularly adopted by the various fish trained to plain glass, evidently presenting considerable difficulties in the normal course.

Fish D8.

Sept. 25, transferred to experimental dish.

Oct. 23-Dec. 13, 77 experimental feedings.

Trained to glass with meshwork of fine lines, as was D7. Detour, 6.5 cm.

The curve depicting the duration of trials is shown in Fig. 12. The average durations of successive groups of five trials during uninterrupted training is as follows:

<i>Serial No.</i>	<i>Average duration.</i>	<i>Serial No.</i>	<i>Average duration.</i>
1-5	6' 22"	16-20	0' 48"
6-10	5' 12"	21-25	0' 33"
11-15	1' 25"	26-30	0' 20"

The manner of this fish differed considerably from that of D7. In early trials it was more active, and a good deal more erratic in its behaviour. More prone to make full turns away from the glass,

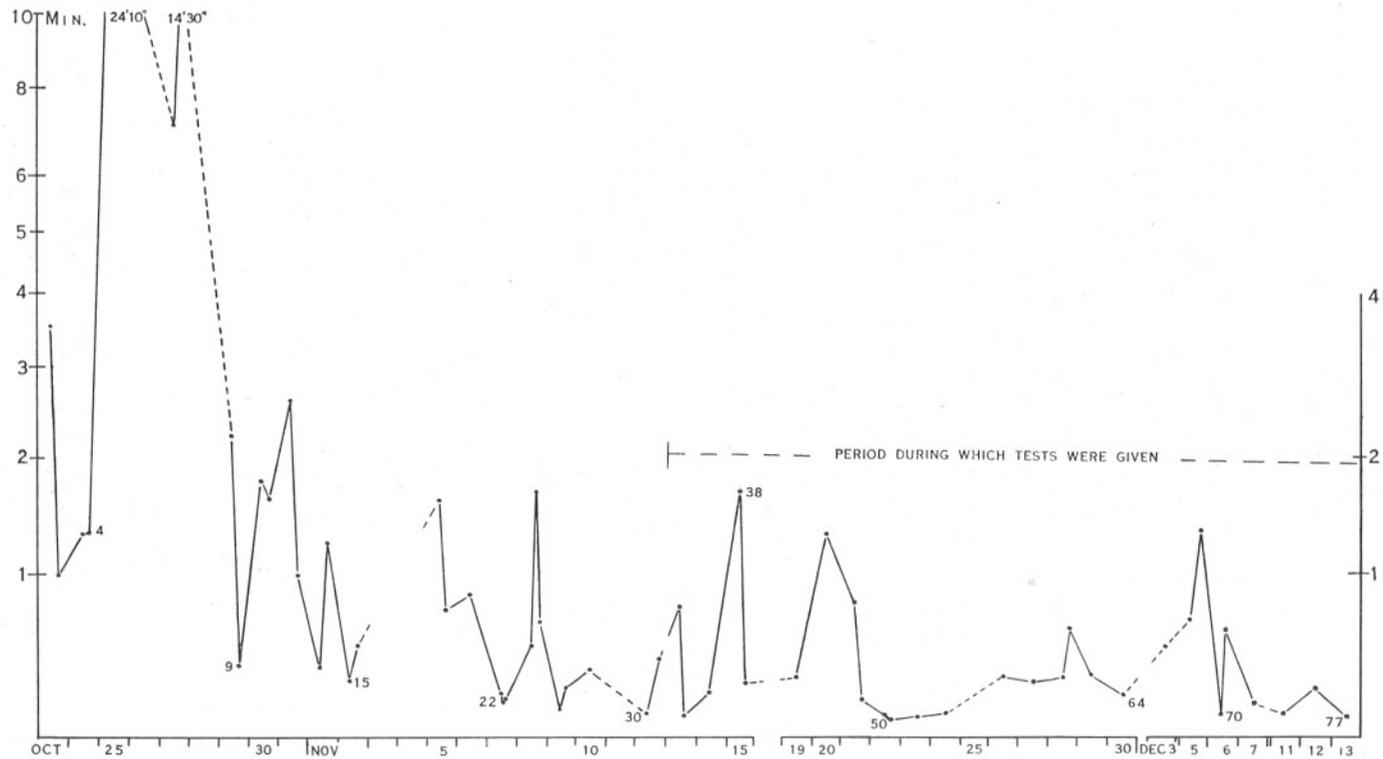


FIG. 13.—Graph of duration of trials of fish DS—as in Fig. 12.

it frequently swam off to other parts of the tank. All through it proved a more unreliable performer, and would doubtless have been long in acquiring a learned response to plain glass.

In spite, however, of this "temperamental" difference, this fish acquired a learned response of the same kind as D7, and the course of learning was in many ways similar, though less regular. The value of the results from this fish lie in the way they tend to duplicate the results from D7, and in the support they lend to inferences derived therefrom.

The solution of the first five trials was fortuitous: the fish happened to reach a part of the tank (region of corner D) from which there lay an uninterrupted path to the food. The trials which followed, however, came to be solved by a complete movement, starting with a left-turn and a right-wheel round the edge. It was this movement, which, as in D7, was established as a learned response: all solutions were effected by this means from trial 6 onwards.

As has been mentioned, the fish was much inclined to give sudden turning movements away from the glass. After giving one of these it often continued to swim right away from the glass. It became unusually inclined to wander over the tank, especially as the trial progressed. This tendency led to two excessively long trials—5, which holds the record of 24' 51", and 7, which lasted 14' 30". Wandering movements, however, decreased greatly after 7, and virtually dropped out after 12.

Among the reactions given to the glass turning movements predominated. The fish was even less inclined to make lateral leftward movements along the glass than was D7. After 11 they virtually disappeared altogether. Withdrawing movements were rare.

A marked improvement came about at the stage of trials 11 to 13. Before 11 no trend of improvement of performance can be observed. At this stage, however, several indications of a change occurred almost simultaneously. (1) 12 was the last trial in which the fish spent any time away from the glass; (2) after 12 turns were all to the left; (3) after 13 the time spent in attempts at reaching the food directly fell to a level minimum; (4) frequency of left-turns showed two sudden increases, one between 11 and 12, the other between 13 and 14; (5) behaviour became standardized from 12 onwards—leftward movements were now definite left-turns.

The subsequent progress was more gradual than in D7, and the fish continued to give occasional lapses. When, at 31, tests were started, the fish had not acquired the same uniform level of efficiency as had D7 by this time. The acquisition of the same learned response was, however, well on its way, and the fish was beginning to turn left immediately, before touching the glass.

Tests in which food was presented on the right. Between 32 and 56 a

similar set of tests were performed as on D7. Probably because the learned response had not been adequately established, this fish did not show such complete "transfer of learning" as D7. Also, the times of the "normal" tests were rather too erratic to justify close comparisons of the tests and their controls. Nevertheless, one feature may be pointed out. The first test showed the fish wellnigh incapable of adapting itself to the changed conditions. It worked persistently at the glass attempting to reach the food directly. It frequently turned to the left, but showed no tendency to turn right. Eventually, after 6 minutes, it reached the food by sheer accident. The next four tests, however, were performed differently, and the performances much resembled those of the corresponding normal trials, showing good "transfer." Though still showing some inclination to turn left, and still spending a longer time before bearing to the right, the fish solved the tests adequately by turning right and left-wheeling round the edge. In 6 and 10 the test was inefficiently performed, but 7, 8, 9, and 11 were done in short times, only slightly worse than the control.

The contrast between test 1 and the four which followed is reminiscent of a similar contrast shown by fish D5, on which comment has already been made (p. 529).

As far as the extent of "transfer" is concerned, if allowances are made for its less reliable behaviour, D8 tends to bear out the features shown by D7.

Tests in which plain glass was substituted for the squared. The fish reacted in a similar manner as D7, but found the test considerably more difficult. Nevertheless, as in D7, it made the detour more readily than if no previous training had occurred; and, again as in D7, the mean of the first five tests fell at the same level as represented by trial 12 in the main series. Other results agree closely with those given above for the other fish. The fish never turned left before striking the glass; the solution was reached by the same method as that to which the fish had been trained; and the variations in the times were mainly dependent on how long it took the fish to turn left.

III. SUMMARY OF THE PERFORMANCES OF INDIVIDUAL FISH.

DETOUR OF 6.5 CM.

Plain glass obstruction.

Fish A. *Efficient learned response*, after 25 trials in which no evidence of improvement was seen. The main steps in progress came at trials 26, 36, and 54.

Response re-learned after a short interval during which the fish was subjected to disturbance. Main improvement at trial 10.

- Fish D5.** *Efficient learned response*, though early trials produced the most inefficient performances of any fish. Important sudden change of behaviour, from which point onwards rapid improvement occurred.
- Fish D6.** *Unexpected efficient response by indirect route.* Glass obstruction with black band at its edges, which was found to make no difference.
- Fish D4.** *Efficient learned response* eventually established, after the first period of improvement had been nullified by a bad lapse. Early on a consistent method of solution was adopted, but it was not established. In the later response the actual movements of the fish still varied.
- Fish D3.** Efficient response not established, though this appeared eventually to be coming on when the trials were abandoned at the 83rd. Response nearly established much earlier on, but a very striking lapse set in.
- Fish D2.** No response established in 45 trials, though one period of steady improvement was passed through.
- Fish D1.** No response established in 45 trials, though at one time it looked as if one was developing. This fish was a steady worker, and its behaviour remarkably uniform. A change to the squared glass obstruction after trial 45 produced a striking effect, showing that something had been acquired.

Glass with Meshwork of Scratched Lines.

- Fish D7.** *Efficient response established.* Note that the method was different from any established, or even partly established when the obstruction was plain glass.
- Fish D8.** *Efficient response established*, as in D7, but not so readily. This fish a more erratic performer.
- Fish D1.** *Efficient response given* after change over from plain to squared glass. (Evidence of similar phenomenon in case of D3.)

Plain Glass.

DETOUR OF 4.2 CM.

- Fish B.** *Efficient response* soon established. When transferred to the 6.5 detour, gave an efficient response at first, but lapsed badly.

DETOUR OF 8.5 CM.

Glass Pot with Black Meshwork.

- Fish D9.** *Efficient response* soon established.

CONSIDERATION OF WHAT IS IMPLIED BY THE TERM
"EFFICIENT RESPONSE."

The training, it is important to remember, involved not so much the acquisition of an altogether new response, but the *modification* of a strongly established natural response—the movement towards a closely situated food-object. The fish had to acquire the habit of moving round to one side to reach the food instead of swimming straight at it. It is necessary, before the method of acquisition of this habit can be discussed, to examine what is known of the basic response, whose presence is a fundamental condition to the subsequent modification of behaviour. Consideration shows that it is not such a simple act as may at first appear.

(i) It is clear that the simple feeding response—the movement up to food-object preparatory to snapping at and swallowing it—is guided by the visual sense. Ample evidence for this has been procured. The olfactory and gustatory senses are evidently brought into play at close quarters, but this fact is irrelevant to the present discussion. The fish can be dependent on its optical receptors alone in discriminating the food-object at a distance, and in controlling its movements towards it. The response which is to be modified is a visual response directed with relation to the "object" which we must suppose is represented in the fish's visual field.

(ii) The movement which the fish performs, though it may be a simple forward motion straight ahead, implies a motor co-ordination of swimming movements. As a simple fact of observation, if the food-object moves, the fish will adjust its movements to the correlated change in its visual field. The ability to do this has been ingrained or acquired during the fish's normal life, and exists before the experiments are started. A high degree of capacity to co-ordinate its movements is possessed by the fish at the outset of the investigation. We can therefore further add that the movements which make up the whole response are directed towards keeping the fish orientated in the direction of the food-object, as forward motion is maintained.

(iii) If an attempt is made to summarize the component events in the series which comprises the response, at least the following must be found significant. (a) Food object is somehow differentiated in the total pattern of stimulation of the optical receptors. (b) Direction of movement is altered to bring this visual object into a certain relative position; and (c) movement is continued and direction is adjusted, so that the visual object maintains its relation, but becomes increasingly larger. (d) Contact is established, swallowing actions bring the food into the fish's mouth, etc.

Further attempting to express these events in terms of neural activity,

we may re-write them as follows. (a) Stimulation of retinal cells, giving rise to an excitatory pattern in the sensory centres of the brain. (b) and (c) Discharge of motor activity in response to the new excitatory pattern and in adjustment to it. (d) Culmination of swimming movements, accompanied by a new gustatory situation with resulting motor discharges bringing about snapping and swallowing.

The neural co-ordination is adequate to the task of producing a unified action (as it appears to observation), involving the integrated activity of the whole fish. If this neural integration is a reality, then it is evident that something has been left out: only the *main* neural events have been mentioned. Coincident with these are doubtless other, subsidiary, though maybe none the less important, neural reactions. Since the activity of the whole fish is involved, something is going on, whether of a stimulatory or inhibitory nature, in the neural pathways not concerned in the main reaction. It is to be inferred that these are of a kind which secure an integrated pattern of neural activity through the whole fish's body, and that habit will have established the most adequate possible. Among the subsidiary reactions those of the visceral system are no doubt important, assisting to maintain the "food perception" situation, and making ready for the discharge of digestive and gustatory reactions. On the whole, in a healthy fish, they will have come to be such as to maintain an appropriate harmony throughout the body, as well as to maintain an appropriate tension which will ensure that the animal reaches its objective in a normal effective manner. If the fish is temporarily frustrated in its movements this neural tension will be maintained. It is perhaps not going too far to postulate that nervous discharges are such that a state of physiological equilibrium is achieved at the culmination of the act, and that, if the movements are frustrated, new nervous discharges will originate maintaining the state of neural tension for a longer or shorter time, until the culmination is reached.

In short, since the activity of the whole fish is involved, the neural processes concerned are seen to be of a complex nature. Mere interference with the performance of the normal reaction will show indications of this complexity. The apparent simplicity of the act is typical of organic systems in general: they degenerate into a welter of complexity when their functioning is obstructed.

Attention has been drawn to the possibilities of subsidiary neural activity. This may play an important role in establishing physiological "states" with which are associated psychological states such as "satisfaction." It is quite possible that the association of motor responses with states of this type may lead to their establishment at the expense of others without such association. In problem learning a basis may be found for interpreting Thorndike's Law of Effect (p. 547).

(iv) To direct observation, at least, the response has the appearance of a unified action. If analysis reveals a complex of nerve reactions, it is evident that some account must be taken of the manner in which the elements of the complex are co-ordinated. No doubt in the main this co-ordination is developed by the type of neural association that has been revealed by the work on conditioned reflexes and responses. Association may be responsible for establishing, or maintaining once established, processes such as the following. (a) The linking of certain sensory or excitatory patterns with certain motor reactions—thus a change in the position of the food-object in the visual field may come readily to bring about a corresponding change in the direction of the fish's movement. (b) The linking of successive motor reactions; a certain reaction *A* may tend to make for an increased readiness of *B*, so that the performance of *B* becomes linked to that of *A*, irrespective of what changes may be going on in the centres of sensory excitation. (c) Certain motor reactions may well, as Washburn (1928) suggests, become associated with certain physiological states, akin to those which accompany emotional states in higher animals. (d) If the food-object is kept in the same relation to other objects in the sensory field, the response may acquire an association to these.

Co-ordinated elements in the neural activity of the fish are clearly of first importance in maintaining the unity of the response against influences which tend to disturb it, or in the development of a more "complex" response if the conditions are modified. Various of these processes may play an effective part in the establishment of an efficient response when the fish, as in these experiments, has to make a detour to reach the food.

The main point to be stressed is that when an obstruction is placed in the fish's path, and when the fish has re-established what we describe as an "effective" response adapted to the new conditions, the change that has taken place essentially involves a re-adjustment of the disturbed balance. If new co-ordinations come to be established, it is on the basis of those which existed at the outset.

Consideration of the nature of the "natural response" has thus inevitably introduced the conception of an "acquired" response adapted to altered external conditions. The features that should characterize an efficient acquired response are already apparent. The two primary observable criteria are as follows. (i) It is performed with a minimum of hesitation and maximum of integration—approximating to as uniform an act as the particular individual fish is capable of giving. (ii) The efficiency of performance is stabilized, and a uniform series of rapid times is shown in the learning curve. Applying the first criterion to the special conditions

of the experiments described above, we have regarded the following characteristics indicative of an efficient acquired response : (i) immediate turning leftwards away from the obstruction ; (ii) persistent leftward movement for a certain distance, far enough to take the fish past the obstruction and leave it an open path to the food ; and (iii) the whole response performed as one continuous act.

DISCUSSION OF LEARNING SHOWN.

CONSIDERATION OF THE LEARNING IN THE LIGHT OF CURRENT THEORIES.

In this section we have to enquire how far the above results are explicable in terms of certain hypotheses which have been brought forward to interpret learning phenomena of the type with which we are concerned. Generally speaking, these hypotheses, even though they may have been dignified by the name of Laws, are at best generalizations which apply under certain conditions within certain limits. Consequently it should be understood that if the application of any to our present results is criticized, it is not to be implied that the hypothesis itself is attacked. The conditions may not have been suitable for the phenomena which it generalizes to have become manifested. What is intended, however, is that the relevance of these hypotheses should be tested in relation to the actual cases of learning which were observed.

THE "LAW OF EFFECT."

It is perhaps most appropriate to treat first an explanation—or rather an approximation to one—which originated from the pioneer investigator in this field, and with certain obvious modifications might well apply generally in spite of the various criticisms that have been levelled against it. The essence of Thorndike's "Law of Effect" is that when, at first, an animal is unable to give an effective response to a situation which evokes action, and gives varied movements of a "trial and error" nature, after a time movements will become established which lead to a *state of satisfaction*, at the expense of others which do not. Successful movements are thus "stamped in" for the very reason that they have been successful, while "useless" movements become "stamped out" because they fail in this respect. Thorndike's own method of formulating this hypothesis is open to the obvious criticism that he is confusing physiological and psychological terms, but it seems that this difficulty can be removed by replacing the term "satisfaction" by one indicating some correlated state of neural (? and humoral) excitation. It seems quite feasible to maintain the Law of Effect on a purely physiological level.

It is supposed, then, that successful movements, by some process of association, are stamped in through their connexion with states of neural excitation accompanying the "attainment of the objective"—achieving a means of escape, reaching a food-object, or whatever it may be. It is, of course, only a first step towards anything that may be considered an *adequate* interpretation; but it is worth while to examine our results and see if they show any indication of complying with this hypothesis. If they do not, there are no grounds for pursuing this line of interpretation any further.

Each fish's performance has been critically studied, and an attempt made to trace any possible influence of successful movements in early trials on the performance of trials which follow, and on the development of any effective response that may be formed. It would be laborious, and unnecessary, however, to recount the details of this examination; for much of the data has to be set aside as of "neutral" character. We shall confine consideration to the main features which have emerged.

(1) Data have been abstracted showing the relation between methods of solution achieved in early trials and the increase in efficiency of subsequent performances. It is seen (*a*) that successful solutions in early stages do not necessarily result in the establishing of the reactions which have led to that solution: that, moreover, methods of solution may suddenly become established which have been rarely or never given before, or, if attempted, have been relatively unsuccessful. (*b*) Also the occurrence of successful solutions does not necessarily lead to an increase in the efficiency of subsequent trials, and increase in efficiency can occur when previous performances have been too varied to give any grounds for expecting immediate improvement.

The frequent early success of the "left-turn" reaction, and its failure to provide the basis of an established response, provide the best instances.

In fishes D1, 2, and 3, the left-turn movement was given from the start, and led to a solution more readily than any other response to the obstruction. Yet it did not lead to a learned response. In the first two fish it dropped out in a surprising way. In fish D4 the movement, on the whole, proved very effective; yet for a long time was only occasionally given, and did not appear at all frequently until an efficient response had been learnt by another method.

These four fish are considered together, as they did not develop a learned response within the first 45 trials. It is important to notice, however, that D3 quite early on came to give many highly efficient performances, though the efficiency was not established; yet the successful trials showed no influence of the early successful left-turn movements. D4 eventually learned satisfactorily, and will be considered again below.

Among those fish which succeeded in acquiring an adequate response comparatively quickly, at any rate D7 and 8 (with the squared glass obstruction) established a response on a movement that had been successful from the start—the “left-turn” movement, in fact. In other fish the situation is more complicated, owing to the fact that more than one type of solution proved effective in the period before efficiency had been achieved. But these provide interesting test cases. Each of them will be considered separately.

Fish A, after it had begun to show improvement, was for a time, so to speak, torn between two conflicting methods of solution—the left-turn-and-right-wheel as opposed to the sideways movement down the glass. The latter, before long, predominated. While there is nothing of special significance in this case taken by itself, it shows agreement with all other instances in the fact that, when the obstruction is of plain glass, the left-turn-right-wheel movement fails to become established in spite of its effectiveness.

It also leads us to the case of fish D6, in which, during the earlier trials, two, and only two, methods of solution were achieved. One of these, again, was the left-turn movement; the other was a withdrawing followed by a right-turn taking the fish into the right-hand regions of the tank, from which it eventually approached the food on the far side. The former movement was not often given, but, when given, led at once to a solution in six cases out of eight. The latter led to a solution after a much longer interval, and by a more circuitous route: *yet it became an established response*, the other completely dropping out after trial 12. In this case, then, where the fish solved the trial by two alternative methods, the most laborious and, at first, inefficient was established at the expense of one that was far simpler and quicker.

The performances of D4 and 5 are considered below illustrating other phenomena of importance. In them it is seen most clearly that efficiency of performance can be established in absence of uniformity of the actual movements given. In other words, learning can still come about even *before a definite predominance has been established between alternative methods of solution*.

It seems definite enough, from the above evidence, that, in so far as the “success” of certain movements leads to their affecting the performance of subsequent trials, certain types of movement (e.g. particularly the left-turn movement) are far less effective in this respect than others.

(2) The case of fish D5, supported in some ways by D4, is of sufficient importance to warrant a more detailed résumé. This fish, it will be recalled, produced the best learned response to plain glass, although its early performances were the worst given by any of the fish (pp. 526–528).

It was prone to wander about the tank, and for the first 12 trials, during which it showed but slight inclination, if any, of tendency to improve, the solution was usually arrived at by the fish eventually *happening* to get into the part of the tank in which a free path to the food was possible. In trials 1, 3, 7, and 8 it swam to the food from corner D; in 2 and 4, it swam up from the back (region A); in 11 and 12 it swam round the edge after withdrawing to the front of the tank. Only in 5 and 9 was a solution given involving a continuous movement from the original position—a left-turn-and-right-wheel movement, as it happened. At 13, however, it eventually solved the trial for the first time by working leftwards down the glass, making frequent contact with it until the edge was reached. The striking feature is that from now onwards all trials were solved by a method resembling this one. The chance methods, and the one given in trials 5 and 9, dropped out completely.

The main characters of the new adopted method of solution were (i) that the fish bore leftwards and made contacts with glass as it did so, and (ii) that it never withdrew from the glass for more than a short distance in the movements that led to the solution—in fact, it gave up altogether making random movements to the other parts of the tank; and (iii) complete right or left turns no longer feature in the fish's response to the glass obstruction. Though, within these limits, the fish's movements still varied considerably, there is decidedly enough in common between these solutions to contrast them with all those given previously. It may be noted that a conspicuous change in the fish's behaviour coincided with the onset of a rapid increase in the efficiency of the response. Are these two effects to be related?

It may well seem that an interpretation on the lines of the "Law of Effect" can be applied. As a result of "trial and error" behaviour, the fish, at the end of trial 13, happened to hit on a "satisfactory" method of solution. This method of attacking the problem became in some way "stamped in," so as to affect the behaviour of all subsequent trials. It so happens that it perhaps did so more effectively than might have been expected; but this fact would enhance rather than vitiate the argument.

It may at once be asked why the solution of 13 should have had such significant effects as contrasted with the solutions of previous trials. For the moment, however, let it be assumed that this has happened, so as to give the theory an adequate chance. We must consider in somewhat greater detail what the effects actually were.

From trials 14 to 23 learning progressed rapidly. The habit of making random movements away from the obstruction suddenly disappeared after 13. The only vestige remaining was seen in a tendency to make occasional short withdrawing movements from the glass obstruction, but

this tendency had almost completely vanished by 21. The fish persistently worked at the glass, and showed increasing inclination to bear leftwards, until eventually getting far enough to the left to pass the edge and reach the food. Both the frequency and efficiency of leftward movements increased.

But, though the general method of tackling and solving the problem was now constant, *the actual movements involved in the solution still varied considerably*. Thus in 13, 14, 15, 17, 19, and 20 the fish kept more or less orientated to the food, withdrawing a little before passing the edge: in 18, 23, and 25 it had made a half-left turn and was orientated towards the edge of the glass; in 21 it passed the edge without withdrawing at all. Good performances (marked by shortest times and least hesitation) did not depend on the method of solution. It was not until after 25 that the method had become approximately constant. It is apparent, therefore, that the fish acquired the habit of giving an efficient performance *before* the actual movements whereby it was effected had become stabilized. Such stabilization as was attained came later.

Evidently, then, whatever had become "stamped in" at trial 13 was not the actual movements involved. It appears, therefore, that in so far as the Law of Effect may be said to hold good in this case, it did not act by the establishing of certain specific motor responses. If the solution of 13 produced any permanent effects, these must have been of some other type. To this question there will be occasion to return later.

Interesting supporting evidence is derived from fish D4. This performer, after a considerable period of erratic behaviour (during which, however, some excellent trials were performed), eventually acquired a satisfactory stable level of efficiency. The most conspicuous feature in the development of this response is that, as in fish D5, but in an even more marked way, the actual method of solution continued to vary long after efficiency had been attained.

Consistently good performances were given between 49 and 69, in which successive 5 trials averaged 22", 17", 15", 15" respectively. Three distinct methods of solution, however, persisted. The efficiency of the general response, therefore, did not depend on the stabilization of the motor reactions involved.

There is little indication in this fish that the "Law of Effect" was operating to any extent; but if some process of this type was responsible for establishing the response, the same conclusion must be drawn as above—it did not act by establishing specific motor responses.

These examples have been considered in some detail as they illustrate most clearly features of which indications were secured in several other fish.

It is to be concluded, then, that if movements which lead to solving the

trial cause any neural changes of a "stamping in" nature, these are not connected with the motor paths. The possibility must not be overlooked, however, that such changes may affect that part of the neural mechanism which is involved in the co-ordination of sensory stimuli. This point will be taken up afresh after other evidence has been considered.

THE CONNEXIONIST AND ASSOCIATIONIST HYPOTHESES.

Attempts at interpreting learning phenomena in terms of the physiological properties of nerves and nerve reflexes lead first to a somewhat elementary type of interpretation which may be distinguished as the "connexionist" hypothesis. It is based on the premise that a neural connexion once made is more readily available on another occasion. To what extent this generalization is justified is not by any means clear, in spite of the fact that it has been widely held. Perhaps the recent demonstration of "facilitation" phenomena in neural reactions of certain invertebrates by Pantin (1935, 1936) provides the best experimental data so far available. It is sufficient, however, for the present purpose to accept the fact that this effect may truly occur in the central nervous system of vertebrates, and that the hypothesis could be justified on purely physiological grounds. Now, if this is so, it is evident that a type of learning will result, due essentially to a facilitation of certain nerve connexions, accompanied perhaps by inhibition of others. This will have come about merely through repetition of the behaviour-act.

The question, however, whether detour learning is adequately interpreted on these lines is another matter. In the first place no facilitation effect is to be expected unless the reactions given in successive performances reach a certain level of uniformity; and it has been seen above that improvement in the fishes' performances did not wait upon standardization of response. More serious still is the obvious difficulty that wherever one out of several alternative responses has to be established, something more is required—something that takes into account the fact that a certain response (or group of responses) is more appropriate than others in the "success" of its outcome. It is at any rate clear that unless the fish performs the same sequence of movements in the solution of each trial, the process of facilitation does not, so to speak, have a chance.

As an illustration the case of D6 may be cited. The movements of this fish were unusually stereotyped. After the twelfth trial the same sequence of movements was given in each trial: the fish passed round to the right and reached the food from the far side of the tank. With successive trials the speed and efficiency with which the course was covered gradually increased. Thus the total time taken over the trial fell from an average of five minutes to a final level of about 45". Now this increase

of efficiency after trial 13, once the habit of taking the path had become established, could well have been due to the facilitation of motor connexions, tending to integrate the sequence of movements. But—and this is the crucial point—facilitation could scarcely have had anything to do with the original “choice” of the particular route taken, as opposed to other possible responses—in other words, with the first acquirement of the habit.

Of the fish given the plain glass obstruction, fishes D1 and 3 afforded the most ample opportunity for the working of this process, as they tended to react in a uniform manner. Nevertheless, no efficient response was established in either. On the other hand, the performances of fishes D4 and D5 varied a good deal, and would scarcely have permitted neural facilitation to play more than a very subsidiary role. Yet both developed an efficient response.

It is quite unnecessary to dwell at any further length on the inadequacies of a simple connexionist interpretation. The facilitation of neural pathways cannot itself account for much, unless considered in conjunction with a related process—the *association* of contiguous pathways.

The association of motor pathways can be conceived as occurring in a manner characteristic of conditioned reflexes. If a conditioning process is at work, and if no assumptions are to be made that go beyond legitimate inferences from experimental results in this field, it is not a difficult matter to deduce the course that learning process, in these cases, should take. There is only one way in which a straightforward conditioning process could have produced the effective detour response: namely, through a linking of certain of the independent motor reactions, at first given at random in response to contact with the obstruction, by backward association with the primary reaction of swimming up to the food.

The established unconditioned response *A* (given to situation *A*) with which others may become associated is the final swimming-towards-and-snapping-at-the-food from a position *P*, clear of the obstruction. The first step will be that the fish in position *P* (situation *A*) becomes habituated to swim straight to the food from this point. “Being in position *P*” thus becomes, by a short step of backward association, conditioned to the final movement to the food. Carrying the process back a step farther, “being at *Q*” (situation *B*) becomes associated with movement to *P* (response *B*); similarly from a position *R* the fish will come to move to *Q*. Finally, the process of association will be carried back to the starting-point, *S*, where the fish first encounters the obstruction; and of various responses the fish may at first give in this position that one will eventually become



established which leads it to position R, then on to Q, then on to P, and so round to the food.

The course of learning, then, would take the form of a process of backward association. The observable effects should be clear enough : for the end part of the detour would be learned first, and the beginning of the final integrated response established last. The experimental results can yield crucial evidence on this point. If they show no indication of the above deduced effects, then learning by motor association must be ruled out of question.

It is not suggested that this interpretation is either one to be expected or one which suggests itself as plausible. A little consideration will show a certain artificiality, as well as raise doubts on whether its application, if permitted by the facts, would not raise more difficulties than it removed. Nevertheless, were there indications that the learning progressed in this way, an opening would still be left for the possibility of a fairly straightforward explanation in terms of conditioned response, and it is obviously necessary, for the discussion which follows, to consider every aspect.

For the purpose of investigating this point the fish's response was conveniently divided into three phases ;—(i) movements against the glass immediately opposite the food, in attempts at reaching the food direct ; (ii) leftward movement taking the fish down the face of the glass plate (or parallel with the face) to its far edge ; (iii) rounding the edge of the glass plate. When the most efficient integrated response had been acquired the first phase was reduced to two or three seconds, and there was no return to this position once leftward movement had started ; the second phase involved a continuous movement down the glass as far as the edge without hesitation ; the third phase involved movement round the edge as soon as the fish had reached this position. The acquirement of efficiency in each of these phases of the response was open to examination.

The interpretation being tested necessitates, strictly speaking, that acquirement of efficiency in the third phase should precede *any* general increase in the second, and that the second and third phases be performed as one unified act before there emerge any signs of increase in the first.

The results obtained were altogether different. Acquirement of efficiency, both in the response as a whole (as the learning curves indicate) and in the separate phases, proceeded irregularly. But there was no question of progress in one of the two earlier phases being arrested while efficiency developed in a later. On the whole, increase of efficiency in all three phases progressed together, often sudden improvements in one coinciding with improvement in another.

But it is still possible that secondary influences may have caused a certain increase in efficiency of the earlier phases while the latter were as yet imperfectly integrated. It is therefore still necessary to examine whether

later phases show any sign of merely being *in advance* of the earlier. In the Appendix (p. 568) is summarized such data as bear on this point. It is seen that not even here is there the least indication of the effects which the hypothesis of backward association requires. For instance, efficiency in the case of fish D5 was established in the first, second, and third phases consecutively—in a forwards, not backwards, direction. The special case of fish D6 is particularly illuminating: the fish found the greatest difficulty over the last section of its circuitous detour, and never, to the end, really acquired efficiency in passing it.

It is therefore quite evident that the learned responses were not being built up in a backward direction from the completion of the trial. This rules out the possible interpretation that learning was effected by a process of backward conditioning.

We reach, then, the conception that processes involving the facilitation and association of *motor* paths could not have produced the effects observed in our cases of detour learning. Any attempted interpretation on these lines proves inadequate. It will be noted that the evidence here brought forward is quite different from that which had already led us to reject the possibility that successful solutions served to "stamp in" the specific movements involved.

Thus one conclusion which has emerged, reached by two independent lines of argument, is that the development of an efficient response to the obstruction was *not* primarily a matter of the linking up of certain movements, i.e. of establishing a motor habit.

IMPROVEMENT IN PERFORMANCE DUE TO CHANGES IN "SENSORY ORGANIZATION."

Learning which involves the effector processes.

The methods of interpretation hitherto considered have one important feature in common: they take no account of possible changes in the *effector* processes concerned in the fish's response. We have merely considered the possibility of associations having become established on the *effector* (motor) side—as a result either of repetition, or of association with some general neurological state produced by relief of tension, or of backward association from the final successful movement. As these possibilities have been ruled out, attention must now be turned to the main alternative interpretation.

Some of the more familiar learning phenomena in animals belong to a class in which the animal, to speak in ordinary language, comes to "detect" certain relations in its surroundings to which it was previously indifferent. In strictly physiological terms, it is in the *effector* processes of the response that the essential change occurs. If there is a change in

the responses given, it is because a new state of central excitation has arisen, and the new state of excitation produces a new response.

Elementary examples are provided by certain simple conditioned reflex and response experiments. In some, a newly applied "stimulus" (or "stimulus complex") acquires the excitatory properties of another stimulus through association with it. The former, "stimulus" A, may formerly have had no conspicuous motor effect, or it may have produced a definite response which is inhibited and replaced by that primarily produced by the latter (unconditioned) "stimulus" B. One aspect of this phenomenon is that a change occurs in the excitatory effects of "stimulus" A.

In other cases, rather less elementary, the animal, giving primary response X to "stimulus" A, is conditioned to give that response to B, but to react negatively to C even when A and C are combined. These are the familiar "choice" experiments, from which the "multiple choice" experiments are a special development. Usually a particular visual object of a certain colour, size, or shape, is associated with the primary "stimulus," i.e. food-object, while another object of contrasting colour, size, or shape, is set against it, often (though not necessarily) associated with a primary "stimulus" causing a negative response. But "stimuli" of a visual nature are not the only ones on which such responses can be built; similar results are obtained involving auditory, tactile, gustatory, and other sense receptors. By such experiments the capacity of the animal is tested for "discriminating" colours, shapes, tones, and various other "sensory" properties. The aspect of this choice-experiment conditioning which we have here to note, is the fact that the animal comes to "detect" a certain contrast, or, more generally, a certain relationship, in its sensible environment, by which, as far as the particular reaction under consideration is concerned, it was primarily unaffected. From the fact that no *new* motor reactions are involved, it is evident that the development of these various conditioned responses is primarily a sensory, or, more strictly, an *affector* phenomenon.

The work of Bull (1928-1934), Herter (1929, 1930), and others, has fully established the ability of teleost fish to develop conditioned responses of various types. With this knowledge, one may enquire whether detour learning, and, more particularly, the manner in which it has been found to occur, is predictable; and if not, what additional factors or conceptions have to be introduced in order to account for it.

If attempts are made to find the points of comparison between detour learning and typical conditioned response effects, or to express the former in terms of conditioned reflexes, it is soon found that the problem is by no means straightforward. If it had emerged that the detour learning occurred by a process of backward association, the phenomena might have

been considered directly comparable, the detour learning appearing as a chain-reflex (or, more strictly, chain-response) effect. But this has been shown not to be the case (p. 554). If, on the other hand, the detour learning compares with the conditioned response in depending on a specific change in the affector processes, then it differs in certain important respects, which at once place it on a higher level of organization, or at least of complexity. The main difference is that a new and more complex motor response develops, and not merely a change over to an alternative response previously given by the animal in other circumstances. If this is to be explained on the grounds that the animal comes to detect some "new" relationship in its surroundings (e.g. spatial and functional relations between itself, the obstruction, and the food-object) in the same sense as this may be said to occur in choice-conditioning, the situation is not in any way simplified. In choice-conditioning the "new" relationship, which the animal, so to speak, is conditioned to detect, is always a straightforward contrast providing stimuli which the sense receptors of the animal are directly capable of analysing.* But the relations which the animal would have to "learn" to detect in acquiring an efficient detour response must evidently be of a more subtle kind, and it would appear that considerable ability for producing a differentiated field of sensory excitation would have to be conceded to the animal. There would appear to be a more highly developed capacity for co-ordinating sensory impulses than might be expected, or than our present knowledge would entitle us to assume.

While, then, conditioned response experiments do not, at first inspection, provide a ready interpretation of detour learning, they do nevertheless demonstrate certain phenomena which are significant for our purpose. The first of these is that associations between nervous paths, at first functionally disconnected, may develop in an orderly and predictable manner; the second is that such associations may develop centrally in that region of the central nervous system which functions in co-ordinating the impulses transmitted by the peripheral receptors. They provide a certain neurological basis for pursuing an attempted interpretation of detour learning as an affector phenomenon.

The affector processes which initiate any given response include both events which occur peripherally in the sense receptors, and those which occur centrally in the sensory centres of the central nervous system. There is first a process involving an analysis of external energy-exchanges into aggregates of unit stimuli, and secondly a re-synthesis of the aggregates of impulses reaching the sensory centres. The mechanisms underlying these complementary functions constitute the affector system. That a distinction should be recognized between sensory analysis and sensory

* See below, p. 558.

synthesis seems inevitable not merely on morphological grounds, but also as an outcome of the conditioned-response work. The conception, in fact, is derived from Pavlov :

“ . . . the nervous system possesses on the one hand a definite analysing mechanism, by means of which it selects out of the whole complexity of the environment those units which are of significance, and, on the other hand, a synthesising mechanism by means of which individual units can be integrated into an excitatory complex. Thus in studying the nervous activity of the cerebral cortex it is necessary to deal with two . . . distinct phenomena, one involving a neuro-analysis and the other a neuro-synthesis.”*

This generalization was intended to apply to Mammalia—vertebrates possessing a cerebral cortex. Nevertheless other vertebrates, as well as some invertebrates, possess centres in the central nervous system associated with afferent nerves and it appears from simple observation that the function of sensory organization—hence neuro-synthesis—is possessed by these animals, however limited that function may be. At the very least it is possessed by teleost fish, which prove capable of producing many of the conditioned reflex phenomena demonstrated in mammals.

Accordingly—to return to the learning problem—if a change occurs in the affector processes, this may involve either the process of neuro-analysis or that of neuro-synthesis. Changes of the first category could involve little more than an alteration of the threshold of excitation of the sensory receptors, though such changes might conceivably have far-reaching effects on behaviour. The second type includes other cases in which a change in the central excitatory complex results. Such could arise through the development of a new neural association. One of its essential features is that it occurs through causes independent of the process of neuro-analysis : it may occur although the external conditions, the stimulation of the sense organs, and the impulses transmitted by them, remain identical.

Since mere changes in the threshold of excitation of the sense receptors could not possibly account even for the most elementary conditioned reflex, to say nothing of detour learning, we may proceed straight away to consider the latter as due to a change in the process of neuro-synthesis. That we are justified in assuming that changes can occur at this stage may be seen by referring back once more to the more elementary conditioned response effects mentioned above. It has been pointed out that these are to be regarded as affector phenomena, occurring centrally, which is the same thing as saying that they involve the process of neuro-synthesis.

* *Conditioned Reflexes*, trans. by G. V. Anrep, 1927, p. 110.

As the change in question is a matter of association of formerly independent nerve-paths, it may be accepted that the process of neuro-synthesis may be modified, under certain conditions, through certain changes which are of the nature of neural associations.

This conclusion has obvious significance in relation to our problem. It may be asked why it was not introduced at the start of the discussion, or at least in the section above (p. 552) dealing with the associationist hypothesis. The fact remains, however, that the type of modification that appears necessarily involved in detour learning is somewhat different, in some respects more complex, than any indicated by conditioned response experiments. It was not justifiable to attempt this line of interpretation before others, which had the appearance of being more straightforward, had been tested.

The first stage of the analysis of our problem brought us to the significant conclusion that the learning shown was not primarily a matter of the development of a motor habit. Having seen that ample precedent exists for doing so, we have now to proceed to test the hypothesis that the learning has resulted from a modification in the process of neuro-synthesis, i.e. in the manner in which the sensory impulses are integrated.

It will first be necessary to consider a body of evidence of a positive character that at least encourages us in pursuing this line of interpretation.

Effects of visible changes in the surroundings.

The evidence now to be discussed illustrates perhaps the most important feature which has emerged during the course of the experiments, namely, that *changes in the details of the conditions presented to the fish were capable of exerting marked effects on the course of learning.* The changes in question concerned visual characteristics of a type the fish proved able to detect, i.e. affected its responses. Also, their *only* effect on the fish was through the visual sense: they did not in any way directly influence the response movements, or require *different* response movements, as would, for example, spatial re-arrangement of the apparatus, or changes like the setting up of currents in the water. If, then, an influence on the response, or cause of learning, could be detected, it could only have been a secondary influence of the changed pattern of sensory stimulation. The significance of this consideration will be seen later.

(i) As described above, some of the experiments were made with the glass obstruction marked with a meshwork of fine lines. The lines, scratched with a glass-cutter, half a centimetre apart, did not seriously interrupt the view through the glass. Fishes 7 and 8 were presented with this "squared" glass from the start. The former proved a good subject and was not long in acquiring an efficient response, which developed during the period between trials 10 and 20. From 21 onwards a series of uniform efficient performances was given, averaging some 11". This was rather quicker than fish D5, the

outstanding performer among the seven fish presented with plain glass. Fish D8 showed more erratic behaviour all through, but eventually became as efficient as D7. Unlike the latter, it showed, to start with, strong tendency to wander over the dish, and for some time its performances fluctuated considerably. There is little doubt that this fish would have encountered great difficulty with a plain glass obstruction, and would probably have ranked with those fish that failed to establish an efficient response.

The evidence points strongly to the fact that the detour round the "squared" glass obstruction was more easily learned than in the case of the plain glass. This might well have been expected, since the fishes showed unmistakable signs of "seeing" the pattern on the glass, fine as the lines were. The evidence for this statement is of two kinds. (i) In early trials the fish often worked close against the surface of the glass: in moving leftwards, they usually moved jerkily from one line to another, in a manner never observed when the glass was plain. (ii) In the acquired response the fish turned leftwards before reaching the glass, at a point about 2 cm. distant, as though they had acquired the habit of bearing away from the obstruction as soon as the pattern came into focus: and this was in strong contrast both with the

TABLE VII.
PERFORMANCES OF FISH D1 IN LATER TRIALS.

Trial No.	Obstruction.	Duration of trial.	Average of five successive trials.	
36	Plain glass	0' 28"	36-40	2' 26"
37	" "	1' 20"		
38	" "	1' 41"		
39	" "	5' 47"		
40	" "	1' 55"		
41	" "	2' 39"	41-45	2' 21"
42	" "	1' 07"		
43	" "	1' 58"		
44	" "	1' 38"		
45	" "	4' 25"		
46	Squared glass	0' 18"	46-50	0' 19"
47	" "	0' 15"		
48	" "	0' 28"		
49	" "	0' 22"		
50	" "	0' 14"		
51	" "	0' 11"	51, 53-56	0' 19"
52	Plain glass	3' 0"+*		
53	Squared glass	0' 43"		
54	" "	0' 16"		
55	" "	0' 12"		
56	" "	0' 12"	57, 59, 60	0' 14"
57	" "	0' 12"		
58	Plain glass	3' 0"+*		
59	Squared glass	0' 13"		
60	" "	0' 16"		

behaviour of other fish presented with plain glass, and with tests on the same fish when plain glass was substituted for squared. Evidently, then, the obstruction was marked with visible characteristics, and it is scarcely surprising that the fish was more effectively enabled to make the detour.

But more significant still, perhaps, is the fact that the learned response given by these two fish was of a *distinctive type*, differing from any acquired

* Abandoned before a solution was achieved.

by the fish which learned to surmount the plain glass obstruction. Both fishes, D7 and 8, made the detour by turning leftwards, before touching the glass, swimming left, and wheeling round the edge in one movement. This manoeuvre, as has already been pointed out, was given by all fish during early trials. In spite of its effectiveness, as again has previously been emphasized, it was never established, sometimes dropping out of the fish's repertory in a striking manner. Where, in short, the obstruction was plain glass, the left-turn movement proved impossible to establish. Yet it provided the effective response in both fish trained to "squared" glass. The conclusion seems unavoidable that the marking on the glass made for this significant contrast. This is made all the more certain by the fact that essentially the same movement is given to an obstruction which has striking visible characteristics, such as the pot presented to fish D9.

The experiments with fishes D7 and 8 thus indicate that the meshwork marked on the glass, endowing it with a visible property, (a) rendered the detour learning easier, and (b) influenced in a marked way the character of the learned response.

(ii) The experiment of substituting the plain glass for squared glass was made in the case of fish D1. This fish, in spite of the uniformity of its behaviour, had shown no signs of establishing a learned response. The result, as may be seen from Table VII, was remarkable.

On the very first occasion the squared glass was introduced a response of marked efficiency was given, and this efficiency was maintained. The average level of the duration of the trial fell to below 25% of its previous value. That no sudden permanent change had taken place, affecting behaviour in both conditions alike, is shown by the results of trials 52 and 58, in which plain glass was used again. In both of these trials the fish proved incapable of making the detour before the trial was abandoned at the end of three minutes. Here, then, the pattern on the glass made all the difference between a laboriously attained solution, and one approaching maximum efficiency.

A similar test was made with fish D3, and the results, as far as they go, are comparable, if not so striking. At the time this fish was tested it was beginning to show gradual improvement, after a period of very inefficient performances. The figures are given in Table VIII.

TABLE VIII.

TESTS WITH SQUARED GLASS ON FISH D3.

Plain glass.		Tests with squared glass.	
<i>Trial No.</i>	<i>Duration.</i>	<i>Trial No.</i>	<i>Duration.</i>
69	4' 01"	70	0' 11"
71	1' 59"		
72	0' 55"	73	0' 16"
74	1' 29"	75	0' 45"
76	1' 35"		
77	1' 19"	78	2' 26"

The first three tests showed a marked reduction in duration as compared with the normal controls, particularly the first. What is also of interest is that the behaviour during the tests differed appreciably from that normally shown by the fish. Most notably, there was a complete absence of withdrawing movements, which characterized all other trials. The fourth test (78) showed a bad lapse, and might appear to vitiate the results. It must be noted,

however, that in this trial the difference in behaviour was conspicuous all the time, and the solution was eventually reached in a manner similar to that in the other tests, and quite unlike that shown normally.

The effect, then, of replacing plain glass by the squared glass, is that the detour is more readily accomplished. This is brought out in a striking way in the above records from the performances of fish D1. At the same time, as indicated by fish D3, the mode of behaviour during the trial, and the method by which the solution is reached, may be affected.

(iii) During the course of the experiments incidents were noted from time to time which indicated that features in the visible surroundings of the fish influenced the behaviour. In one case quite a trivial feature was responsible for so affecting the fish's response that the efficiency of performance was altogether impaired. This incident, which occurred in the training of the first animal investigated (fish A), is worth recording in detail.

During the second series of trials with this fish, after an efficient method of solution had been re-established, unexpected failures occurred in three trials, in which the fish failed to get straight round the edge of the glass first time. It was then noticed that a strip of white paper inserted into the groove supporting the glass plate (see description of apparatus, p. 505) was protruding a little from the groove, and ended a little short of the edge of the glass. For the purpose of testing whether the presence and position of the strip of paper had any influence on the extent of leftward movement of the fish, the paper was re-adjusted and made to protrude *beyond* the edge of the glass. The fish was again tested and now gave a perfectly efficient performance. Tests were continued, amounting to seven altogether on this particular day. The results are given below in Table IX. Situation A denotes that the edge of the glass lay beyond the edge of the paper, and B that the edge of the paper protruded beyond the edge of the glass.

TABLE IX.

PERFORMANCES OF FISH A, 23.2.34.

Situation.	Performance.
A	2 unsuccessful moves before frame removed at 20".
B	<i>round first time (at 11").</i>
B	<i>round first time (at 8").</i>
A	3 unsuccessful moves before frame removed at 20".
B	<i>round first time (at 7").</i>
A	5 unsuccessful moves before eventually reaching food at 45".
B	<i>round first time (at 30", but fish by now not hungry).</i>

It seems clear enough that the position of the edge of the paper was responsible for the fish's failures. This suggests at once that the fish was using the visible protruding strip as a guide to the position of the invisible edge of the glass. Be this as it may, a further test showed that the learned response itself was not at all dependent on the presence of a white paper strip. The next day the white paper was replaced by light brown paper fitted well into the groove so as to be invisible from below. There was therefore nothing which could be taken as a "sign" of the edge of the glass. With this arrangement the fish gave perfectly satisfactory trials. It was thus shown that the fish had not learned the position of the edge of the glass by association with the white paper.

It is therefore to be concluded that the presence of the slightly protruding strip of paper, ending before the edge of the glass, had *distracted* the fish in some way. No doubt, this was because the fish, relying by habit on its vision, had a tendency to pick up visual clues when there was the least chance

of being enabled to do so, and in this case had begun to develop an association with a clue that turned out to be a *false* one. But, however this may be, the point to be brought out is that details in the visual field can exert significant effects on the response.

The above examples illustrate how changes induced in the conditions presented to the fish—changes of kind which do not modify the detour problem, or affect the fish's response movements in any direct way, but which are detected by the fish through its visual receptors, and thus presumably affect the visual pattern to which it reacts—can affect the response in a significant manner. We have considered cases in which there is a *contrast* between two different experiments, and cases in which *changes* are introduced at some point in one series of trials. The same kind of effects are noticed in both.

Where contrasts, or changes, are noted in the response, the cause can only reside in a contrast, or change, in the sensory situation (however we may visualize or define this event) to which the fish reacts. Situation A evokes response *a*, while situation B evokes response *b*. We are not now concerned with what causes the particular characteristics of *a* or *b*. The point that must be made is that the differences observed in the response of the fish are induced in this way—by a difference in the situation which evokes them.

It may finally be observed that differences in the external conditions have been seen to exert two types of effect. First, there is the more immediate effect on the behaviour shown in the particular trials concerned. Secondly, as in the example of fishes D7 and D8, they may exert a more "long-range" influence, by affecting the selection of that form of behaviour which is eventually established as a learned response.

Detour learning an affector phenomenon.

The observational data just considered have a significant bearing on our problem. In showing that externally induced changes in the affector processes of the fish's reaction have marked effects on the learning process, they virtually demonstrate that *any* change in the affector processes can exert such effects. For those occurring peripherally are farthest removed from those that constitute the final central state of excitation through which the motor centres are activated. If, then, neural changes occur more centrally—such as in the process of neuro-synthesis (see p. 558)—they must be at least as capable of affecting the fish's performance as those induced peripherally.

Though internal changes affecting neuro-synthesis are hidden from direct observation, we have seen that it is necessary to infer their existence in interpreting the results of conditioned response experiments (p. 558). But, furthermore, from evidence considered earlier, it is concluded that

they are necessarily involved in the present case. The detour learning observed involves some internal neural change: this change does not involve the motor, or effector, processes of the response (p. 559): therefore an appropriate change in the affector processes remains the only alternative.

Taken together these two main conclusions leave room for only one plausible interpretation of the learning observed. The latter assuredly depends on a change involving the processes of neuro-synthesis. It is an *affector* phenomenon.

For some purposes it is preferable to express this reasoning in a rather different form, lest any shortcomings of the neurological concepts hitherto employed should be supposed to vitiate the deductions.

We may consider the situation (to which the animal's movements are adjusted and modified) as a whole, and call it the *perceptory situation*. This term is employed in its most general sense to express, objectively, the "sensed" situation to which the fish reacts, whatever it may be, whether an aggregate of stimuli, or whether something that has to be distinguished as a "gestalt" or organized pattern. The two main conclusions now may be expressed as follows. (i) The observed learning is not a motor habit; the only apparent alternative is that it involves a significant change in the perceptory situation to which the motor reactions are directed and adjusted. (ii) Changes in the perceptory situation, externally induced, can exert significant effects on the fish's response; therefore any changes in the perceptory situation, including those which may arise internally, have at least comparable effects. The final conception to which we are led is that learning takes place because a new perceptory situation arises which renders possible a more adequate response.

A picture of the process by which the wrasse learnt the detour path may now be sketched in its broad outlines. When first the food is presented behind the obstruction, the fish does not adequatelyprehend* the relations of the objects external to it, or adequately co-ordinate its sense impressions to enable it to give an effective response. It makes various ineffective movements which tend to become increasingly random, until by chance it gets into a position from which it can reach the food. With repetition of the situation, sooner or later a change occurs in the way in which the fish prehends its surroundings, and a new response is given (to what is essentially a new situation). The change, further, is such that the fish can give a more adequate response, enabling it to circumvent the obstruction, and so evidently involves a prehension of some

* This term is introduced to express the relation between the animal and the elements of (or relationships in) its surroundings which it proves able to differentiate. It may be defined as equivalent to the term "detect" shorn of its subjective implications. An animal can be said to "prehend" an object or contrast with no commitment as to whether the event involves consciousness on the animal's part.

significant relation, not detected before, between the fish itself, the obstruction, and the food. In the end the main relations are sufficiently well prehended to enable it to make the detour with a maximum efficiency.

It is perhaps not so much the fact that the problem of detour learning appears to be essentially a problem of sense-perception which is important, as the evidence from which this judgment is derived. Investigators who adopt the theories of the Gestalt school have stressed the probable importance of changes taking place in the perceptual field (see, e.g. Wheeler, 1929). As mentioned at the outset (p. 501), E. S. Russell has drawn attention to this aspect of the problem, and has suggested that the interpretation of simple detour learning shown by sticklebacks is rightly to be conceived on these lines. But, perhaps without exception, interpretations of this type have had their origin not so much in logical deduction from experimental results as from the metaphysical viewpoint from which the results have been described. This is not to say that the interpretations are false, but they will be unsatisfactory scientifically until they can be shown to be *required* by the results of experiment. In so far as they have hitherto been thought inappropriate may lie merely in the inadequacy of the necessary experimental data. This remains to be seen. However, since the course of the present discussion is guided by the principle of procedure from fact to hypothesis (and back again), it seems that "organismal" theories of learning (if they may so be called) are most conveniently introduced at a later stage, when the consideration of the data presented above is complete—when, in particular, the nature of the perceptory change involved in the learning has been more closely examined.

It is concluded, then, that the improvement in performance which characterizes the learning we have been studying is the result of a more adequate perception of the conditions presented to the fish. It will be noticed that this does not actually solve the problem of learning, but it does, at least, define where the problem really lies. The crucial point to be established is how the change in the perceptory field comes about, and why the change should be of the particular type found. It will be necessary to turn once again to the experimental data to discover if any light has been thrown on this problem.

I wish to express my gratitude to Dr. E. J. Allen for his encouragement and sympathetic advice given to me on various occasions during the course of this work; to those with whom I have had profitable discussions on problems bearing on animal learning, particularly Dr. E. S. Russell and Dr. C. F. A. Pantin; and to Dr. S. Kemp for reading the manuscript, and offering some helpful suggestions for its final preparation.

SUMMARY.

1. This paper deals with certain experiments on training fish (*Ctenolabrus rupestris* L.) to swim round obstructions to reach food, for the purpose of investigating how their learned response was developed. The whole question as to how learning which involves "problem-solving" is rightly to be interpreted and harmonized with our knowledge of conditioned responses, presents difficulties which have not yet been adequately faced.

2. A description is given of the results of experiments carried out on eleven fish. The fish had to learn a detour route either into a pot or round glass plates. Attention may be drawn to the great diversity in the behaviour of individual fish, both in their reactions to the obstruction at different stages of training, and in the method by which they succeeded in passing it. Some individuals are evidently more capable of profiting by experience than others.

3. As complete a record as possible was made of all performances; and these data were carefully analysed with a view to exposing the conditions under which efficient responses developed, and to detecting any possible causal influences. The results of this analysis, of which the main features are summarized below, may be partly summed up by saying that learning could progress in spite of considerable and significant irregularities in the fishes' performances. These were such as to preclude all the more straightforward* interpretations of the learning that can be suggested.

4. No general connexion was apparent between the behaviour shown in early trials and that in later trials, when the behaviour, if not perfectly integrated, was at least more uniform. It proved impossible, from examination of behaviour in early trials, to predict whether an efficient learned response would be established, or, if established, what particular movements would be involved. The experiments in which the obstruction was of clear glass, and the detour learned with difficulty, if at all, afford the most critical tests.

5. In particular, the movements which had led to successful solutions in early trials were by no means necessarily "stamped in" or reproduced in an efficient response, if and when this was achieved. Moreover, an efficient response can be established even before the movements by which it is carried out are at all stabilized. The possibility, therefore, that the learning had arisen, in accordance with the "Law of Effect," as a result of the recurrence of those movements which came most frequently to be associated with the solution of the problem, is excluded.

* i.e., from a physiological point of view.

6. While an efficient response was developing, the integration of the later movements did not proceed in advance of that of the earlier. The data are quite incompatible with the hypothesis that the response developed from independent movements linked by a process of backward association.

7. Since also the "connexionist" hypothesis fails to account for the facts, the possibility that the learning involved nothing more than the development of a motor-habit is now finally eliminated.

8. Only one alternative remains to be explored, namely, that the learning is an *affector* phenomenon. It would thus be associated with the synthesizing, or organizing, processes which must be assumed to occur in the sensory centres of the central nervous system.

9. A certain body of evidence is shown to encourage this view. Details in the external conditions which cannot affect the fish's activity except through the medium of the sense-organs, are found to exert considerable effects on behaviour—both on the performance of individual trials and on the trend of behaviour as a whole through a series of trials. Thus if a meshwork of fine lines is scratched on the glass plate, learning is greatly facilitated, and the movements by which the fish make the detour are significantly different.

10. The conclusion of the evidence considered is that learning is essentially due to the discrimination of some general relation in the external situation which had not previously been prehended (or "detected"). With a clearer appreciation of its surroundings the fish is enabled to give a more effective response. It remains to examine how this critical change takes place, and how its essentially adaptive character is to be explained.

REFERENCES.

- BULL, H. O. 1928. Studies on Conditioned Responses in Fishes. I. Journ. Mar. Biol. Assoc., N.S., Vol. XV, pp. 485-533.
 — 1930. *Idem.* II. *Ibid.*, Vol. XVI, pp. 615-637.
 — 1935(a). *Idem.* III. *Ibid.*, Vol. XX, pp. 347-364.
 — 1935(b). *Idem.* V. *Ibid.*, Vol. XX, pp. 365-370.
 — 1934. *Idem.* IV. *Ibid.*, Rep. Dove Marine Lab., N.S., No. 2 (59).
 HERRICK, C. J. 1927. An Introduction to Neurology. 4th edition. Philadelphia and London.
 HERTER, K. 1929. Dressurversuche an Fischen. I. Zeits. f. Vergleich. Physiol., B. X, pp. 688-711.
 — 1930. *Idem.* II. *Ibid.*, B. XI, pp. 730-748.

- LACK, D. 1933. Habitat Selection in Birds. *Journ. Animal Ecology*, Vol. 2, pp. 239-262.
- LLOYD MORGAN, C. L. 1900. *Animal Behaviour*. London.
- PANTIN, C. F. A. 1935. The Nerve Net of the Actinozoa. *Journ. Exp. Biol.*, Vol. XII, pp. 119-164, 397-399.
- 1936. On the Excitation of Crustacean Muscle. II. Neuromuscular Facilitation. *Ibid.*, Vol. XIII, pp. 111-130.
- PAVLOV, I. P. 1926. *Conditioned Reflexes: an Investigation of the Physiological Activity of the Cerebral Cortex*. Translated and edited by G. V. Anrep. Oxford, 1927.
- RICH, W. H., and HOLMES, H. B. 1928. Experiments in Marking young Chinook Salmon on the Columbia River, 1916-1927. *Bull. Bureau U.S. Fisheries*, Vol. XLIV, pp. 215-264.
- RUSSELL, E. S. 1931. Detour Experiments with Sticklebacks (*Gasterosteus aculeatus*). *Journ. Exp. Biol.*, Vol. VIII, pp. 393-410.
- 1932. Conation and Perception in Animal Learning. *Biological Reviews*, Vol. VII, pp. 149-179.
- RUSSELL, F. S. 1931. The Vertical Distribution of Marine Macroplankton. X. Notes on the Behaviour of *Sagitta* in the Plymouth Area. *Journ. Mar. Biol. Assoc., N.S.*, Vol. XVII, pp. 391-414.
- STEVEN, G. A. 1936. Seals (*Halichoerus grypus*) of Cornwall Coasts. *Journ. Mar. Biol. Assoc., N.S.*, Vol. XX, pp. 493-506.
- WASHBURN, M. F. 1926. *The Animal Mind*. 3rd edition. New York.
- WHEELER, R. H. 1929. *The Science of Psychology*. London.

APPENDIX.

DATA BEARING ON THE POSSIBILITY OF BACKWARD ASSOCIATION.

FISH A.

First series of trials.

The component phases of the learned response were acquired in the following stages.

- Trial 8. Random movements to other parts of the tank mainly eliminated.
- Trials 25 to 30. First permanent reduction in time spent in attempts at swimming straight at food before any leftward movement. Fish now gets into the habit of working steadily down the glass.

Trial 36. From now on usually moves straight down the glass and passes round the edge first time on 4 occasions out of 5.

Trial 55. Proficiency in the above virtually established.

Trials 55 to 60. Further reduction in the duration of the first phase, before first leftward movement, and final proficiency acquired.

There is no indication here of later movements acquiring efficiency earlier.

Second series.

The main step in the re-establishment of the learned response came in trials B9-11, and was marked by rather an increase in efficiency of both the first and third phases of the response.

FISH D5.

Phases of the learned response were established in the following order.

1. First phase, over which the fish hardly ever spent any length of time.
2. Second phase: the habit of moving as far as the edge of the glass plate in the first leftward movement.
3. Third phase: the habit of passing round the edge at first attempt.

Note that the integration of the response proceeded from the beginning forwards, and not from the end backwards.

FISH D7.

No one phase can well be said to have acquired proficiency before any other. Progress affected the response as a whole.

FISH D8.

This fish first became proficient at moving leftwards in a half-circle (full left-turn followed, after a longer or shorter forward movement, by a wheeling to the right), simultaneously reducing the time spent in attempts at reaching the food directly.

It was a long time, however, before it became proficient in passing round the edge of the glass on its first leftward movement. A considerable delay in establishing perfect integration was entirely due to errors made in the last phase of the response.

FISH D4.

The first phase never occupied any length of time, and the fish developed a habit of moving leftward efficiently at an early stage.

Until behaviour changed at trial 41, when a bad lapse set in, the perfection of an efficient response only depended on the ability of the fish to

pass round the edge of the glass, once it had moved far enough to the left (third phase). But consistency in this habit was not acquired during this period.

In the eventual learning which set in after trial 42, the fish at first was taking a considerable time to reach the edge of the glass. But reaching the edge in short time did not wait upon the acquisition of the habit of moving round the edge at the first attempt. Integration of the second and third phases progressed simultaneously.

FISH D6.

The data provided by this fish are particularly instructive, as the long route taken fell into three natural stages, namely (i) withdrawal from L and passage round Q, (ii) passage through K round P, and (iii) passage through J round O.

On page 537 figures are given for the times taken for the respective stages, and it is at once apparent that the last phase was never really efficiently learned. The average times for the passage round O are consistently high.

It is quite evident that the rapid passage from Q to P did not depend on the association with an efficiently integrated passage from P to O. Still less did the habit of turning away from the food at L and rounding Q depend in any way on the complete integration of the rest of the response.