

THE BEHAVIOUR AND BRAIN FUNCTION OF THE CICHLID FISH *HEMIHAPLOCHROMIS PHILANDER*

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ABSTRACT

Forebrain extirpations from *Hemihaplochromis philander* (Pisces: Cichlidae) resulted in a decrease of aggressive (territorial), courtship, and spontaneous behaviour. The stimulus-response latency was found to be increased by the extirpations. Forebrainless males were unable to distinguish between male and female conspecifics on a visual basis. Abnormal responses to certain stimuli occasionally resulted in accidents suggesting a failure of neural feedback mechanisms.

It was suggested that the teleost forebrain houses a primitive limbic system the main functions of which would be general arousal and the selection of appropriate responses to the incoming external and endogenous (motivational) stimuli.

KEYWORDS:

Brain Function, Teleost, telencephalon, Cichlid fish behaviour, limbic system, hippocampus.

The anatomy and location of the teleost forebrain led earlier workers to assume that the function of this part of the brain was exclusively one of integration and correlation of olfactory information. This error is perpetuated in current textbooks despite a good deal of evidence to the contrary from Janzen (1933), Noble (1937), Hale (1956a and b), Segaar and Nieuwenhuys (1963) and others, who have shown that the forebrain is involved in non-olfactory behaviour.

This paper draws attention to several of the more important non-olfactory behavioural changes which occurred as a result of the surgical removal of the forebrain of a small cichlid fish, *Hemihaplochromis philander* (Wickler).

PROCEDURE

The experimental fish were caught by netting in lakes of Natal and Zululand, from where they were transferred to the laboratory. The males, which were to be used in the experiment were maintained in a cold water aquarium (at $17 \pm 1^\circ\text{C}$) for fourteen days prior to the commencement of the investigation, in order to obtain a degree of pre-experimental conformity of the behaviour and physiology of the fish.

Each male was then placed in a separate aquarium where its behaviour could be observed from behind a one-way mirror. All these aquaria were of the same size (40 cm x 30 cm x 35 cm); had equal artificial illumination for 14 hours per day, a sand substrate, two small aquatic plants, and contained two spent female and three juvenile male conspecifics. The water temperature was then raised over a twelve hour period to $25 \pm 1^\circ\text{C}$, and maintained at that temperature throughout the experiment.

These conditions were known to promote territorial and reproductively oriented behaviour in *H. philander* (Ribbink 1971).

The ensuing aggressive and courtship behaviour of the subject fish was assessed every day for fifteen days, commencing approximately 36 hours after the fish had been placed in the experimental aquaria. The 36 hour period was considered to be a necessary recovery period for those fish which had undergone surgery.

Three categories of experimental fish were used. Each group or category contained seven adult males, between six and eight centimetres in length. The categories were as follows:

- (i) Normal males, which served as normal controls.
- (ii) Sham operated controls, in which the surgical procedure went as far as the severing of the choroid tela.
- (iii) Experimental males from which the forebrain had been surgically removed.

Surgical Procedure

The fish were anaesthetised with Sandoz MS 222, the concentration of which was adjusted so that respiratory movements were maintained but other movements were suppressed. The bodies of the fish were held in a foam rubber lined clamp and the heads were secured by two "V"-clamps into which the supra-orbitals were fitted. The mouth and gills were submerged but the top of the head was exposed. A longitudinal incision was made on either side of the supra-occipitals, the hypaxial muscles were then parted and held by retractors in order to expose the roof of the cranium. A dental burr was used to drill through the skull to expose the choroid tela. In the sham operated controls the tela was severed and the wounds were closed. In the experimental fish the forebrain was removed by separating the telencephalon from the diencephalon with a LM₄ Lesion Maker (Grass Instrument Company), and removed from the cranial vault by means of suction. The wounds were sewn closed with ophthalmic needles and silk, and treated with aureomycin cream to prevent infection.

Measurements of aggressive behaviour

Under natural conditions aggressive behaviour is elicited by a male conspecific entering the territory of the resident male. The normal patterns are active aggressive display, lateral display, and circling (Ribbink 1971).

Aggression was induced by lowering a round-bottomed flask, which contained a sexually coloured male conspecific, into the aquarium/territory of the subject fish. The object fish was always 5-10 mm smaller than the resident male. On all occasions the flask was lowered into the centre of the aquarium, and suspended between three and five centimetres above the substrate.

After a 60 second pause had been allowed for the subject fish to recover from any disturbance caused by the flask, all the behavioural displays were recorded verbally by the observer on a tape-recorder for exactly 300 seconds. The total time spent in each display pattern was then determined from the playback of the recording.

Aggressive activities such as tail-beating and biting, which are performed during the behavioural displays, were also enumerated during the 300 seconds.

Measurements of sexual behaviour

Under normal conditions a gravid female is invited to the male's nest by a series of invitation behaviour patterns, and once there the nest activities which lead to spawning are elicited (Ribbink 1971).

Courtship behaviour was evoked experimentally by lowering a flask which contained a gravid female into the aquarium. The time spent in courtship was recorded and transcribed by the methods described earlier. The number of courtship activities performed during the 300 seconds was also counted.

RESULTS

Results of surgery

After the experiment every fish was sacrificed and a microscopic examination and measurement of the brains of the forebrainless and sham operated fish was made to determine whether the operations for this experiment had been performed as intended.

Aggressive behaviour

(a) *Time*

The measurements of aggressive behaviour revealed that the fish from which the telencephalon had been removed spent very little time in aggression during the course of the investigation (Fig. 1). By contrast, the two control groups increased their aggressive behaviour until 255 or more of the 300 seconds were spent in aggression.

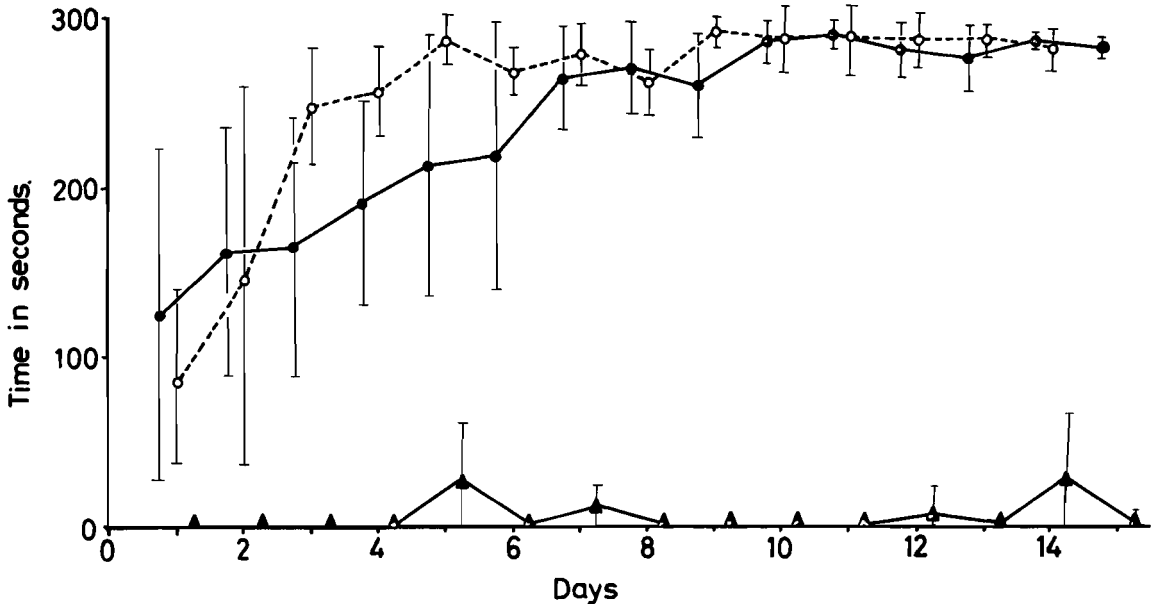


FIGURE 1

The time *H. philander* spent in aggression during each experimental period. The measurements of behaviour were taken on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

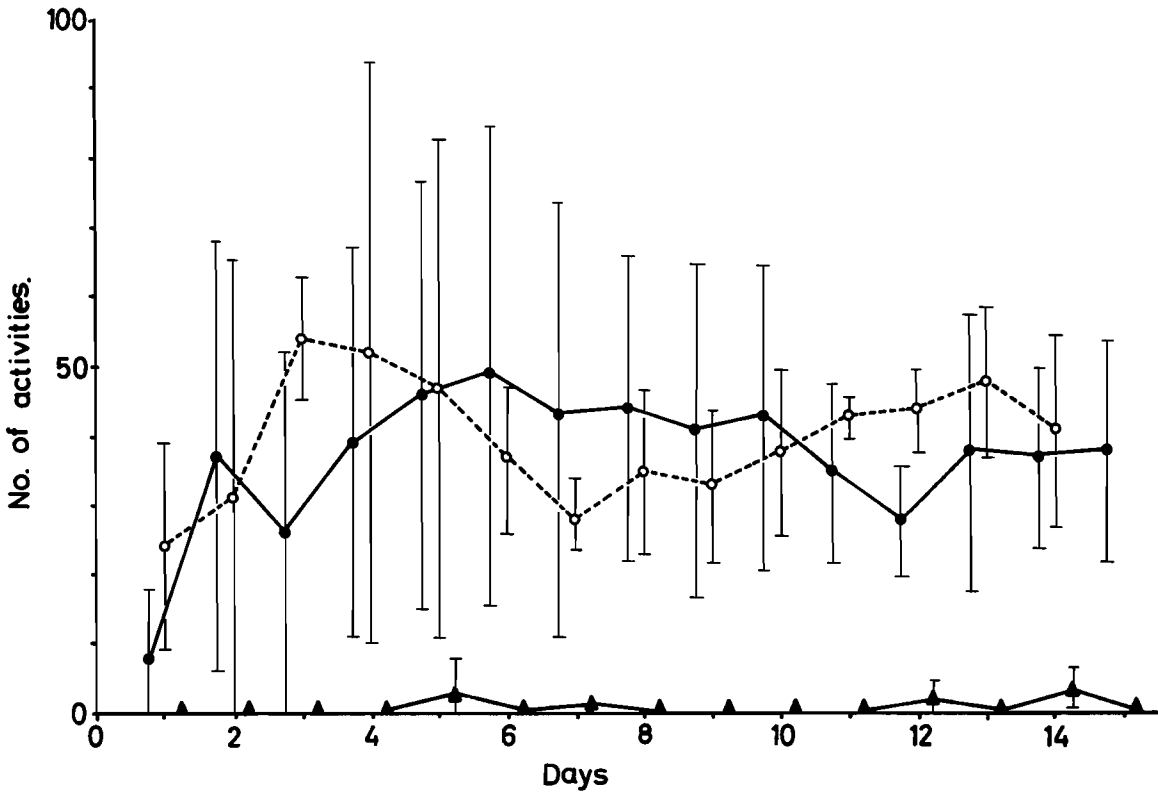


FIGURE 2

The number of aggressive activities *H. philander* performed during each experimental period, on successive days. The points on the graph represent the mean values (N=7), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

The amount of variation in the behaviour of the normal and sham operated fish was remarkably small after the sixth day. It is suggested that the more variable behaviour during the first six days may be attributed to the "uncertainty" which exists during the establishment of a territory.

(b) *Aggressive activities*

The form of the curves which illustrate the number of aggressive activities performed was found to be similar to those curves depicting the time spent in active aggression (Fig. 2).

(c) *Other behaviour in the presence of a male conspecific*

The remaining periods of the 300 seconds were occupied either in passive displays or by swimming. The passive displays (Fig. 3) took two forms; the fish either did not do anything, or

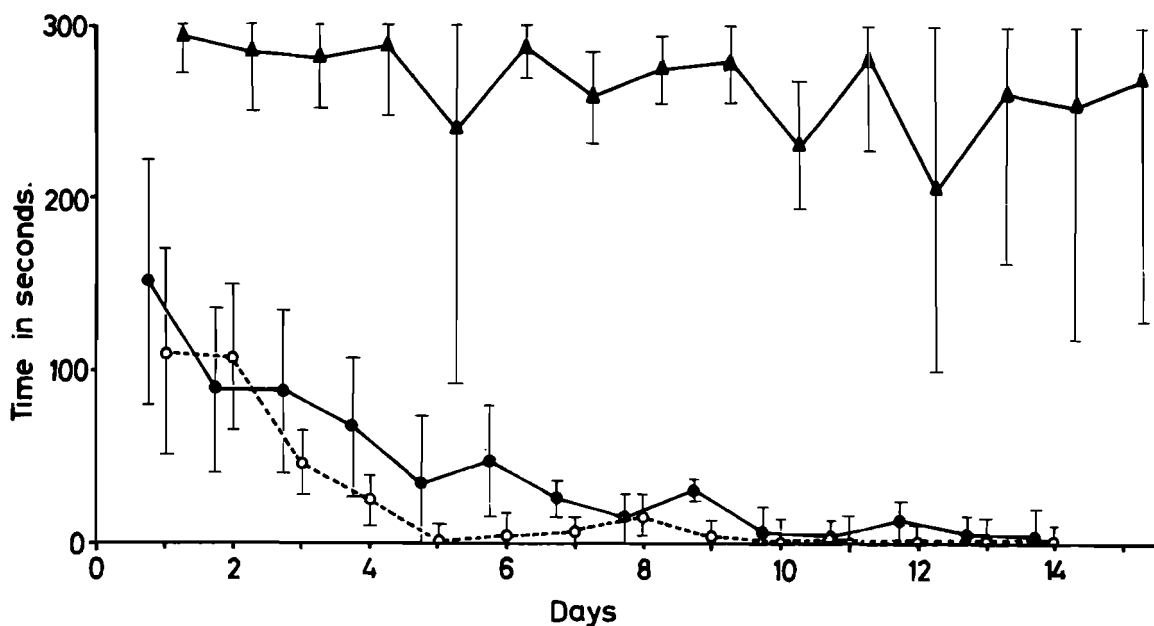


FIGURE 3

The time *H. philander* spent in passive behaviour during measurements of aggression in each experimental period, on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

exhibited a passive aggressive display during which it remained motionless with fins fully extended. The swimming also occurred in two behavioural forms, either swimming to the flask to initiate or resume aggressive behaviour, or the chasing of other fish in the aquarium. This chasing of other fish appeared to be redirected aggression, since this activity could be increased markedly by placing a larger object fish in the flask.

The two control groups were found to chase frequently during the initial stages of the investigation, but the number of chases decreased later in the experiment (Table 1). These findings indicate that the proportion of redirected activity is high during establishment of the territory, but once territoriality reaches a maximum the aggression becomes more appropriately directed, which may account for the decrease in the number of chases.

An unexpected behaviour pattern appeared in the fish from which the telencephalon had been removed. These fish were found to court male conspecifics which were presented in the usual manner. This suggests that they were unable to distinguish between males and females on a visual basis. This aspect of their behaviour will be dealt with more fully later in this paper.

TABLE I
THE TOTAL NUMBER OF CHASES PERFORMED BY *H. philander* MALES DURING THE EXPERIMENTAL PERIODS IN WHICH AGGRESSIVE BEHAVIOUR WAS MEASURED. THE MEASUREMENTS WERE TAKEN ON SUCCESSIVE DAYS

Day	Control	Sham	Forebrainless
1	13	14	0
2	30	17	1
3	32	22	0
4	21	14	3
5	17	17	0
6	14	14	10
7	16	21	3
8	19	10	2
9	11	9	1
10	13	10	0
11	9	8	14
12	5	14	7
13	13	3	4
14	12	4	5
15	10	4	1

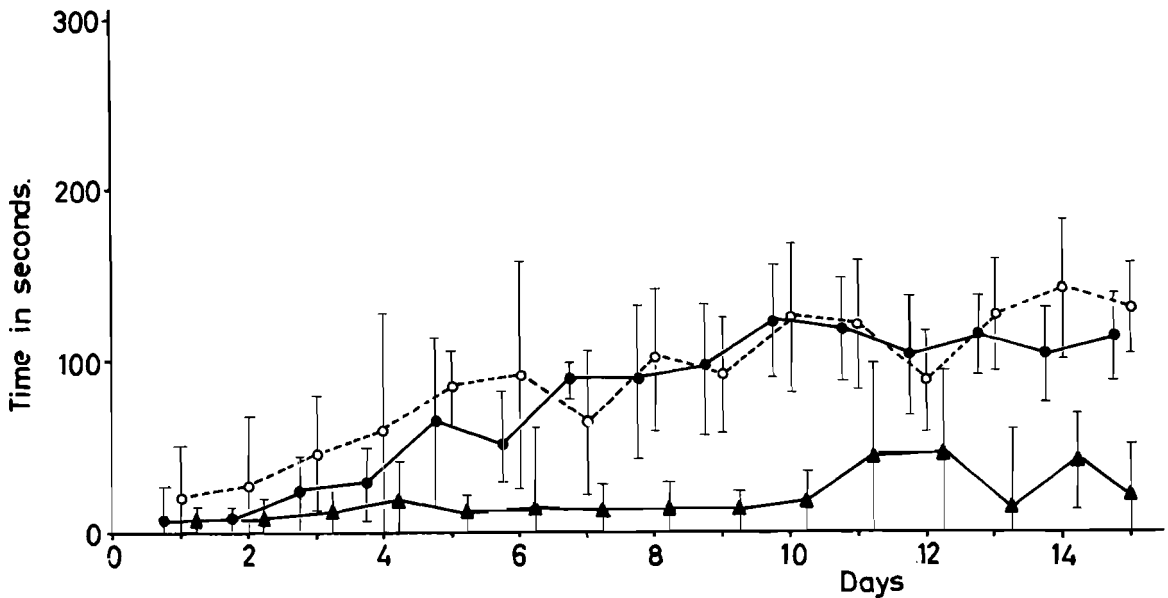


FIGURE 4

The time *H. philander* spent in courtship during each experimental period, on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

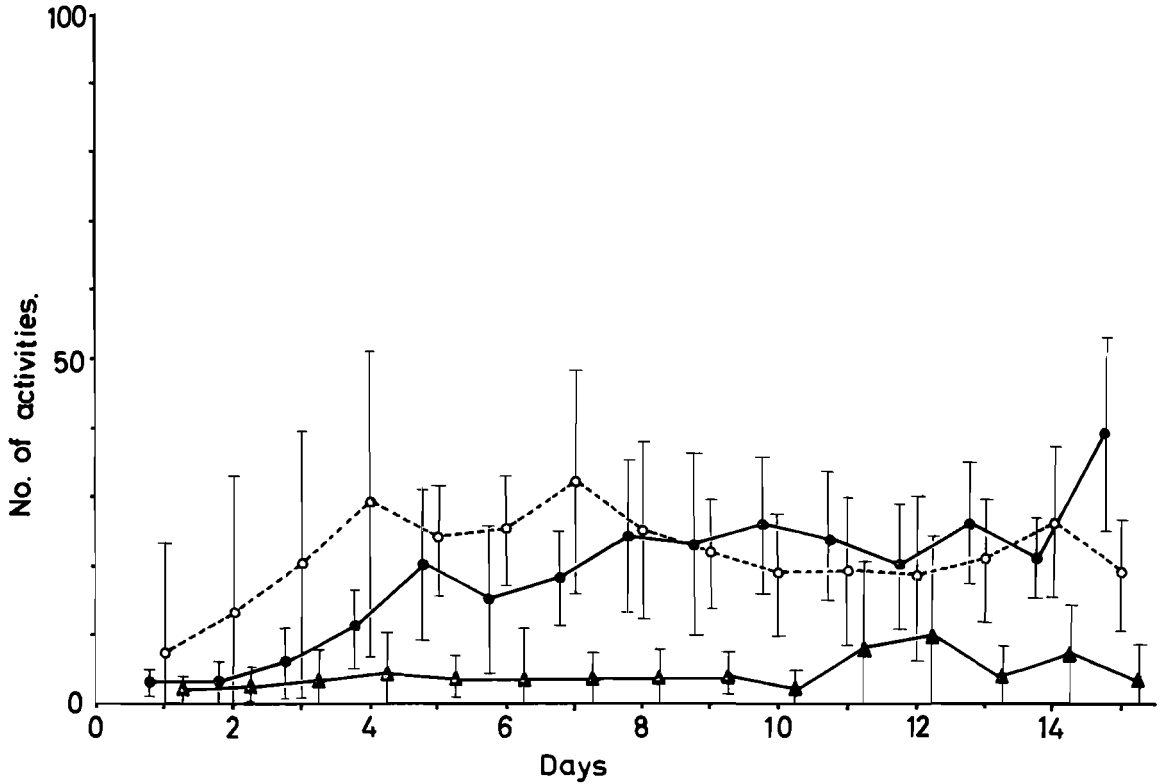


FIGURE 5

The number of courtship activities performed by *H. philander* during each experimental period, on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

Courtship behaviour

(a) *Time and activities*

Fish without their forebrain spent less time in courtship (Fig. 4) and performed fewer courtship activities (Fig. 5) than the sham operated and normal males.

(b) *Aggression during courtship measurements*

Aggressive behaviour in the presence of a gravid female also occurred. This aggression was evident in the two control groups, but was virtually absent from the forebrainless fishes (Figs. 6 & 7). Aggression in the former groups was especially marked during the establishment of the territories, when intruders were treated aggressively regardless of sex. In the later stages of the investigation, aggression was also evoked when the female in the flask failed to follow the courting male. This

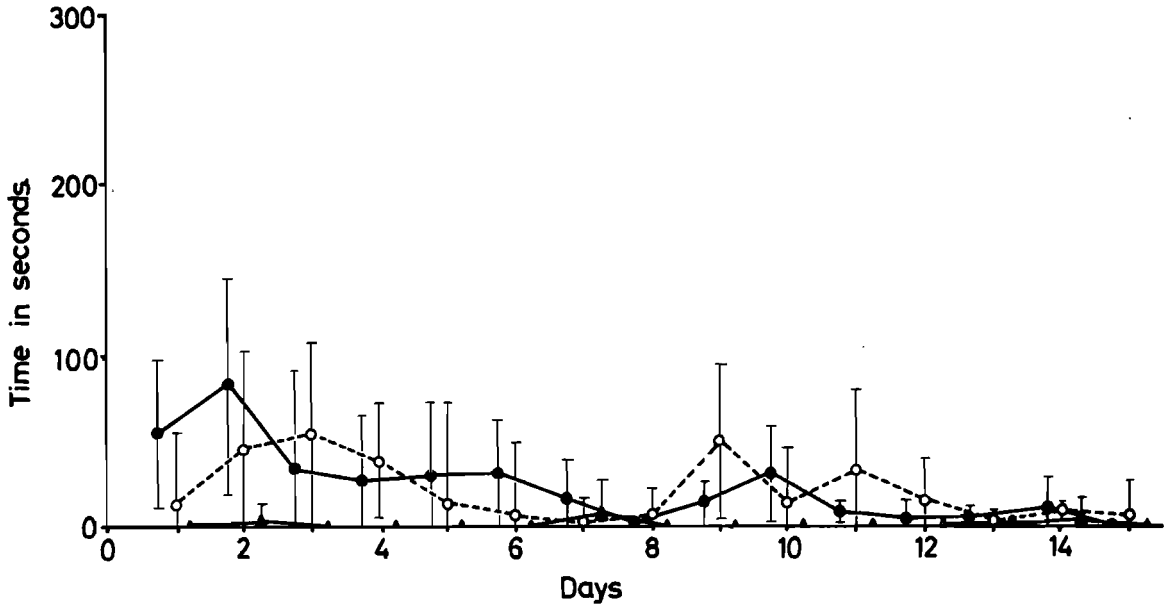


FIGURE 6

The time *H. philander* spent in aggressive behaviour during courtship in each experimental period, on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○) and forebrainless fish (▲).

TABLE 2

THE TOTAL NUMBER OF CHASES PERFORMED BY *H. philander* MALES DURING THE EXPERIMENTAL PERIODS IN WHICH COURTSHIP BEHAVIOUR WAS MEASURED. THE MEASUREMENTS WERE TAKEN ON SUCCESSIVE DAYS

Day	Control	Sham	Forebrainless
1	15	26	2
2	35	22	0
3	17	31	0
4	31	25	4
5	38	36	3
6	35	42	2
7	35	21	1
8	37	43	0
9	28	43	1
10	36	38	2
11	28	24	12
12	25	36	2
13	29	23	8
14	45	29	0
15	36	31	0

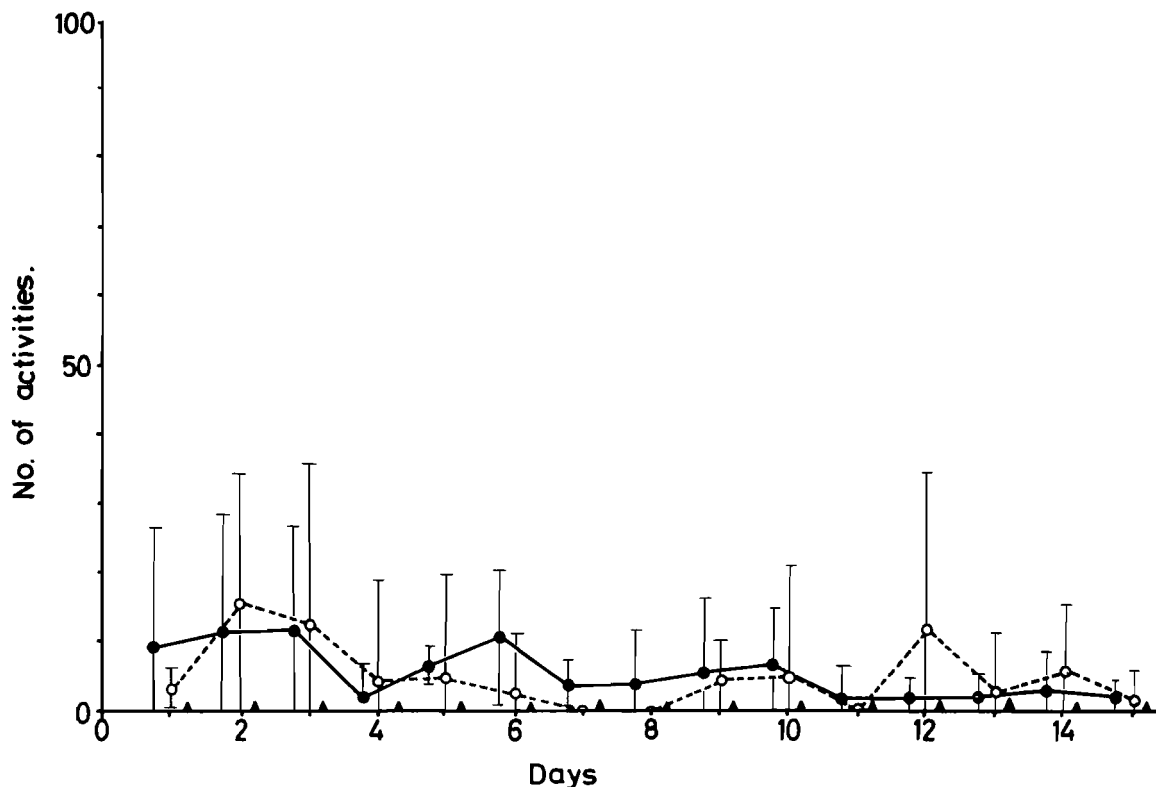


FIGURE 7

The number of aggressive activities performed by *H. philander* during courtship in each experimental period, on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors.

Normal controls (●); sham operated controls (○); forebrainless fish (▲).

aggression was often directed at the female in the flask but it was more commonly redirected, as manifested by an increased number of chases (Table 2).

The number of chases in the presence of a gravid female is greater than when in the presence of male conspecifics (Table 1), probably due to the aggression being more appropriately directed in the latter instance.

(c) Passive performances

When in the presence of a gravid female the two control groups spent less time in passive behaviour than the forebrainless fish (Fig. 8). A comparison of the time spent in inactivity when in the presence of a male conspecific (Fig. 3), with that when in the presence of a female conspecific (Fig. 8), shows that the time spent by the forebrainless fish in passive behaviour was similar in both instances. However, the two control groups were found to spend more time in inactivity

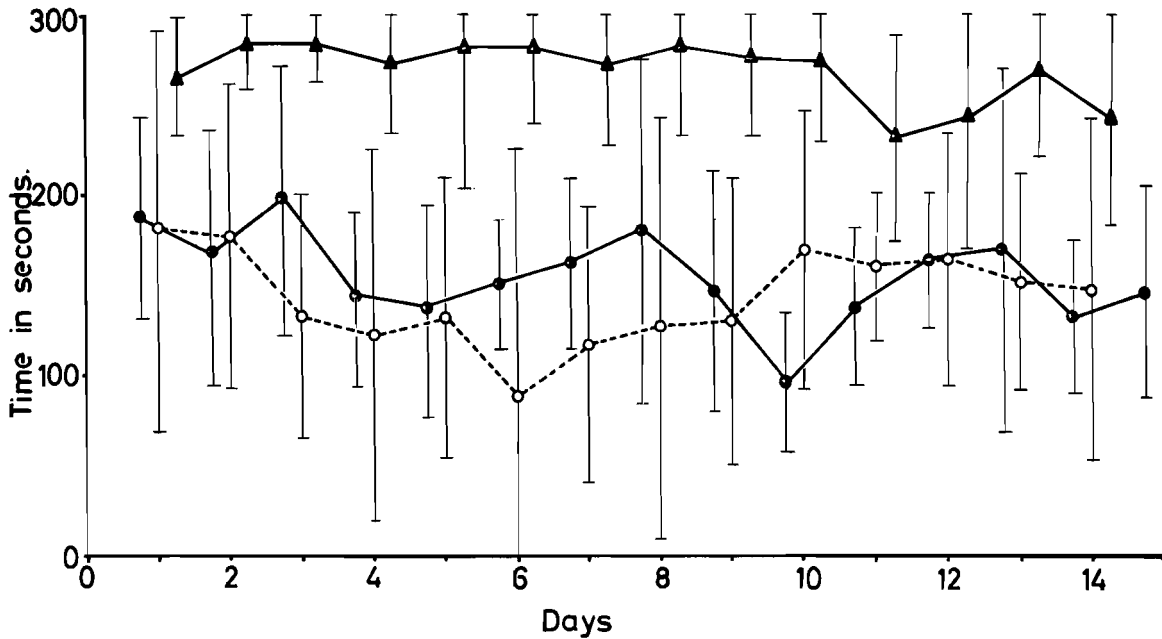


FIGURE 8

The time *H. philander* males spent in passive behaviour during each experimental period, when in the presence of female conspecifics. Measurements of behaviour were taken on successive days. The points on the graph represent the mean values ($N=7$), and the variation is expressed as two standard errors. Normal controls (●); sham operated controls (○); forebrainless fish (▲).

when presented with a gravid female. This increased inactivity of the sham operated and normal males could be partly attributed to the time spent in waiting for the females to either turn towards them, or waiting for the females to follow them to the nest.

(d) *Courtship sequences*

Thus far, the total number of courtship activities and the total time spent in courtship have been considered. This overlooks the fact that the courtship sequences are composed of a number of behavioural components. By considering each component of the courtship behaviour as a percentage of the total courtship pattern (Figs 9a and 9b) it is clear that the forebrainless fish spent the greater proportion of time in sideshake (SS). The forebrainless fish showed no nest-shake activity (NS) and the time spent in vertical-nest-shake (V) was increased. During the course of the experiment, the forebrainless fish spent 79 seconds in vertical-nest-shake whilst the normal fish spent five, and the sham operated fish spent four seconds in vertical-nest-shake.

This indicates that the relative occurrence of components of the courtship sequence was disproportionately altered by the ablations.

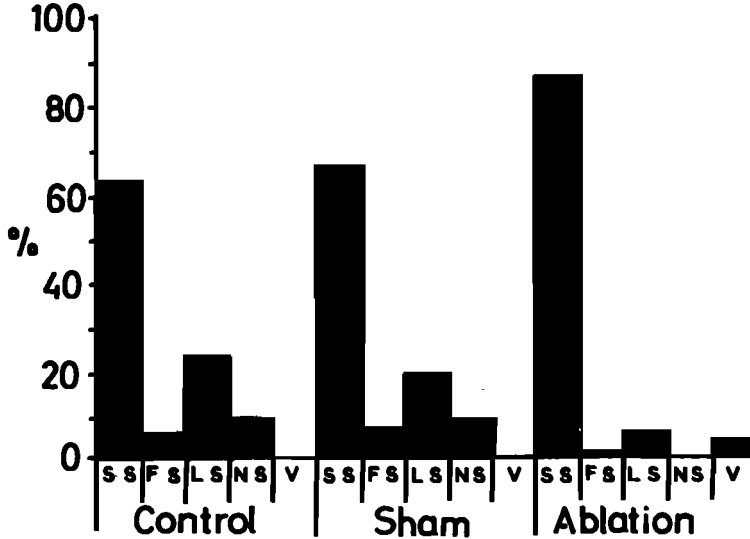


FIGURE 9a

The number of performances of each courtship component by *H. philander*, expressed as a percentage of the total number of courtship activities.

SS = side-shake; FS = follow-shake; LS = lead-swim; NS = nest-shake; V = vertical-nest-shake.

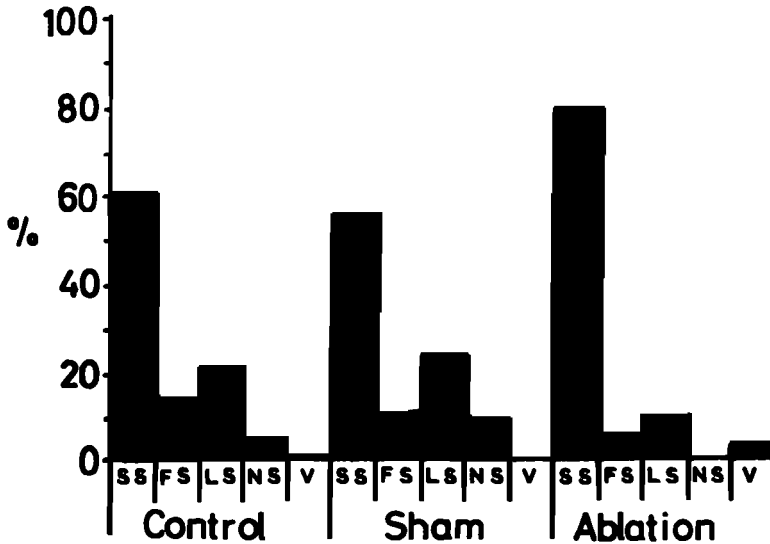


FIGURE 9b

The time *H. philander* spent in each component of courtship expressed as a percentage of the total time spent in courtship.

SS = side-shake; FS = follow-shake; LS = lead-swim; NS = nest-shake; V = vertical-nest-shake.

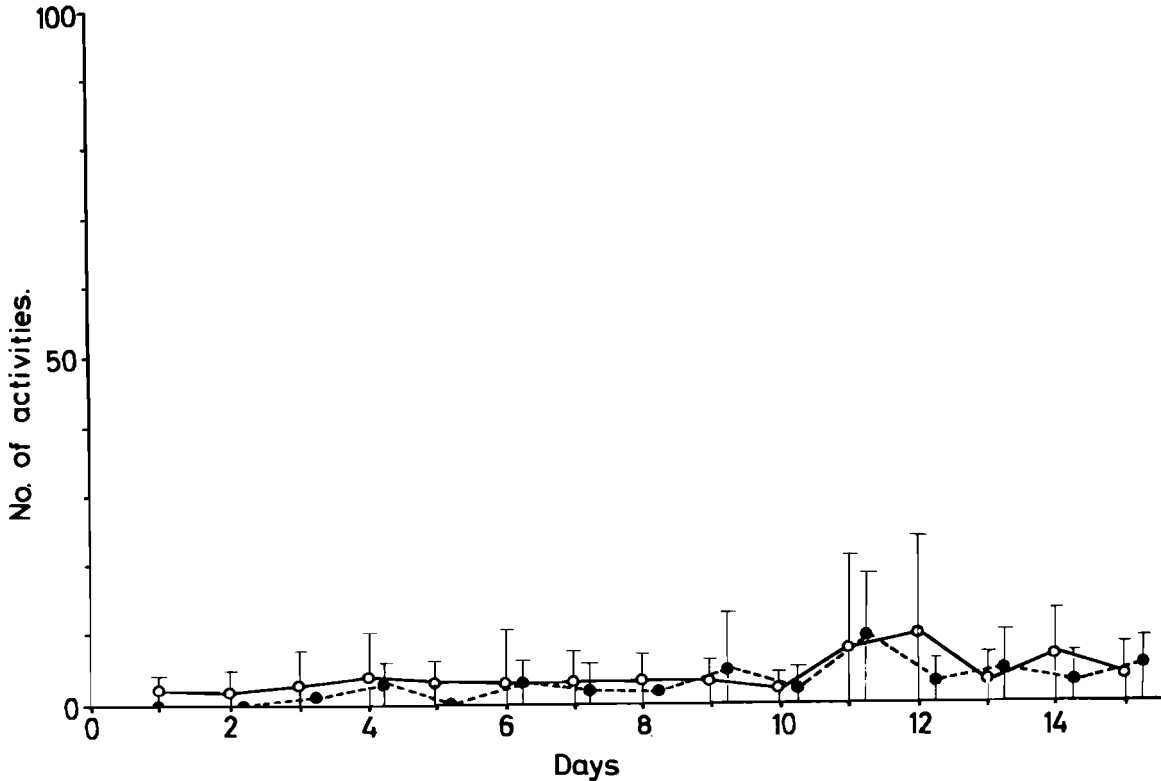


FIGURE 10

The number of courtship activities performed by forebrainless male *H. philander* to gravid conspecific females (solid line) and conspecific males (broken line), during each experimental period. The measurements were taken on successive days. The points on the graph represent the mean values ($N=7$) and the variation is expressed as two standard errors.

(e) *Sexual recognition*

It has already been mentioned that the forebrainless fish would court both sexes. It was thus of interest to compare the courtship activities (Fig. 10) and the time spent in courtship display (Fig. 11) of the forebrainless fish when in the presence of conspecific males with those performances when in the presence of conspecific females. These results show a striking similarity which demonstrates that the forebrainless fish were unable to distinguish between males and females, using the visual information provided under the conditions of this experiment.

The behaviour of the forebrainless fish under less restrictive conditions was investigated. On twenty-eight different occasions during the course of the experiment, a free-swimming conspecific male was released into the aquaria of the forebrainless fish. A normal male would not tolerate the

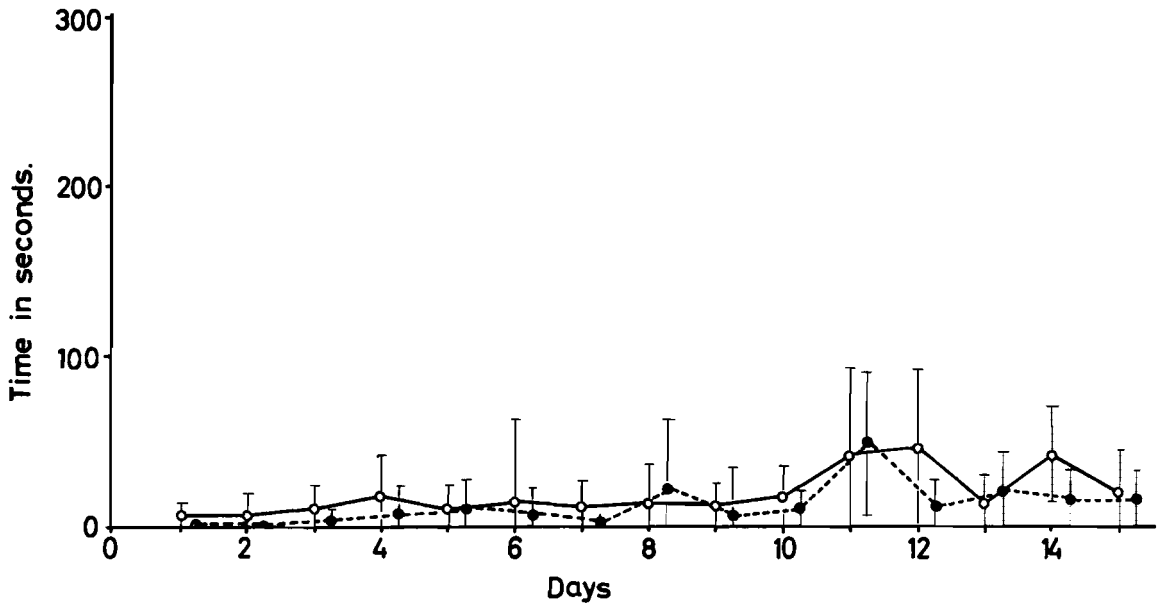


FIGURE 11

The time forebrainless *H. philander* males spent in the courtship of conspecific males (broken line) and conspecific females (solid line), during each experimental period. The points on the graph represent the mean values ($N=7$) and the variation is expressed as two standard errors.

presence of the intruder (Ribbink 1971) but the forebrainless males were found to court the intruding males.

The general pattern of behaviour, under these conditions, was as follows. The free-swimming normal male would begin to explore the aquarium. The forebrainless male would remain in inactivity from twenty to three hundred and sixty seconds, after which delay it might swim towards the intruding male. More frequently however, the exploring normal male would find the forebrainless fish. The approach of the normal male would elicit courtship in the forebrainless fish, to which the intruder would respond in an aggressive manner with bites and tail-beats. The forebrainless males usually continued with their unsuccessful sexual overtures for some time after the assault from the normal male had begun. Thereafter, a brief show of lateral display and possibly one or two tail-beats would appear, and then on every occasion the forebrainless fish was easily and rapidly defeated.

These results indicate that aggressive behaviour was inhibited by the forebrain ablation, and could only be elicited by repeated tactile assaults. Further, it would appear that males from which the telencephalon had been removed could not distinguish between the sexes on a visual basis, and it is doubtful if they can do so on a tactile basis, since the response to the tactile assault may be considered to be one of self defence and not sexual recognition.

TABLE 3
THE TOTAL NUMBER OF NESTS CONSTRUCTED BY EACH GROUP (N = 7) OF FISH DURING THE COURSE OF THE EXPERIMENT

Day	Control	Sham	Forebrainless
1	0	0	0
2	0	0	0
3	3	5	0
4	6	7	0
5	8	7	0
6	8	9	0
7	13	11	0
8	14	12	0
9	16	15	0
10	16	18	0
11	17	18	0
12	19	18	0
13	22	18	0
14	25	18	0
15	25	18	0

Additional results

Forebrainless fish failed to explore their environment and new objects, and failed also to dominate aquaria even when they were substantially larger than the other fishes. Furthermore, forebrainless males would allow themselves to be dominated by females.

Feeding behaviour was normal in execution, but the stimulus-response lag was considerably greater than that of normal and sham operated males. Nest building behaviour was entirely absent (Table 3).

On many occasions the response to a stimulus was abnormally powerful, which sometimes resulted in accidents. For example, the normal escape response elicited by a movement of a hand over the water surface is for the fish to dive down to settle on the substrate. It was not unusual for a forebrainless fish to dive into the sand substrate and become buried. Similarly the forebrainless fish often swam forcibly into or past the flask which contained the object fish. This did not occur in the control groups.

DISCUSSION

(i) Decreased activity

The most apparent alteration to the behaviour of *H. philander* resulting from the extirpation of the forebrain, was that these fish became less active than those in the control groups. The forebrainless fish spent most of their time motionless just above the substrate, usually in a corner or near a plant. They only occasionally showed any spontaneous activity, and exploratory

behaviour appeared to be completely absent. By contrast, the fish in the control groups initially explored their aquaria, and later they readily investigated new objects placed within the aquaria. They were perpetually employed in some form of activity; when presented with object fish the behaviour of the fish in the control groups was directed at these. At other times the males occupied themselves by establishing or maintaining their dominance, by digging or enlarging their nests and by chasing and foraging.

Telencephalic ablations in other fish have also been reported to result in severe decrements or loss of spontaneous and exploratory behaviour (Janzen 1933; Hosch 1936; Hale 1956a). It seems probable that the decreased activity of forebrainless fish is due to a decrease of spontaneous behaviour. A further contributing factor would be the increased stimulus-response latency found during measurements of feeding, courtship and aggressive behaviour of *H. philander*. This effect is not confined to *H. philander*, but has also been found by Aronson (1967), Aronson and Herberman (1960), Aronson and Kaplan (1963; 1965; 1968) and Hale (1956a) in other fish. Thus, in *H. philander*, and presumably in other teleosts, the decreased activity which results from telencephalic ablations can be partly explained by the apparent decrease or loss of spontaneous and exploratory behaviour, and by the increased stimulus-response lag period.

The observed decrements of all forms of territorial behaviour may be due to direct inhibition of such behaviours, or they may represent 'artifacts' of an increased stimulus-response latency.

(ii) *Aggressive behaviour*

With few exceptions it appears as though removal of the entire forebrain from teleosts results in a marked depletion of aggressive behaviour, accompanied by a loss of social status and other dependent territorial behaviours. Segaar (1961) also found that certain forebrain lesions in *Gasterosteus aculeatus* males resulted in a decrease of aggression so that they were unable to protect their territories. Similar reductions of aggressive, territorial and social behaviour were also found by Aronson (1948) using *Tilapia macrocephala*, and Hale (1956b) working on *Lepomis cyanellus*. Noble and Borne (1941), however, found no apparent reduction in vigour in the fighting of *Betta splendens*, *Hemichromis bimaculatus* and *Xiphophorus helleri* after partial or complete forebrain destruction. An assessment of their work is difficult, since it appeared only as a brief abstract.

It is not clear whether the loss or decrease of nest-building behaviour in *H. philander*, *G. aculeatus* and *T. macrocephala* can be linked with the apparent inhibition of aggression, or whether this represents a separate inhibitory phenomenon. Certainly the loss of social status and the inability to form and hold a territory can be partly ascribed to the decrease of aggressive behaviour after forebrain ablation.

One aspect of territorial behaviour which could be evoked by visual stimuli in forebrainless *H. philander* was that of chasing. The forebrainless fish chased on relatively few occasions (Table 1), and the chases differed from those of the normal fish insofar as they were incomplete. The forebrainless fish appeared to be unable to pursue a fleeing intruder which changed direction during the course of its flight. As a result of this the duration of the individual swimming pursuits was shorter in the forebrainless fish than in the control groups. A similar observation was recorded by Noble (1936) using other cichlids from which the forebrain had been removed. These fish were "unable to follow the school through rapid turnings". It seems likely that the lag period between

stimulus and response was too great for the deprived fish to maintain the stimulus-response communication.

(iii) *Courtship Behaviour*

As early as 1936/37 Noble reported that lesions in the corpus striatum (=forebrain) resulted in permanent defects in the sexual behaviour of some cichlid fish. Later, Noble and Borne (1941) found that forebrain extirpation from *H. bimaculatus* and *B. splendens* resulted in the complete loss of sexual activity in these fish, whereas in *X. helleri* all elements of sexual activity persisted after forebrain lesions. They claim that in *H. bimaculatus* and *B. splendens* both partners play an active role in courtship, while in *X. helleri* the female is the passive partner. They therefore concluded that the forebrain of *H. bimaculatus* and *B. splendens* regulates sexual activity by co-ordinating and synchronizing the behaviour patterns of the partners, whereas it is implied that in *X. helleri* the forebrain plays little or no part in the mediation of sexual behaviour.

In a more detailed study by Aronson (1948) it was found that the early courtship patterns of *T. macrocephala* were not reduced by "total decerebration" (forebrain ablation), whilst the later patterns, which were more directly associated with spawning, suffered a reduction in frequency of occurrence. Work on *Xiphophorus maculatus* (Kamrin and Aronson, 1954) showed that all sexual acts, except gonopodial swinging, decreased in frequency as a result of forebrain lesions. Segaar (1961) and also Segaar and Nieuwenhuys (1963) using *G. aculeatus*, demonstrated that sexual, aggressive and parental behaviour are in some form of balance in normal males. A series of different telencephalic ablations altered the normal balance of these drives in different ways, depending on the size and position of the ablation. They concluded that the function of the telencephalon of the stickleback is to regulate the timing and strength of expression of the components of aggressive, sexual and parental behaviour.

In *H. philander* the forebrain extirpations reduced the amount of invitation (early) courtship behaviour, and also changed the percentage occurrence of side-shake and other courtship behavioural components in a disproportionate manner. Furthermore, the ablations resulted in the inability of these fish to distinguish between male and female conspecifics on a visual basis.

(iv) *The execution of motor-patterns*

Both agonistic and courtship behaviour were drastically reduced by the ablations. However by means of visual stimuli courtship behaviour could be evoked, and a combination of visual and tactile stimuli could provoke intraterritorial aggressive behaviour. In both cases it appeared as though the behavioural motor-patterns were normal in execution. Because the execution of these patterns appears to be normal in fish without the forebrain it is likely that the organization of the execution of these motor-patterns takes place in brain centres posterior to the telencephalon. Since the motor-patterns appear to be organised elsewhere in the brain, the role of the forebrain in the mediation of these non-olfactory behaviours requires an explanation.

(v) *Interpretation of forebrain function*

There are at present two opposing schools of thought concerned with the non-olfactory functions of the telencephalon of bony fish. On the one hand, it is considered (Noble 1936; 1937; Noble & Borne 1941; Segaar 1961; Segaar & Nieuwenhuys 1963) that the integration of agonistic

(territorial), sexual and parental behaviour takes place in the forebrain. Those holding this opinion do not necessarily attribute the control of the behavioural motor-patterns to the telencephalon, but they suggest that the forebrain provides the necessary integration (co-ordination, synchronisation and adjustments to drives) of incoming information, thereby producing the correct responses in normal fish. It therefore seems, that although the control of the execution of the motor-patterns is seated in lower brain centres, it is the forebrain which is partially responsible for the translation of sensory input into the behavioural output.

The second school are of the opinion that integration of non-olfactory behaviour does not take place in the telencephalon, and suggest that the forebrain acts as an "activator", "facilitator" or "arouser" of these behaviour patterns. These ideas originated from the work of Janzen (1933) who observed that goldfish without their forebrains showed a decreased response to external stimuli, and very little endogenous activity such as exploration. He therefore suggested that the telencephalon is responsible for "initiative" and "spontaneity". Support for these suggestions comes from Herrick (1933) who suggested that one of the functions of the cerebral hemispheres of all vertebrates, including fish, is to serve as a "non-specific activator". Experimental work on *T. macrocephala* led Aronson (1948) to conclude that the telencephalon — "does not integrate any behaviour patterns, but rather facilitates the functioning of other parts of the brain which more precisely control these activities". Aronson's contentions were reinforced by Hale (1956b) who suggested that the behaviour patterns of the sunfish, *Lepomis cyanellus*, are organised in lower brain levels and that the telencephalon acts by facilitating these patterns. More recently Aronson and Kaplan (Aronson 1967; Aronson & Kaplan 1968; Kaplan & Aronson 1963) furthered their hypothesis by means of avoidance conditioning experiments, in which it was demonstrated that the stimulus-response latency of *T. macrocephala* was markedly increased by forebrain extirpations. Although Hale (1956a) found that all previously established associations were lost as a result of forebrain extirpations, Aronson and Kaplan (1968) found that previously conditioned responses were not obliterated by the operations, and therefore concluded that forebrain ablations cause a decline or change of behaviour patterns, but not the elimination of these patterns. Aronson and Kaplan (1968) suggested that the forebrain does not organise behaviour but exerts a strong influence over almost every behaviour pattern studied. They suggested that the forebrain functions are (1) non-specific and (2) facilitative i.e. the forebrain functions as a "non-specific arousal system". They drew support for their hypothesis from the electro-encephalographic (EEG) recordings of Enger (1957), and Schadé and Wieler (1959), in which the EEG activation was associated with reduced reaction time (=arousal). Furthermore, an anatomical examination of the brain of *T. macrocephala* revealed major fibre tracts running from the telencephalon to the di- and mesencephalon, which suggested to Aronson and Kaplan (1967) that the forebrain might exert a "dynamic influence on the midbrain". Probably it is the midbrain which organises the behavioural motor-patterns.

On the basis of this hypothesis Aronson (1967) prefers to interpret his own work, and the decrements and alterations to behaviour reported by other workers, as a failure of the "arousal system" rather than the removal of excitatory or inhibitory systems as interpreted by Segaar, Nieuwenhuys, Noble and others.

The effects of forebrain ablations on the behaviour of *H. philander* cannot be satisfactorily explained by the interpretations of one school of thought to the exclusion of the other, but

requires both interpretations to account for the behavioural modifications found. This suggests that an interpretation of the function of the forebrain of teleosts should incorporate both of these views.

The conversion of the endogenous and exogenous sensory input into a behavioural output must be considered as a process involving neural integration, and the resultant behavioural response would represent the final balance of the incoming information. The elucidation of the role of the telencephalon in the mediation of non-olfactory behavioural responses cannot be fully explained in terms of adjustments to the balance of the excitatory and inhibitory nuclei. In fact, were it not for the experimental evidence to the contrary, the involvement of the telencephalon in these behaviours would seem unnecessary, because with the possible exception of nest-building behaviour, it has been shown that the non-olfactory behaviour patterns are organized in lower brain levels.

The non-specific arousal hypothesis could explain (incorporating neural integration) the involvement of the telencephalon in visually oriented behaviour. It could also account for the increased stimulus-response latencies, the loss of spontaneous behaviour (exploratory), and partially account for the decreased frequency of occurrence of aggressive/territorial, courtship and swimming behaviour which resulted from telencephalic extirpations. This hypothesis, however, is too general to yield much information about the precise mechanisms involved. Furthermore; (1) the inability of forebrainless *H. philander* to distinguish between males and females; (2) the disproportionate relative decrements to the frequency of the occurrence of the components of courtship behaviour and (3) the abnormal escape response cannot be explained in terms of a failure of an arousal mechanism, but rather as a disruption of the balance between excitatory and inhibitory nuclei.

Although Enger (1957), Schadé and Wieler (1959), and Gusel'nikov *et al.* (1964) have shown that electrical patterns associated with 'arousal' occur infrequently in the telencephalon of fish, Timkina (1965) and Zagorul'ko (1965) have shown that some electrical transfers do take place between the telencephalon and mesencephalon. It therefore seems possible that the arousal system is present in certain teleosts, but it is poorly developed.

Arousal is one of the functions of the limbic system of higher vertebrates, and several authors (Aronson & Kaplan 1968; Gusel'nikov *et al.* 1964; and Segaar & Nieuwenhuys 1963) have drawn attention to the similarity of function of the limbic system of mammals and the teleost forebrain. Other important functions of the limbic system, and particularly the hippocampus, are those associated with the focussing of attention, motivationally oriented behaviour (drives) and the selection of the appropriate behavioural response to a situation (total stimulus input).

Anatomical evidence (Ariens Kappers, 1921; Nieuwenhuys, 1959) indicates that much of the limbic system of mammals is represented by precursors in the teleost telencephalon. In addition Ariens Kappers (1921) and Gusel'nikov *et al.* (1964) (by implication) are of the opinion that the epistriatum of teleosts is an analogue of the primordium hippocampi of amphibians and other vertebrates.

The presence of a limbic system, albeit primitive, in the teleost forebrain could account for most behavioural modifications resulting from telencephalic ablations. Those behaviour patterns which cannot be explained in terms of the arousal system, could be accounted for by other limbic systems. For example, the ability to distinguish between male and female conspecifics would

depend upon an evaluation of the incoming information, and upon the selection and initiation of an appropriate behavioural response. If the teleost epistriatum is the analogue of the hippocampus of higher vertebrates, then the fish forebrain would be expected to house the neural apparatus for the assessment of sensory input and for the selection of appropriate behavioural output. The inability of forebrainless *H. philander* to distinguish between the sexes could then be explained in terms of an alteration or removal of such a selection mechanism.

The arousal hypothesis has been used to explain the increased stimulus response latency. An alternative suggestion is that the removal of the usual mechanism for response selection makes it necessary to use compensatory selection routes where possible. These compensatory mechanisms would take more time to select the appropriate, or in *H. philander* some inappropriate, behavioural responses. Aronson and Kaplan (1964) have evidence for the presence of long term compensatory mechanism in the cerebellum.

Since the regulation of motivationally directed behaviour is partly attributed to the limbic system in mammals (Guyton 1966), it may also be possible to account for the alterations to the balance of drives, described by Segaar (1961) and Segaar and Nieuwenhuys (1963), in terms of an interference with the limbic system. Should limbic structures be present in fish then it is probable that they would influence each other, and thus the final behavioural response would represent an integration of numerous centres.

It is suggested that the forebrain of *H. philander* functions not only to provide a general excitation (arousal) of non-olfactory behaviour patterns, but also functions in a more specific manner by which it selects the behavioural response(s) appropriate to a given situation. This not only indicates that a limbic system may be present, but also suggests that a partial organisation of non-olfactory behaviour occurs in the forebrain.

Finally, Gusel'nikov *et al.* (1964) found good EEG responses in the forebrain of amphibia and reptiles to photic and acoustic/lateral line stimuli, but very poor responses in the forebrain of the goldfish. They therefore concluded that the conduction of all forms of sensation to the telencephalon begins in the amphibia, and that this has been the basis of telencephalic development in the vertebrates. In view of the involvement of the teleost forebrain in behavioural responses to visual and tactile stimuli, it would appear that sensations, even if modified by the tectum, are transferred to the telencephalon. Thus it seems possible that the progressive development of the vertebrate forebrain began in early fishes.

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