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THE UNIVERSITY OF ALBERTA

REINFORCEMENT PROPERTIES OF AGGRESSION AND SEX PROVOKING STIMULI
IN THE SIAMESE FIGHTING FISH

by



STEPHEN R. GOLDSTEIN

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
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UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Reinforcement Properties of Aggression and Sex Provoking Stimuli in the Siamese Fighting Fish", submitted by Stephen R. Goldstein in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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To my parents

ABSTRACT

The general problem of experimental interest centered around the reinforcing properties of stimuli associated with reproductive behavior of the male Siamese Fighting Fish (*Betta splendens*). The specific purpose of the research was to determine whether live male and live female *Bettas* were effective reinforcers for conspecific males. Using an operant conditioning procedure, the research objectives were achieved by the manipulation of schedule, deprivation and display conditions. A second purpose was to investigate the role of social and physical stimulus factors in controlling operant behavior. Finally, the validity of the operant measure was assessed by matching combatants against each other on the basis of their conditioning rates.

It was found that both live male and live female *Bettas* function as strong positive reinforcers. However, the data suggest that there may be unique differences between the two with regard to schedule controlled responding. Stimuli capable of specifically engendering either frontal or lateral display were found to support different rates of responding; lateral display supported the higher rate. The physical stimulus of light was found to have a powerful effect on the temporal distribution of operant responding in that a suppression occurred during the twilight phase of a light-dark cycle while a noisy circadian rhythm, containing 23, 24, and 25h components emerged with continuous illumination. Finally,

mirror-supported conditioning rates were found to predict the outcome of fighting contests.

Reinforcing effects were discussed in terms of Premack's law, naturalistic contingencies, and emotionality. The concept of agonistic behavior was used as basis for contending that the male reinforcer elicits both approach and withdrawal tendencies making it an ambivalent reinforcer. This ambivalence may be related to its unique schedule effects. Aschoff's rule, a generalization about the circadian rhythms of day and night active animals under monophasic light conditions, was used in conjunction with known facts about the reproductive activity of *Betta* to account for the appearance of disturbed circadian periodicities in operant responding.

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CHAPTER I

I N T R O D U C T I O N

Domestic strains of Siamese Fighting Fish (*Betta splendens*) are the end product of a relatively short history of selection for aggressive behavior (Smith, 1945). However, so highly refined is this selection that today it is safe to say that a random matching of any two adult males would probably result in an immediate aggressive encounter. An appreciation of the intensity of this behavior can be gleaned from the fact that if the combatants were not separated at the end of the contest the loser would likely die in a short time.

The aggressive behavior of *Betta splendens*, which is characterized by a highly complex display that eventually gives way to fighting (Simpson, 1967), appears to be visually mediated as its release can be effected by exposure to either a "model", a mirror or a rival male in an adjacent aquarium (Lissmann, 1933).

In a now classic study Thompson (1963) demonstrated that stimuli capable of releasing aggressive display could also function as positive reinforcers. Since this demonstration forms the basis of the experimental work reported in this dissertation it is important that it be considered in some detail.

Thompson studied the relative reinforcement properties of the fish's mirror image and of stationary and moving wooden models of displaying male *Bettas*. A ring with a 3 in diameter was placed in

an aquarium about 3 in from a two-way mirror. The ring was constructed in such a way that upon swimming through it the fish would interrupt light coming from a photocell system thereby shutting off a bright light bulb located behind the two-way mirror. This produced a mirror to which the fish could display for a fixed period of time (20 sec). At the end of the 20 sec the light bulb located behind the mirror turned on and thereby destroyed the mirror effect. Further exposure to mirror could only be had by further ring swimming responses.

Under these conditions, Thompson found that fish would, at asymptote, emit over 600 responses in a 24 h day; an effect sustainable over several days. The unusual nature of this demonstration lay in the suggestion that the stimuli which engender aggressive behavior act as positive reinforcers.

At least three related control problems were raised by this demonstration. First, the dependent measure used was ring swimming and not display. Therefore it became possible to argue that "light off", as opposed to mirror display, was supporting the ring swimming behavior since the illumination change was also response contingent. Besides being logically defensible, the above argument is supported by evidence showing that light changes have reinforcement properties for rodents (Lockard, 1963).

Secondly, since displays were not recorded it is possible to take the position that the fish may not have consistently emitted the display response upon exposure to mirror image. If this were the case, the logical chain connecting mirror-aggressive display

reinforcer would be broken or at least seriously weakened.

Finally, it is known that upon exposure to mirror image a *Betta* will show a general increase in activity and a specific increase in circling behavior (Evans, Abramson, & Fremont-Smith, 1958). It is therefore possible that the increased rate of ring swimming may have had nothing to do with the response-reinforcement contingency but could instead have been attributable to the activating effect of mirror image (Goldstein, 1967).

These three control problems have been subjected to experimental analysis and have yielded essentially negative results. Thompson (1963) found that removing the two-way mirror entirely, but leaving the light off contingency still intact, resulted in a rate of responding equal to or less than that obtained in a previous extinction session. Thompson and Sturm (1965,b) measured display as well as the operant response and found that the fish displayed about 97 per cent of the time the mirror was presented. And finally Goldstein (1965, 1967) and Hogan (1967) used yoked control designs to account for the activating effect of mirror image and found that heightened activity played a minor role in determining response rate.

Though the control problems are not exhausted in the above analysis, it is probably safe to assume that the effect demonstrated by Thompson is valid. Scientific knowledge about a new bona fide phenomenon is usually accumulated and advanced by the identification and analysis of the factors which influence its occurrence. In case of the mirror-image-as-reinforcer demonstration, relatively little is known about the

controlling variables. Therefore, it seemed desirable to survey a number of factors of a general nature known to control operant behavior and some specific factors peculiar to the Siamese Fighting Fish which might also have been a source of behavioral control.

Generally speaking there are three broad classes of factors manipulated in the experimental analysis of operant behavior. These deal with various intrinsic and extrinsic aspects of the *reinforcement* situation, such as its magnitude or schedule characteristics; with properties of the *response*, such as its force or specific typography; and, with a variety of *stimulus factors* which may be either antecedent to, coterminous with, or totally independent of, the response. In the following, attention is focused only on reinforcement and stimulus factors.

Reinforcement

This section is concerned with intrinsic and extrinsic characteristics of the reinforcer.

Intrinsic Properties

The intrinsic properties of the reinforcement situation under consideration deal with distinctions involving live fish and mirrors, males and females, and with heteroplastic or different plane mirror stimulation.

Live Fish: Every operant study to date employing male Siamese Fighting Fish has used either the mirror image of the fish or a model of a *Betta* as the reinforcer. The use of a live male *Betta* as a reinforcer has never been reported in the literature. Further questions about the possible

artifactual nature of the demonstration would be attenuated by showing that a live male also acts as a positive reinforcer. Thus Gallup (1968) in a review article offers the suggestion that the reinforcing effect can be attributed to novelty associated with mirror image stimulation.

There is an additional reason for considering the reinforcement properties of live males. Thompson (1963) concluded that "the relative reinforcement properties of visual stimuli, similar to male fish in aggressive display, covary with the degree to which stimuli will evoke unlearned aggressive display". Baenninger (1966) used a free choice situation and found that *Bettas* displayed more frequently to mirrors than live fish. If Baenninger's results are interpreted to mean that mirror is a more effective releaser of aggressive behavior than live fish, the implication would be that mirror should sustain a higher operant rate. However, an alternative interpretation is that the mirror is a less intimidating stimulus, an interpretation that leads to no specific a priori prediction. Since both interpretations are justified by the data, differential prediction based on these results would seem highly arbitrary. However, it is desirable to utilize live fish reinforcement since it may provide a first step toward the establishment of a rough response range which can be used to evaluate the relative reinforcement properties of live fish and mirrors.

Male-Female: At the outset it was stated that the placement of two males together in an unpartitioned tank would result in an elaborate mutual display that eventually would give way to fighting. Interestingly, if one of these males had been exposed to a mature female *Betta*, a display,

which in many respects is indistinguishable from the one the combatants show each other, would have occurred. This implies that if the response is regarded as the reinforcing event, and two qualitatively different stimuli produce this response, the principle of equivalence predicts that if one were a reinforcer the other would be too. Specifically this would mean that the female *Betta* should act as a positive reinforcer for the male. It was a major purpose of this dissertation to determine if the female did in fact operate to reinforce behavior of the male. There is evidence that sex-provoking stimuli can act as positive reinforcers in rats (Sheffield, Wulff, & Backer, 1951) and that visual access to a female can act as a positive reinforcer for male sticklebacks (Sevenster, 1968).

Heteroplastic Mirror Stimulation: By way of anticipating one outcome of the present experimental research it may be indicated that some subjects failed to achieve high rates of responding. A host of reasons could, of course, be given for this, not the least of which asserts that this kind of variability, far from being atypical, should, in fact, characterize a species if enough subjects are tested. The consequence of this approach, however, is that to enhance further understanding it is necessary to look for organismic differences between species members in an attempt to correlate such difference with differences in performance. While there are merits to this approach, it suffers from the threefold disadvantage that (1) it is not always evident what the critical organismic factors are, (2) given the existence of a critical factor, it is not always possible to obtain subjects that

vary along a continuum of this factor, and (3) since the experimenter usually cannot randomly assign the organismic factor to the subject, there is an ever present problem of interpretive difficulty arising out of covariation with traits incidental to those of experimental interest. An alternative approach is to look, not in the subject, but rather in the subject's environment to account for differences in behavior.

One interesting and potentially important situational difference between the present and earlier work (i.e. Thompson, 1963; etc.) was the area of reinforcement available for display. Both Thompson (1963) and Hogan (1967) used the entire wall of a standard 2.5 gal. aquarium for mirror image presentation and Goldstein (1967) used an area 4 in high by 8 in wide to reinforce subjects. In the present study, however, it was necessary to use an area of reinforcement slightly less than 3 in wide by 8 in high in order to effect control over stimulus presentation. One consequence of this, which was evident from casual observation of displaying subjects, was that during lateral display the subject would almost immediately leave the area of reinforcement because of a propensity to swim in the horizontal plane during display. Doing this, however, eliminated the visual feedback of the reinforcer. Other subjects were seen displaying in the frontal position during the time reinforcement was available. Therefore, on the basis of these observations, it was postulated that the reinforcement area initially used favored the performance of frontal display and discouraged the emission of lateral display. Finally, to account

for differences between this and previous work, it was assumed that frontal display would be a less potent reinforcer than lateral display. Therefore, the aim of the study on heteroplastic mirror stimulation was to determine whether different display components differentially affect operant responding.

Extrinsic Properties

The reinforcement schedule and deprivation were two extrinsic reinforcement properties dealt with in the present study.

Schedule Properties

With an aim of further extending the reinforcement nature of male and female *Bettas*, the particular schedule characteristics investigated were the operant rate, the response contingent rate under continuous reinforcement (CRF), variable ratio reinforcement (VR) and variable interval reinforcement (VI), and finally, the nonresponse contingent rate under extinction.

Operant Level: In operant conditioning studies the organism is required to emit some specified response in order to procure reinforcement. Since the rate at which this response is emitted constitutes an important dependent variable, it is necessary to have some idea of the frequency with which this response normally occurs. That is, a reward-free baseline is needed against which subsequent response-contingent behaviour can be compared. The effectiveness of the reinforcer and of the response reinforcement contingency can be ascertained by noting departures from the baseline operant rate. As in earlier work with Siamese Fighting Fish, the present study incorporates the operant level determination.

Response-Reinforcement Contingency: When a reward-free baseline level of responding has been established, the effectiveness of a presumed reinforcer may then be ascertained by programming arrangements which make reinforcement presentation contingent on the emission of the operant response. There is a relatively large number of response-reinforcement contingencies and these are collectively referred to as schedules of reinforcement (Ferster and Skinner, 1957).

If each operant response results in the acquisition of reinforcement then a continuous reinforcement schedule (CRF) is in effect. Before the completion of the present experimental work this schedule was the only one ever reported in the literature to control operant behavior in *Betta*.¹ In general, response rates ranging from 600 (Thompson, 1963) to 1400 responses in a 24 h day have been reported with this schedule. It is used again in the present study with a mirror reinforcer, and for the first time, with live male and live female reinforcers.

Reinforcements do not have to follow each response. This schedules can be arranged in which reinforcement is primarily controlled by the emission of a specified number of responses (a ratio schedule) or by the passage of a given period of time (an interval schedule) and these schedules may either be fixed or variable.

¹ See Discussion Section for consideration of more recent work.

It is a common practice in operant research to maintain behavior under some form of intermittent reinforcement schedule (Morse, 1966). Prior to the completion of this study, however, mirror reinforced operant behavior in *Betta* had never been reported on anything but a CRF schedule. If mirror image is indeed a viable reinforcer, it should be possible to maintain operant behavior under various schedules of intermittent reinforcement. In this study an attempt was made to maintain operant behavior on variable ratio (VR 3) and variable interval (VI 30) schedules.

Variable interval and VR schedules have the property of producing high constant rates of responding throughout an experimental session (Teitelbaum, 1966). This is a convenient property because it tends to make schedule behavior sensitive to change as indicated by departures from this constant rate. This departure can be used as an index of the effectiveness of superimposed treatment conditions and a number of treatment conditions are used in the present study.

In the operant conditioning situation, if contingencies are arranged so that reinforcement no longer follows the response, the rate of responding will eventually deteriorate to pre-reinforcement levels (Skinner, 1938). This response attenuation is known as extinction.

Extinction demonstrates the reversible nature of the operant behavior with the discontinuation of the reinforcement contingency. This reversibility is a final step in the chain from operant level to contingent level to extinction level, demonstrating that contingent reinforcement can alter and control the probability of an

arbitrary response.

In this study the main purpose of applying the extinction procedure was to demonstrate the reversibility of the reinforced behavior. The actual time to reach a near operant level was also of particular interest as the extinction level in earlier work (e.g. Thompson, 1963; Goldstein, 1967) was well above the baseline operant rate. The actual course of extinction or the absolute number of responses emitted are given secondary consideration as a variety of treatment conditions and an extremely protracted extinction session would likely confound traditional schedule effects.

Deprivation: A condition of deprivation is created by temporarily eliminating the availability of stimuli capable of releasing consummatory behavior. Usually these are unconditioned or reinforcing stimuli. In the learning experiment the definition is expanded to include the elimination of the response manipulandum so as to prevent confounding with extinction.

There is a conceptual tie binding deprivation and reinforcement which is based on an empirical fact showing a functional relationship between response strength and deprivation time (Miller, 1957). Though the relationship is by no means simple, depending as it does on the response measure, the motivational system, and a variety of organismic factors, some form of covariation usually emerges. This has lead some theorists to assume that deprivation creates a "drive" state which in one form or another, is presumed to be necessary for learning to occur (e.g. Hull, 1943). Others take a more conservative position

maintaining simply that deprivation merely facilitates response acquisition (Skinner, 1938). Clearly both positions regard the motivational properties of deprivation as important for learning and indeed an experiment involving positive reinforcement would almost never be attempted before a deprivation state had been created.

That is what makes mirror image reinforcement in *Betta splendens* so interesting. All the available data indicate that a deprivation state in the usual sense is not needed to effect response acquisition or to maintain high rates after learning has occurred, though this does not preclude the possibility of a deprivation effect emerging. Indeed, in the present study, the effects of deprivation from the male reinforcer and deprivation from the female reinforcer are given systematic consideration.

Stimulus Factors

Two categories of stimulus factors were investigated. One of these, which may be termed social stimulation, involved prolonged visual free access to a fish of the opposite sex of the reinforcer. The other, which may be regarded as physical stimulus, was the light-dark cycle.

Exposure: Exposure refers here to a treatment in which an experimental fish (i.e. a fish working for reinforcement) is given unrestricted visual access to a fish of the opposite sex of the reinforcer. Exposure is not concurrent with reinforcement stimulation.

Since two types of reinforcement are used, two exposure conditions are possible.

In one condition a male reinforced by another male is given temporary access to a female. In the other, a male reinforced by a female is given temporary access to a male. Presumably exposure to female stimulates and facilitates the expression of reproductive activities (Aronson, 1945) while exposure to a (rival) male induces increased aggression. Two experimental questions are asked:

(1) Does exposure to a female (i.e. the arousal of sexual behavior) affect the intensity of aggressive behavior (as reflected in the frequency of ring swimming) towards the reinforcing male? and

(2) Does exposure to a rival male affect the intensity of subsequent sexual reinforced operant behavior??

These questions are of interest because social interactions of this sort may be important modulators of aggressive and sexual behavior..

Light: In fishes, as in most other phylectic groups, one of the most important determinants of appetitive behavior in general and reproductive behavior in particular, is light (Pickford & Atz, 1957; Lockard, 1963). For this reason, it is standard procedure among fish researchers to precipitate reproductive behavior by modification (usually lengthening) of the day-night cycle (Hoar, 1962).

In previous research with mirror image reinforcement (e.g. Thompson, 1963) subjects were tested on an around-the-clock basis. However, in order for the two-way mirror system to work effectively, it was necessary to maintain continuous light conditions

over the experimental apparatus. This, it turns out, corresponds to one aspect of a basic procedure used by biologists to investigate innate periodicities of a physiological and behavioral nature (Sollberger, 1965).

There exists a large body of experimental evidence which demonstrates that organic activity, from simple vegetative processes occurring in plants and microorganisms to complex behavioral patterns occurring in higher vertebrates, can be characterized by a reliable waxing and waning in frequency over time (Harker, 1964). The most commonly studied periodicities are those approximating the length of a day, and are usually designated as circadian (circa = about; dies = day).

In order to establish the existence of a circadian rhythm an organism is tested under constant light and temperature conditions. This favors the production of a characteristic distribution of response throughout the "day" which presumably reflects an underlying biological clock. Constant conditions are used in an attempt to eliminate periodic external cues which might act to control responding. Under such constant conditions the underlying rhythm is allowed to "run free" at speeds slightly less or slightly more (depending upon the species) than 24 h.

Since continuous illumination was used in earlier research with *Betta*, it was repeated here in an attempt to determine whether male-reinforced and female-reinforced operant behavior followed a circadian pattern.

Conditions may also be arranged, however, in which a periodic external signal synchronizes the underlying rhythm to its own

phase. Such stimuli are called entraining stimuli by Pittendrigh (1960) or Zeitgeber (time giver) by Aschoff (1960). Illumination and temperature are the most frequently used Zeitgeber. Typically, when illumination is used as an entraining stimulus, response is restricted to a specific phase of the light-dark (LD) cycle, depending primarily upon whether the organism is normally day or night active (Aschoff, 1960).

Studies of entrainment are an integral part of circadian rhythm research since it is usually necessary to demonstrate the existence of a fixed pattern from which the circadian rhythm can deviate. In the present study an attempt is made to entrain the operant behavior for both reinforcers to a light-twilight cycle.

Validity of the Operant Technique:

It is necessary at this point to deal with a problem that is basic to this entire study and to much of the operant work previously reported on *Betta*. The point at issue is whether the operant rate can be considered a valid measure of the presumed underlying motivational state supporting the operant behaviour.

To consider this question in more detail, assume that two subjects are placed on a CRF schedule reinforced by mirror image. One subject emits 500 responses a day and the other emits 100 responses a day. On the basis of this, one might conclude that the first fish was more aggressive than the second. The reasons supporting this conclusion are, (1) the aggression provoking stimuli are not available to subject prior to his response; (2) therefore, the more subject responds the more

often does he produce his mirror image to which he may exhibit the aggressive display and (3) a fish which displays most frequently or puts himself in a position to do so, must be the more aggressive of the two.

Stated this way, the assumptions underlying the operant analysis of motivation become clear. Specifically, in the operant analysis of aggression and sex the measure of the intensity of these presumed motivational states is the rather indirect one of the arbitrarily defined operant. What gets measured, in other words, is not some property of aggressive display, like its latency or even its occurrence, but rather the number of times the fish swims through a ring per unit time. Clearly, swimming through the ring is not an aggressive or sexual response. It is assumed, however, that these motivational states are operative, since the operant is the means by which subject can show aggressive or sexual behavior, just as opening a refrigerator door is the means by which one gains access to food. The operant technique, therefore, gains its validity as an index of the intensity of the underlying motivational state if (a) there is a high correlation between the occurrence of the operant response and the subsequent occurrence of the species typical consummatory response (i.e. display) or better yet, (b) if a high rate male can defeat a low rate male in a fighting contest. With regard to the first of these conditions, Thompson & Sturm (1965, b) have found such a correlation to exist. With regard to the second, it was the purpose of a further experiment to determine whether a relationship existed between operant performance and fighting.

Summary

The general problem of experimental interest centered around the reinforcing aspects of stimuli associated with reproductive behavior in the Siamese Fighting Fish. The main purpose of the study was to determine whether live male and live female *Bettas* could reinforce operant behavior in the conspecific male. It was purposed that the manipulation of schedule, deprivation and mirror components would be conducive to such an analysis. A second purpose of the study was to investigate the role of various stimulus factors in control of operant behavior. One of these was a social stimulus and concerned the possible effect of exposure to a fish of the opposite sex of the reinforcer; the other was the physical stimulus of light as manifested in the light-dark cycle. A further objective was to assess the validity of the operant as a measure of aggressiveness. In the next chapter, the methodology used to implement these objectives is discussed.

CHAPTER II

M E T H O D S

This chapter is devoted to a detailed description of the subjects, apparatus, and experimental procedures used to investigate the problems and issues considered in the first chapter.

Subjects: The experimental subjects included in this study were twelve adult male Siamese Fighting Fish. Ten of these were from a larger group of fish obtained from a local breeder and were about seven months old at the start of the experiment. These were fairly uniform in color, being a mixture of blue and red. The remaining two subjects were part of a larger shipment obtained from a local dealer through his agent in Toronto. These subjects, which were used towards the end of the study, were about 3 in long, one being red-blue, the other blue-green in color. Their exact age was not known though they were perhaps about eight months old when the experiment began.

The seven male and eight female exposure and reinforcement fish were all obtained from the local breeder. Five males and three females had to be replaced because of death. The females all appeared to be "ripe," judging from the swollen abdomen and, in some cases, the appearance of the "egg spot" at the urinogenital opening.

All subjects were fed once daily, at various times during the day, on a diet of San Francisco freeze dried brine shrimp.

This was supplemented at frequent intervals with live white worms (*Enchytraeus albinus*) and with freeze-dried *Tubifex* worms.

Apparatus: Eight standard 10 gal. aquaria, housed in separate roofless compartments, were arranged along two rows of shelves. Each tank was equipped with an under-gravel filter, gravel, a thermostatic automatic heater and a thermometer. The undergravel filters, which could be independently operated, were powered by a Titan II air pump.

Each tank was partitioned into three glass water-tight chambers, one for the reinforcer fish, one for the experimental subject and one for the "exposure" fish. A diagram of the tank is shown in Fig. 2.1. Compartment R, the reinforcement chamber, housed a male (or in once case, a mirror) in the male-male condition and a female in the male-female condition. The face of this chamber was formed by two sheets of glass separated by a $\frac{3}{8}$ in water-tight pocket. A shield, $3\frac{1}{2}$ in wide by 11 in high was attached to a wooden pendulum and hung freely in this water-tight pocket. The pendulum, in turn, was attached to a 12 v DC solenoid, such that activation of the solenoid resulted in the movement of the shield from its normally closed position (1a in Fig. 2.1) to an open position (2a in Fig. 2.1). When the shield was in the closed position it concealed the reinforcement chamber containing the stimulus fish. In the open position the contents of the chamber became visually accessible to an occupant of the experimental space (section E in Fig. 2.1).

The main features of the experimental chamber (so called because the experimental subject was continually housed in it were that it contained an underwater photocell system (PCE) and a pair of window channels at points x and y into which an opaque partition could be placed. With such a partition in place, a deprivation chamber, or an exposure chamber (depending upon further manipulations) was formed at section S.

The light portion of the photocell system was a GE TL 1 3/4 lens-end lamp (2.5 v) designed for long term continuous operation. The lamp and the photocell were embedded into plexi-glass tubes which, in turn, were enclosed in a tightly fitting glass sleeve. The face of both the photocell and the light sleeves, which were 1 in in diameter, were made of quartz to minimize the refraction of light as it passed from the source to the receiver. This whole assembly was placed into a support mounted on top of the aquarium so that the light sensing part of the system was 3 in from the bottom of the tank and 3 in directly opposite the stimulus chamber. The light source and the photocell were kept 1 in apart by this mounting arrangement and by a small bridge joining the separate halves.

Interruption of the light beam activated the solenoid causing the shield to swing to its open position. The interval through which the shield remained in this open position was controlled by a Hunter Timer.

Section W of Fig. 2.1 is the third major division of the aquarium. In the male-male situation this compartment held a female

while in the male-female condition it held a male. Normally the fish in this chamber was not visually accessible to the experimental subject because of an opaque partition immediately in front of this chamber. The exposure condition could be created by simply removing this partition and placing it at points x and y in the diagram. Leaving the partition in its original position and placing a second partition at points x, y, formed the deprivation chamber in which the experimental fish could neither see nor gain access to the contents of the rest of the aquarium. All eight tanks were designed in this way, thus forming a system that allowed the imposition of various treatments without the necessity of handling the fish.

Two Gerbrands interval, and two Gerbrands ratio programmers were used to arrange the variable interval and variable ratio schedules of reinforcement. Responses were recorded by electromagnetic event counters, and by an Esterline-Angus 20 channel event recorder using time correlated chart paper moving at 3/4 in/h. The event counters were read daily at noon and in addition were photographed by a Revere 16mm camera at half hour intervals, 24 h a day for the duration of the study. Water temperature was maintained at $80^{\circ}\text{F} \pm 2^{\circ}$.

Procedure: In accordance with the original design of this study, it was anticipated that all subjects would start and end each phase of the experiment at about the same time. This would have facilitated between group comparisons. In practice, however, this was not possible since large individual differences existed in conditioning various subjects and because, especially during the first month of the experiment,

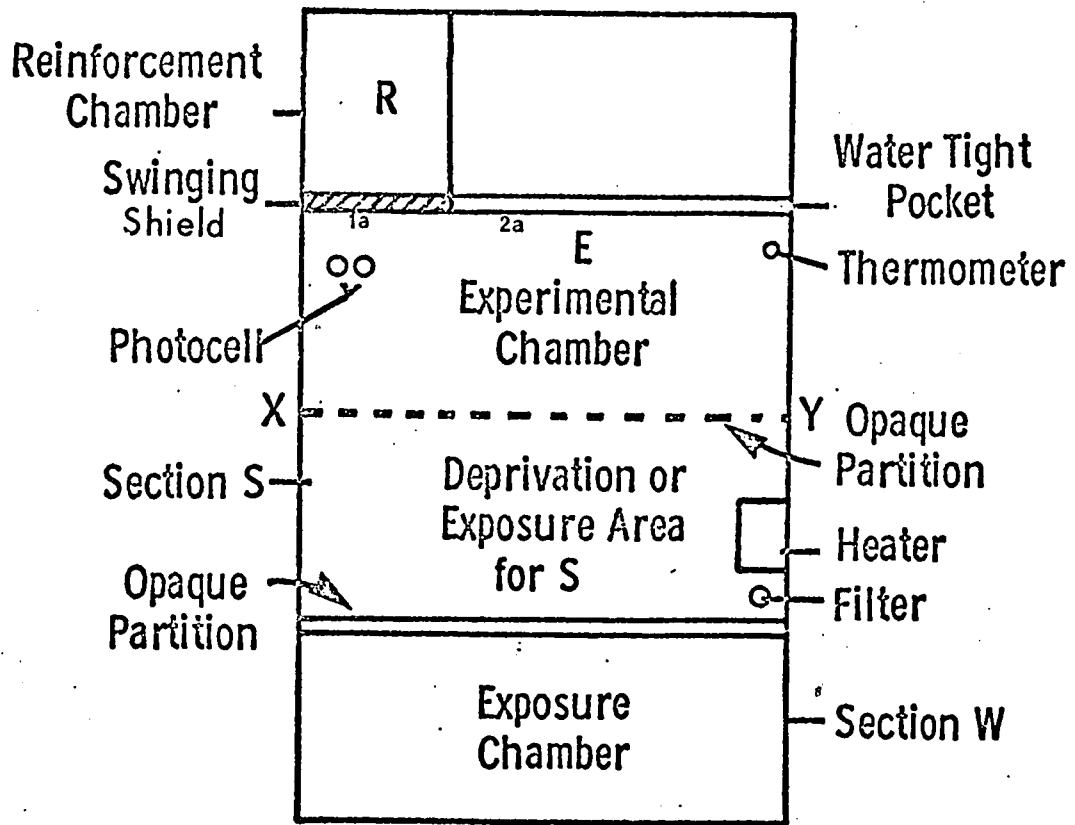


Fig. 2.1. Overhead view of a partitioned aquarium used to implement various treatment conditions in the study of conspecific-reinforced operant behavior.

several subjects died. Therefore, a within-subject strategy was adopted in which each fish received the various treatments at different points in time depending upon when he started the experiment and upon his own performance.

Table 2.1 outlines the conditions received by the twelve subjects used in this study. Since the implementation of any treatment condition followed the same procedure regardless of which subject received it, a general description is still possible. Departures from the general plan are described separately.

During the operant level determination, which lasted four days for all subjects, (except for the two that were tested near the end of the experiment and received a two day operant level), a response was recorded every time the fish swam through the photo-cell ring device. At the moment the response occurred, the shield concealing the stimulus chamber swung open and maintained this position for 20 sec. This exposed the fish to an empty chamber. At the end of the 20 sec. the shield returned to its closed position. The purpose of this was to establish a baseline rate of responding.

During conditioning, a female in the MF condition, and a male in the MM condition, was placed into the reinforcement chamber. Whenever the experimental subject made a response, the shield swung open as before but this time exposed the reinforcer fish to the experimental subject. As in operant level determination the shield stayed open for 20 sec after which it returned to its closed position. If the fish happened to stay in the ring during the entire 20 sec of

Table 2.1. Design of Experiment I

<u>Reinforcer</u>	<u>Schedule</u>	<u>Treatments</u>							
Mirror	CRF	LL	LD	LL	Dep ₁	Dep ₂	Exp	Ext	
Male	CRF	LL	LD	--	----	----	----	----	
Male	CRF	--	LD	LL	Dep ₁	Dep ₂	Exp	Ext	
Male	CRF	LL	LD	--	----	----	----	----	
Male	VI 30	LL	LD	LL	Dep ₁	Dep ₂	Exp	Ext	
Male	VR 3	LL	--	--	----	----	----	Ext	
Male	VR 3	--	LD	LL	----	----	----	----	
Female	CRF	LL	LD	LL	Dep ₁	Dep ₂	Exp	Ext	
Female	CRF	--	LD	LL	Dep ₁	----	----	----	
Female	CRF	LL	--	--	----	----	----	Ext	
Female	VI 30	LL	LD	LL	Dep ₁	Dep ₂	Exp	Ext	
Female	VR 3	LL	LD	LL	Dep ₁	Dep ₂	Exp	Ext	

CRF Continuous Reinforcement

VI 30 Variable Interval 30 Seconds

VR 3 Variable Ratio 3

LL Continuous Illumination

LD Light 18 hours - Twilight 6 hours

Dep₁ Deprivation from Reinforcement 2 Days

Dep₂ Deprivation from Reinforcement 4 Days

Exp Exposure to Sexual Stimulus or "Rival"

Ext Extinction

reinforcement presentation the shield would, at the appropriate time, still return to its closed position, and could not be activated again until the light reaching the photocell was again interrupted.

All subjects receiving the VI and VR schedules were first maintained on CRF until a high rate of responding relative to the fish's previous performance was established and then switched to the respective schedules. In the case of the two subjects in the MM condition, this was done quite early because one subject was started late in the experiment and the other case provided a favorable opportunity to evaluate subsequent treatment conditions (i.e., deprivation and exposure) early in training rather than late.

Deprivation was achieved by attracting the fish with food towards the deprivation side of the tank and then lowering an opaque partition behind the fish at points x, y (see Fig. 2.1). Under these conditions the experimental subject could not see any other fish nor could he see the photocell ring device. Subjects received two deprivation periods, the first lasting for two days, the second for four days. Deprivation was terminated by removing the opaque partition, thus permitting the fish immediate access to the manipulandum and, consequently, the reinforcer.

Exposure was achieved in exactly the same way as deprivation. Once, however, the fish was in the new chamber, the opaque partition covering the exposure chamber was removed, thus giving the experimental fish full view of a female in the MM condition or a

male in the MF condition. This exposure condition lasted two days, during which time the experimental fish could not see nor gain access to the manipulandum or the reinforcer. The exposure condition was terminated by returning the opaque partition back to its original position concealing the exposure chamber. This then gave the experimental subject free access to the manipulandum and, if a response occurred, the reinforcer.

During LL the overhead lights were left on 24 h a day each day until this condition was altered to an LD cycle. The study started under LL on 26 June 1967, continued under these lighting conditions until 30 July 1967 when an 18h light, 6h twilight condition was imposed, and was returned, for the remainder of the study, to LL conditions on 18 October 1967. Twilight began at 1:00 a.m. and ended at 7:00 a.m. Central Standard Time. A "twilight" condition was created by the operation of two 40 w light bulbs placed on a wall opposite the experimental aquaria which operated while the fluorescent lights were off. Additional light was also provided in the aquarium itself by the 2.5 v light source of the photocell system. It was not possible to measure illumination inside the tank but it was, however, determined that the experimental fish could see the reinforcer during twilight by mechanically opening the shield and observing display behavior.

In extinction, whenever the fish swam through the ring, the response was recorded but the shield did not move. Thus the reinforcer was no longer available to the test subject. This condition

lasted for at least seven days. The end of extinction marked the end of the experiment.

Data Analysis: Several statistical analyses were used to evaluate the data obtained in this study. These included (1) a simple description of rate changes as indicated by adding successive data points to produce a cumulative response curve (Skinner, 1938); (2) nonparametric tests to assess the effects of given treatments on given individuals and, where possible, between groups of individuals. Such tests tend to be more conservative than parametric tests in rejecting the null hypothesis, vis-a-vis the power-efficiency for a given sample size. A further advantage is that no assumptions about the normality or equity of variance in the underlying distribution of the data is made (Siegel, 1956); and (3) auto and cross correlation with Fourier analysis to evaluate periodicity. Of these procedures the last requires extensive comment.

If the behavior under investigation is suspected to contain periodicities of varying durations, these may be detected by a variety of recording and mathematical-statistical techniques.

The recording procedure most frequently used in studying periodicities is an event marker which indicates response on time correlated chart paper. The rationale for this approach is given by Richter (1965).

Data display techniques of this type are limited by the fact that they may not be sensitive to hidden periodicities or periodic phenomena masked by noise, and if this is the case, they may

not provide an exact value of period length.

Several statistical-mathematic techniques, mainly the outgrowth of work in information theory, are now available to extract periodicities from otherwise noisy data and to more or less accurately define these periods. These are known as auto and cross correlation and are often coupled with Fourier analysis.

Autocorrelation is a statistical procedure developed by Yule (1927) and by Bartlett (1948) which is designed to remove random components from presumably periodic data. The end product of autocorrelation is the correlogram which is simply a plot of correlation coefficients as a function of "lags". The correlation coefficients are obtained by correlating the original wave form with itself (hence autocorrelation) starting from successive points in time (the lags).

Crosscorrelation is the same as autocorrelation except that instead of correlating the waveform with itself, a different input waveform, usually with known characteristics, is correlated with the original. Crosscorrelation is therefore, more powerful than autocorrelation because in the latter case two noisy signals are correlated while in the former case, a noisy signal is correlated with a perfectly periodic one. The output of both analyses is a new wave with most of the noise removed. Frequently, simple inspection of the waveform is all that is necessary to determine the existence of periodicity and period length.

More accurate determinations may be made by a power spectrum analysis based upon a Fourier transformation of the correlogram.

The Fourier transformation simply separates the complex waveform into its constituent elementary components in the form of sine and cosine functions. The power spectrum is derived directly from this and is usually presented in the form of a histogram. The height of any bar in the histogram indicates the relative contribution of that component to the waveform. Thus a negatively decelerated histogram indicates a predominance of low frequency components, a negatively accelerated histogram indicates a predominance of high frequency components and a flat power spectrum means that all elements contribute about equally (i.e. noise). Further discussion of these procedures can be found in Mercer (1960) and Sollberger (1965).

It may be said that these procedures involve a tremendous amount of computational labour and are, therefore, primarily restricted to computer use. All the frequency analyses reported in the present paper were executed by a Link-8 computer.

Heteroplastic Mirror Stimulation

The methodology used to study the effects of mirrors in different planes is somewhat different than the preceding work and is therefore given separate consideration.

Method

Subjects: The subjects were 16 adult male *Bettas* purchased from a local breeder who in turn received his shipment from an agent in Toronto.

The fish were purchased in two lots of ten each at three week intervals. The extra fish were ordered to cover the possibility of losses though these did not occur. The subjects were blue-green and blue-red in color and all were approximately 3 in long. All subjects were fed once daily, about 10 min after the daily experimental session with San Francisco freeze dried brine shrimp.

Apparatus: The apparatus employed here was essentially similar to apparatus described elsewhere (Goldstein, 1965, 1967). Two operant conditioning units were employed. These consisted of standard 2.5 gal aquaria, Warner photocell systems, under water ring devices, Hunter event counters and two-way mirrors.

The light portion of the photocell system was mounted over the aquarium while the photocell was located below the aquarium. The ring device was placed into this system so that light could pass uninterruptedly through the ring. The area of the "ring" through which the fish could swim was 1 in wide by 3 in high. Whenever the fish swam through the ring, a 100 w light bulb located behind a two-way mirror switched from a normally on, to an off position for an interval controlled by the Hunter timer. Responses were recorded by the Hunter event counter and on an Esterline-Angus event recorder.

Procedure: Three display components were tested in this study, "frontal", "lateral" and "full." In the full display condition, fish were permitted complete access to mirror image by using the entire rear wall of the aquarium as a mirror (10 in by 8 in). In both the frontal and lateral display conditions, a matte cardboard sheet was placed directly

in front of the two-way mirror. In the lateral condition, this sheet had a $\frac{1}{2}$ in wide by 6 in long cutout in the central horizontal plane, whereas in the frontal condition a cutout of identical dimensions was placed in the central vertical plane. Thus, when a fish swam through the ring, the entire rear wall became a mirror in the full condition, a narrow vertical mirror appeared in the "frontal" condition and a narrow horizontal mirror appeared in the lateral condition.

Table 2.2 outlines the design of this study. Two repetitions of eight subjects each were employed, and in each repetition subjects were assigned at random to the different groups. A two day operant level was determined for all subjects in which response produced no systematic stimulus change in subject's environment, but responses were, of course, recorded. The next 14 days of the study were all response contingent days in which ring swimming produced mirror image for a period of 20 sec.

During the first seven response contingent days, four subjects had access to full mirror image, whereas during the last seven days, two of these were switched to frontal mirror and two to lateral mirror. Of the remaining four subjects, two started under lateral and were later switched to full mirror, and two started under frontal and were later switched to full. This constituted one repetition of the experiment. A second repetition commenced a week after the end of the first repetition.

Subjects were tested 4 h a day with an average 20 h intersessional interval for the 16 days of a repetition. The daily

time of testing was systematically varied for each fish in a latin square design so that each subject was tested at every possible testing time during the course of the study. Testing times were from 8:00 a.m. to noon, noon to 4:00 p.m., 4:00 p.m. to 8:00 p.m., 8:00 p.m. to midnight. After the last subject had been tested, the tanks were cleaned and refilled with aged tapwater.

Validity of Operant Technique

The method used to determine the relationship between operant responding and fighting differs from the preceding methodologies and therefore requires separate consideration.

Method

Subjects: The subjects were 11 adult males selected after the termination of the study on heteroplastic reinforcement.

Apparatus: The apparatus consisted of a 15 gal. plexiglas tank which contained a removable opaque partition dividing the tank in half.

Procedure: One week after the termination of the study on heteroplastic reinforcement, fish were matched on the basis of their average full-mirror response rates. The matching was done so that high rate fish (over 200 responses/4h) would fight low rate fish (less than 30 responses/4h), intermediates (100-200 responses/4h) would fight high rate fish, intermediates would fight against low rate fish, and finally lows would fight against lows. Because of the lack of an available male a high-high encounter was not held.

Fish were placed on either side of the partition and allowed 5 min adaptation to the chamber. The partition was removed when the fish were oriented toward each other. The fish were separated when it became clear that the contest had been decided, thus making victory or defeat the dependent measure. Defeat was evident when one of the combatants attempted to flee, hid in a corner, backed off from his opponent, did not counter-attack, showed colour bleaching, etc.

Table 2.2. Experimental Design for Study II

<u>N</u>	<u>Operant</u>	<u>Conditioning</u>	
		2 Days	7 Days
4	Full	Full	Lateral
4	Full	Full	Frontal
4	Lateral	Lateral	Full
4	Frontal	Frontal	Full

CHAPTER III

R E S U L T S

In order to simplify the presentation of the data, the results for the different treatment conditions are considered first for the male-female condition and then for the male-male condition. In addition to this separate treatment, an explicit comparison is made in describing the effects the various treatments have on the two classes of reinforcers. Finally, the results of the research on heteroplastic mirror reinforcement and the relationship between operant rate and fighting are considered in separate sections. A brief summary of all the results appears at the end of the chapter. Before undertaking these tasks, however, some general remarks are in order.

During the first month or so of the study most of the experimental subjects in both the MM and MF condition died and therefore had to be replaced. It was not at all clear why these deaths occurred as the fish showed no obvious signs of disease. Some fish seemed sluggish and did not eat for a day or so prior to death, but others did not show this syndrome. Fish #4, in Fig. 3.7, showed a high rate of response up to the time of his death. It may be of some significance that all the subjects that died in this experiment were maintained in the laboratory under LL for about a month and a half prior to the onset of the study which also began under LL. The possible implications of this finding are pursued in the next chapter.

A second general finding was the large individual differences both between subjects and within a given subject over time, a finding recently confirmed by other workers (Hogan et al, 1970). Thus, some subjects showed very low rates of responding, others showed intermediate rates and still others moderately high rates. The very high rates reported earlier by Goldstein (1967) and Hogan (1967) were not obtained in this study.

Finally, the combination of deaths, the protracted nature of the study, and the physical nature of the experimental area (which precluded complete control over individual tanks) resulted, upon introduction of replacement subjects, in the unsystematic confounding of various experimental conditions. This coupled with the large within and between subject variability and the small number of subjects tested made various interaction effects very difficult to interpret. Therefore, the use of statistical tests on comparisons involving deprivation and exposure for example could not readily be justified since significant differences, degrees of freedom notwithstanding, could easily be spurious. Instead, the data are analyzed in the hope of discovering trends which might be suggestive of bona fide.

Male-Female

Reinforcer: Figure 3.1 shows the cumulative response output as a function of days for the five subjects used in the MF condition. Each data point represents the sum of responses emitted in 48 successive

0.5 h intervals, plus the sum of all preceding days. The slope of the curve is an index of rate of change; the steeper the slope, the greater the rate of responding.

It can be seen that the operant rate, represented by the first four days of responding, was very low ($\bar{X} = 5.65$ responses/day) and that when the contingency went into effect responding accelerated at different rates for different subjects. Table 3.1 shows these changes together with a sign test evaluating the proposition that mean conditioning rate exceeds mean operant rate. The sign test is significant ($n = 5, x = 0, p = .031$).

Response curves for subjects trained entirely under conditions of CRF are numbers 1, 2, and 3 in Fig. 3.1. Subjects numbered 4 and 5 started training under CRF and were later shifted at the points indicated, to VR and the VI schedule for the remainder of the acquisition phase of the study.

Consider first the acquisition curves for the CRF subjects. Perhaps the most striking characteristic is the rate differences shown by the three subjects. Thus subject 1 maintained a very low rate (about 25 responses/day), whereas subjects 2 and 3 maintained much higher rates (106 responses/day and 155 responses/day respectively).

Of interest also is the fact that both subjects 2 and 3 showed an initial high rate of responding at about 275 responses/day and then shifted to a new lower rate at about 75 responses/day (for subject 2) and 83 responses/day (for subject 3).

Subjects 4 and 5 were also initially maintained under

Table 3.1. Mean Operant and Conditioning Rates

Male-Female						
	<u>Operant Level</u>			<u>Conditioning</u>		
	<u>Responses</u>	<u>Days</u>	<u>\bar{X} R/D</u>	<u>Responses</u>	<u>Days</u>	<u>\bar{X} R/D</u>
CRF	36	4	9.00	7,873	97	81
CRF	4	2	2.00	4,242	24	177
CRF	14	4	3.50	1,740	76	23
VI	43	4	10.75	27,180	98	277
VR	12	4	3.00	26,149	119	219
* Sign test n = 5, x = 0, p = .031						
Male-Male						
(MIR)CRF	106	4	26.50	7,229	122	59
CRF	8	4	2.00	11,658	27	431
CRF	1	4	0.25	7,775	78	99
VR	65	2	32.50	10,120	23	440
"VR"	5	2	2.50	1,900	74	26
VI	1	4	0.25	4,388	51	86
CRF-"VI"	29	4	7.25	3,688	60	61
† Sign test n = 7, x = 0, p = .008						

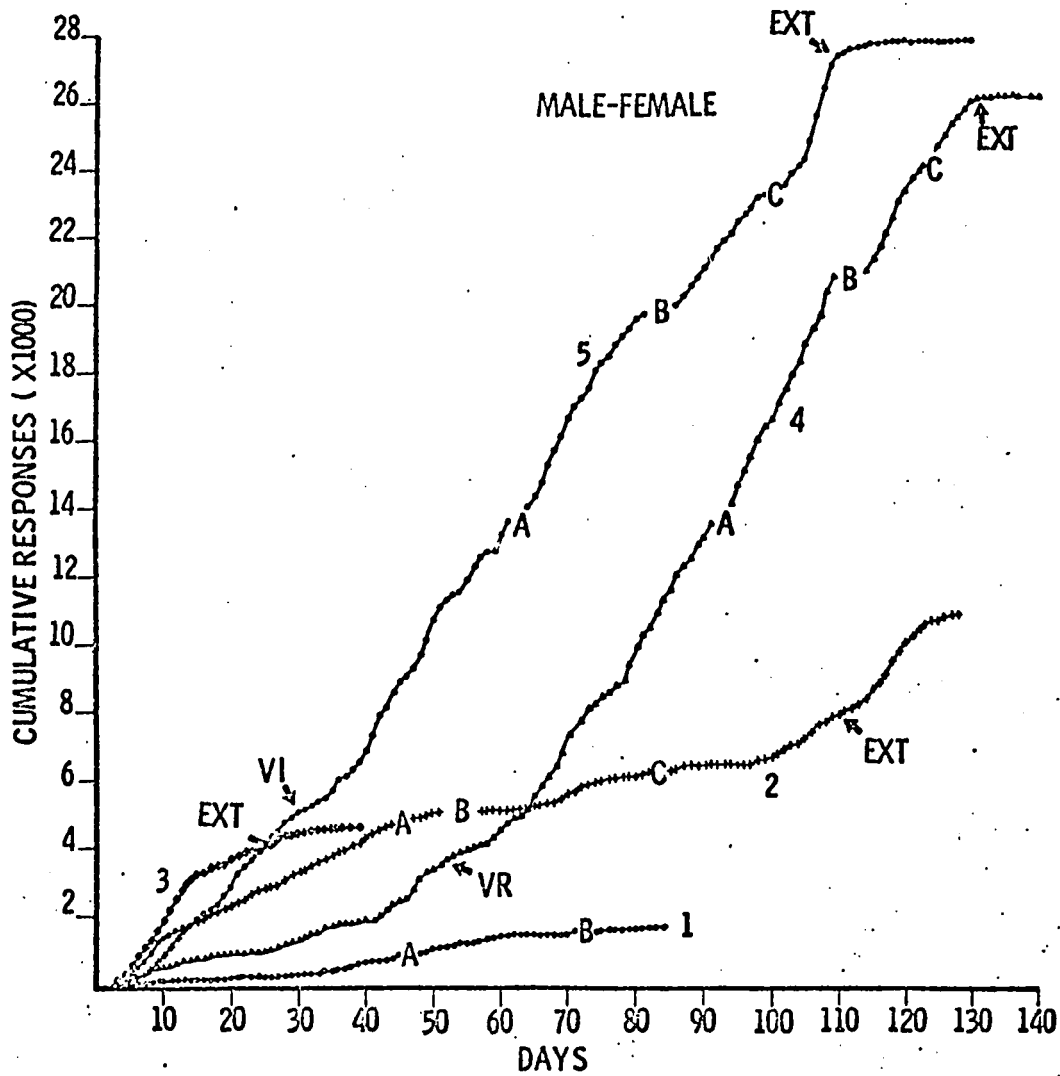


Fig. 3.1. Daily cumulative operant responding of male *Bettas* reinforced by the presentation of a female. "A" and "B" are 2 and 4 day deprivation conditions and "C" is exposure to a rival. Response rates vary considerably from subject to subject.

CRF and their response rates are intermediate with respect to the others. Thus, while on CRF, subject 4 maintained a low rate, but this tended to increase irregularly between the 25th and 50th day of responding. On the other hand, subject 5 maintained a relatively stable response rate throughout the CRF phase of the study. Neither of these two subjects showed the initial high rate followed by a new lower rate characteristic of subjects 2 and 3.

Schedule: After extensive training on CRF, subjects 4 and 5 were switched to the VI and VR schedules. It is evident from Table 3.2 that the transition from CRF to schedule is associated with a rate decrease of several days' duration. This is then followed by a recovery period which eventually exceeds the CRF rate. Thus, the VI subject averaged about 218 responses/day in the week prior to the introduction of VI and about 131 responses/day in the first VI week. However, several weeks later, in the week prior to extinction, the fish was averaging about 545 responses/day. Similarly, for the 25 CRF days before transition to schedule, the VR subject emitted an average of 102 responses/day whereas for the next 25 days on VR this subject emitted an average of 208 responses/day. Data for the 6 day period before and after transition are shown at the bottom of Table 3.2. Finally, both subjects maintained their high rates of responding, with occasional brief plateaus, for the remainder of the acquisition phase of the study.

Deprivation: Table 3.2 shows mean responses/h, 2 days, 1 day and 4h before and after the 2 day and 4 day deprivation conditions. Two subjects on CRF and two on intermittent schedules received deprivation

Table 3.2. Female Reinforcement

Responses Per Hour

	<u>Before</u>			<u>After</u>		
	Deprivation (2 days)					
	<u>2 Days</u>	<u>1 Day</u>	<u>4h</u>	<u>4h</u>	<u>1 Day</u>	<u>2 Days</u>
CRF	2.46	4.75	4.00	4.50	1.46	1.33
CRF	2.82	3.92	5.00	3.00	3.96	3.08
VI	18.58	15.58	11.75	13.25	16.67	14.58
VR	10.29	16.00	21.25	20.00	25.71	24.58
	Deprivation (4 days)					
CRF	0.96	1.17	2.50	3.00	0.79	0.21
CRF	2.37	1.79	2.00	1.50	1.13	0.71
VI	11.25	5.75	4.25	10.25	11.96	9.54
VR	26.67	16.46	24.50	19.00	7.17	18.33
	Exposure to Male					
CRF	1.17	1.95	1.50	9.00	2.95	2.67
VI	7.92	6.42	2.00	3.75	11.67	12.67
VR	16.50	7.88	4.50	0.00	18.33	12.58
	Schedule					
	<u>\bar{X} 6 Days</u>	<u>1 Day</u>	<u>1 Day</u>	<u>\bar{X} 6 Days</u>	<u>\bar{X} 6 Days</u>	<u>Before Ext.</u>
VI	9.11	9.12	7.66	5.46	22.77	
VR	7.86	8.17	4.88	3.33	15.83	

periods. Consistent trends are not readily apparent from the data. Thus for the first deprivation condition one CRF subject showed a decrease in responding from the day prior to the day after deprivation but a small increase from the last 4h prior to deprivation to the first 4h after. This could mean that behavior immediately prior to and after deprivation is a more sensitive measure of change. When the data of the remaining CRF subject is considered, however, a reverse effect occurs. The data for the VI and VR subjects shows the same kind of inconsistencies.

Exposure: Table 3.2 contains the exposure data for the VI, the VR, and a CRF subject. Exposure seems to exert a relatively consistent effect on all subjects that received this treatment. This is manifested by a general tendency for subjects to show an increased rate of responding after exposure to a "rival" male. The pre-day and post-day treatment measures, and the pre-4h and post-4h measures reflect these changes most clearly except for the VR subject who failed to respond in the first 4h post-exposure.

Cyclicity: Figures 3.2 and 3.3 show Esterline-Angus data records for two of the five subjects in the MF condition. A clear impression of periodicity is not evident under conditions of LL. There is, however, a faint hint of a shift in response density towards the left as would occur if a strong 25h component were present. This is obscured by the fact that responding is not restricted to a limited portion of the day, but rather occurs continuously throughout the day.

Figure 3.4 shows Link-8 generated autocorrelograms and corresponding power density spectra during both LL and LD for three

MALE-FEMALE CRF-VI30 SEC

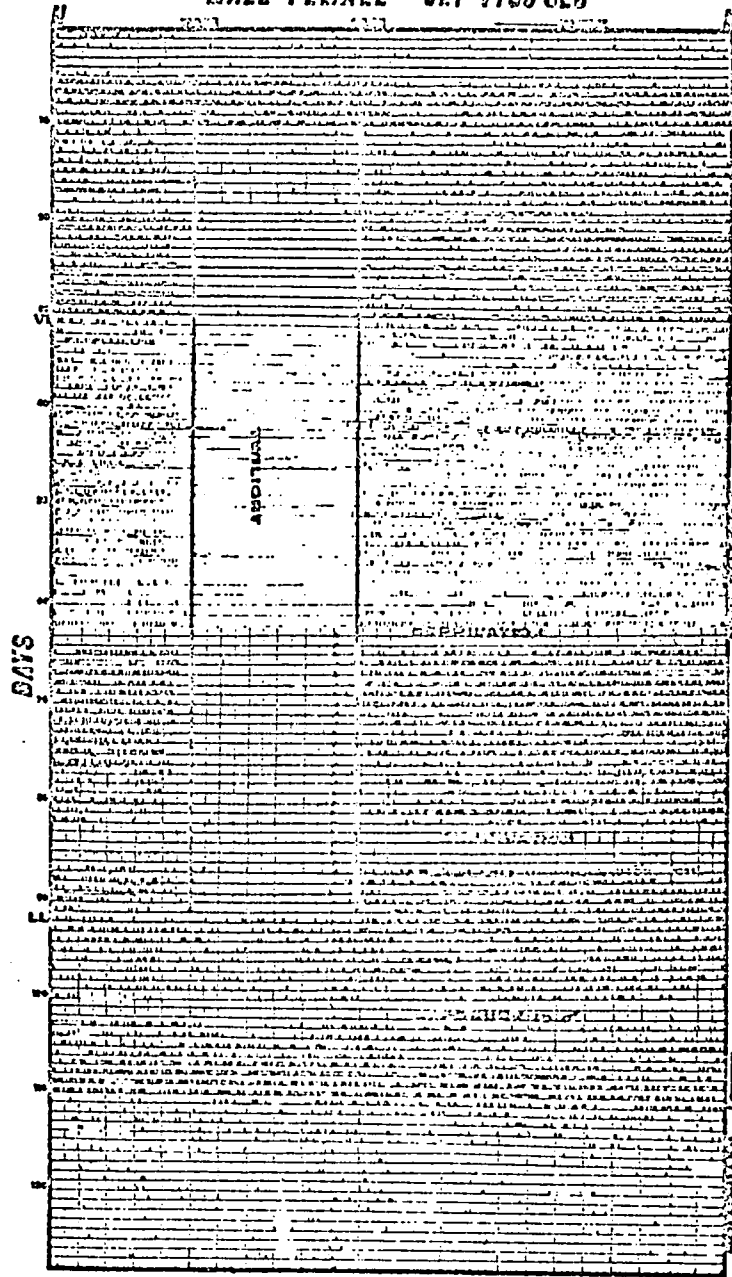


Fig. 3.2. Actogram showing the complete within and between day distribution of operant responding for a subject maintained on VI 30 second schedule under various experimental conditions. The record provides a quick visual impression of the gross temporal patterning of responding.

of the five subjects in the MF condition. Consistent trends exist in the fish not shown. Both the autocorrelogram and the power spectrum fail to show a clear periodicity in the operant behavior under conditions of LL. Thus, the autocorrelogram drifts in a linear fashion towards zero correlation and the power spectrum is relatively flat. Both these analyses indicate a predominance of noise with a high frequency component.

It is only when cross-correlation is applied to the original data that underlying periodicities appear. Figure 3.5 shows a series of cross-correlograms for the three fish represented in Fig. 3.4 under LL. It can be seen that there are strong 23, 24 and 25h components and that other components, for example, a 6h component, are negligible.

Figure 3.6 shows the number of responses over days emitted by the VI, VR, and a CRF subject. Each day contains eight data points (i.e., the sum of 3h intervals) plotted as a continuous record. There is some indication of long term periodicities under both LL and LD with the LD lasting about three times longer than in those in LL. Because of the relatively small number of cycles present, however, a more precise analysis was not performed. The dramatic shifts in the daily response distributions under LL and LD are also readily apparent from these records.

Entrainment: The actograms of Fig. 3.2 and 3.3, nicely demonstrate entrainment of the circadian rhythm. Thus, it is evident that during the twilight phase of the LD cycle responding virtually ceases for the subjects shown. (A similar effect was obtained for the other subjects

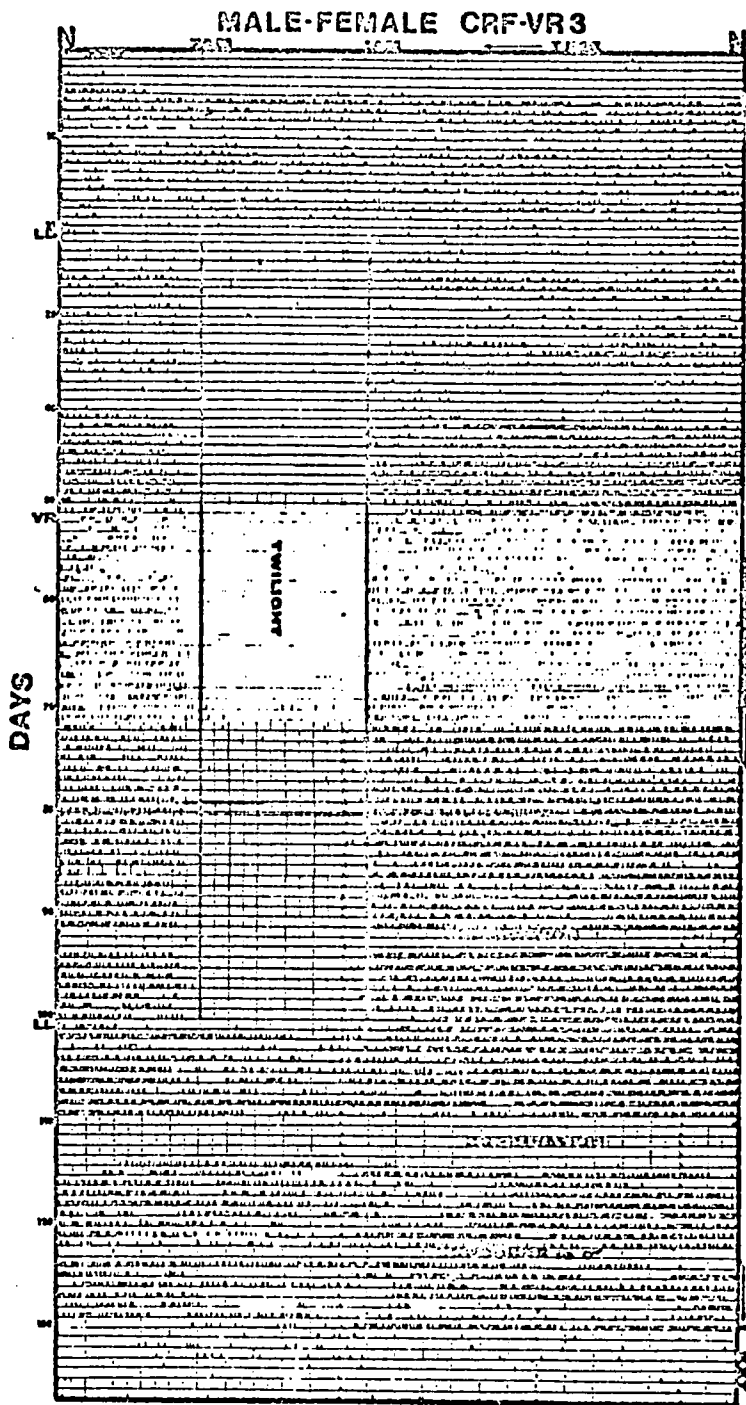


Fig. 3.3. Actogram for a VR3 subject reinforced by presentation of a female *Betta* under a variety of experimental conditions.

not shown.)

The data records also suggest that during the transition from light to twilight there is a slight tendency for responding to "spill over" into the twilight phase. On the other hand, there is a good indication that the fish does not immediately respond to light onset as indicated by the fact that on many days a half hour or more passes before the first response is recorded. The record, however, also shows exceptions to this.

There is also some indication that a fish that begins the study under LD conditions is less likely to respond in the twilight phase than a fish that starts the experiment under LL. This effect, which is not very large, is evident from an inspection of the actograms presented.

Finally, reference to Fig. 3.4 shows that when a LD cycle operates a clear 24h periodicity in operant responding is established. This is particularly striking in view of the fact that the autocorrelogram fails to detect any periodicity in the same fish under LL. This is strongly suggestive of entrainment.

Extinction: When a response occurred in extinction the shield concealing the stimulus chamber did not open. Under these conditions, response rate declines and rapidly approaches zero for all subjects except fish #2.

Shortly after exposure to the rival male, subject 2 began to maintain a new high rate of responding. This new rate was only slightly affected by the onset of the extinction procedure, but

CONTINUOUS ILLUMINATION
(LL)

LIGHT 18h - TWILIGHT 6h
(LD 18:6)

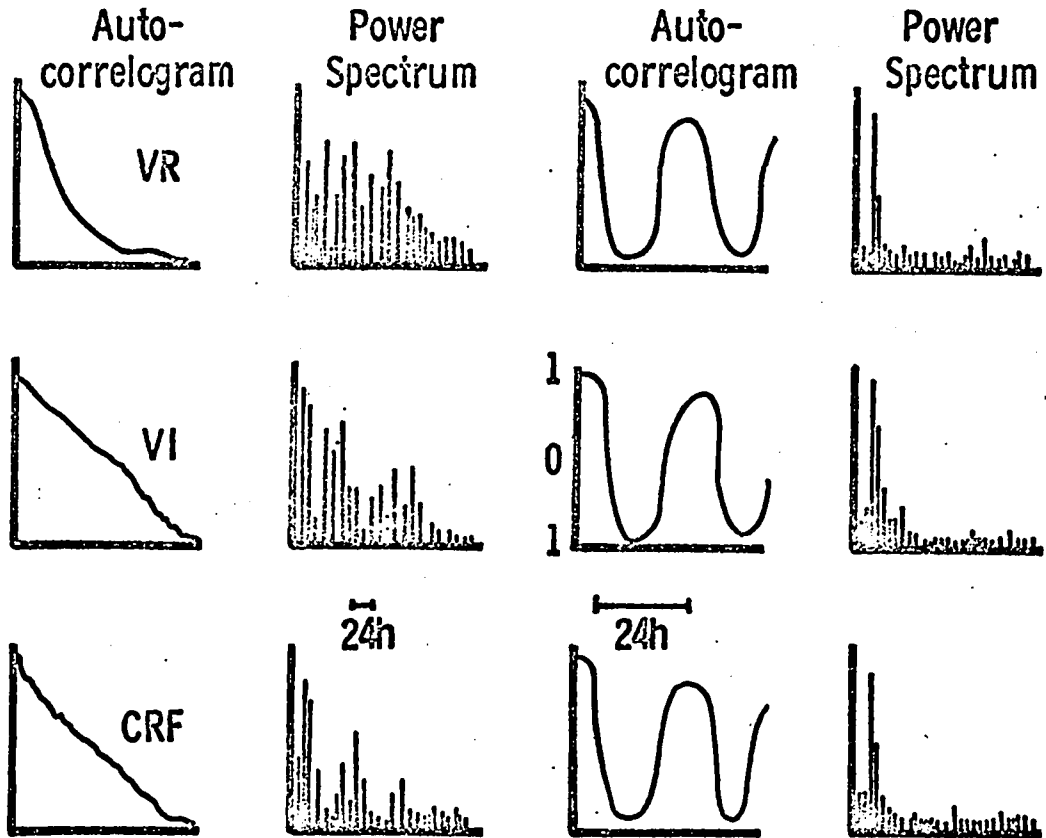


Fig. 3.4. Autocorrelograms and corresponding power spectra for representative ten day samples of operant responding of subjects maintained by a female reinforcer under various schedules. The figure suggests high frequency noise under LL and entrainment under LD 18:6.

CONTINUOUS ILLUMINATION

CROSSCORRELOGRAMS

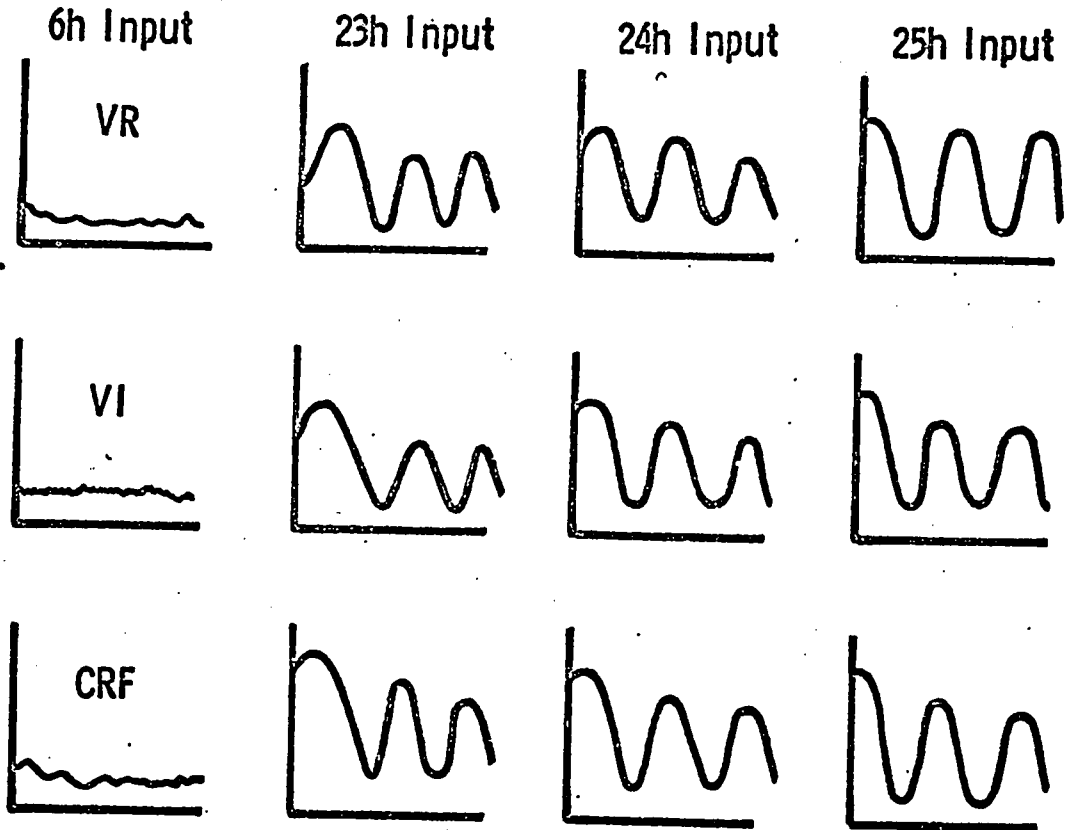


Fig. 3.5. Cross-correlograms for representative ten day samples of operant responding maintained by a female reinforcer under the various schedules and under LL. Strong 23h, 24h, and 25h, components are evident.

thereafter a second rate increase occurred. This new rate exceeds the highest acquisition rate. Finally, however, after about ten days the rate starts to approach zero.

Of the three remaining subjects whose response output is under the influence of the extinction procedure, the VI and CRF subjects show the most gradual decline while that of the VR subject is quite precipitous, 336 responses being emitted on the day prior to extinction and 14 the first day of extinction!

Male-Male

Of the four original experimental male subjects that started this experiment on 26 June 1967, only one finished. In all, a total of five males died in the MM condition. These subjects, as indicated earlier, were local stock housed under LL for about a month and a half prior to the start of the experiment. The only subject to last from the original starting date to the termination of the study was reinforced by a mirror rather than a live male.

Reinforcer: Figure 3.7 shows the cumulative response output as a function of days for seven subjects in the MM condition. Subjects numbered 1, 2, 3, 4, were maintained under a CRF schedule; subject 5 and 6 were exposed to the VR schedule and subject 7 was exposed to the VI schedule. Subject 5 was taken off the VR after a relatively brief exposure and placed back on CRF since it was evident that the schedule was not supporting the behavior of this normally low rate subject.

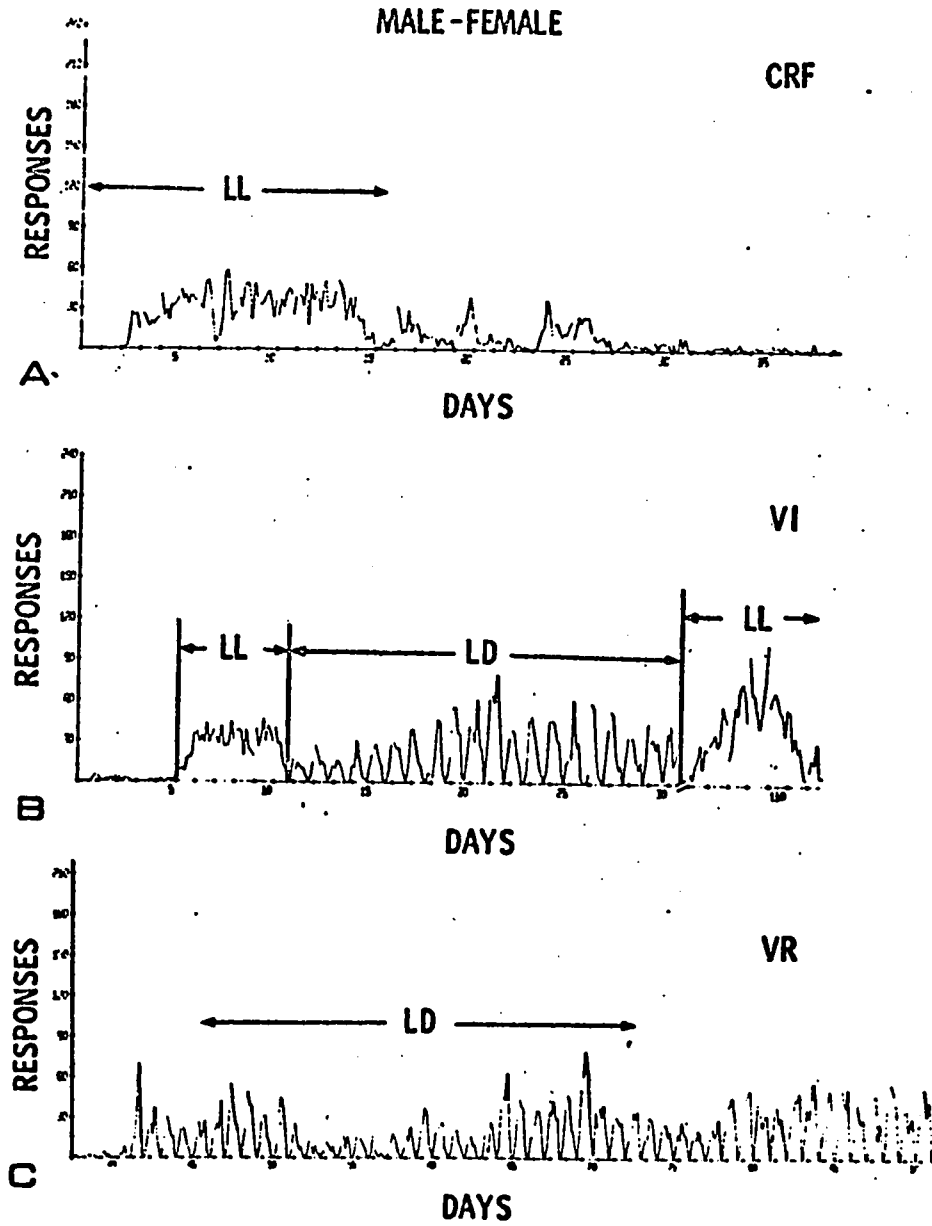


Fig. 3.6. Daily number of operant responses during successive three hour periods for subjects maintained by the indicated schedules under continuous illumination (LL) and under a light-twilightcycle (LD). A clear indication of twilight suppression of operant responding is evidence from these records.

This subject was eventually replaced by number 6.

The variability in the effectiveness of the conspecific male as reinforcer is shown in Fig. 3.7, when the response reinforcement contingency is established. Three of the seven subjects show high rates of responding, with an average of about 400 responses/day, while the remaining subjects are either unaffected by the onset of contingency or else establish low rates of responding with an average of about 50 responses/day. The baseline operant rate for the group is an average of 11 responses per day. Table 3.1 shows that the conditioning rate is significantly above the operant rate ($n = 7$, $x = 0$, $p = .008$).

The figure also shows that the low rate subjects began to take on new higher rates of responding between about the 20th and 40th day of the study.

Schedule: When it became apparent that the conspecific reinforcer sustained a high rate relative to the past performance of the fish on CRF, subject 6 was switched to the VR schedule and subject 7 to the VI. According to the original plan of the experiment, subject 5 was marked for the VR condition and thus was eventually, though temporarily, placed on this schedule. The very large rate increase that marked a similar transition in the MF condition did not occur here.

Subject 6 was the VR replacement for subject 5. The new VR subject was maintained on CRF for five days during which time he emitted about 700 responses/day. On day six of acquisition, the subject was placed on VR 3. As Table 3.3 suggests, two fairly distinct rate decrements appear after the onset of schedule. The first occurs

Table 3.3. Male Reinforcement

Responses Per Hour

	<u>Before</u>			<u>After</u>		
	Deprivation (2 days)					
	<u>2 Days</u>	<u>1 Day</u>	<u>4h</u>	<u>4h</u>	<u>1 Day</u>	<u>2 Days</u>
MIR CRF	2.12	1.75	1.00	4.50	4.04	3.00
CRF	2.46	2.71	2.00	3.00	3.29	5.12
VI	5.71	8.79	12.25	24.00	12.83	7.25
Deprivation (4 days)						
MIR CRF	3.87	5.57	10.25	12.00	7.17	3.54
CRF	4.92	3.79	3.25	10.00	5.54	6.04
VI	0.50	8.33	14.00	17.75	10.37	7.29
Exposure to Female (2 days)						
MIR CRF	2.71	2.50	3.00	5.00	2.79	2.63
CRF	5.71	4.21	5.75	4.50	5.59	4.87
VI	10.29	11.79	8.25	1.50	1.39	0.33
Schedule						
	<u>\bar{X} 6 Days</u>	<u>1 Day</u>	<u>1 Day</u>	<u>6 Days</u>	<u>6 Days Before Ext.</u>	
VR	30.17	27.21	21.62	20.49	9.59	
VI	7.27	5.63	6.46	7.46	0.13	

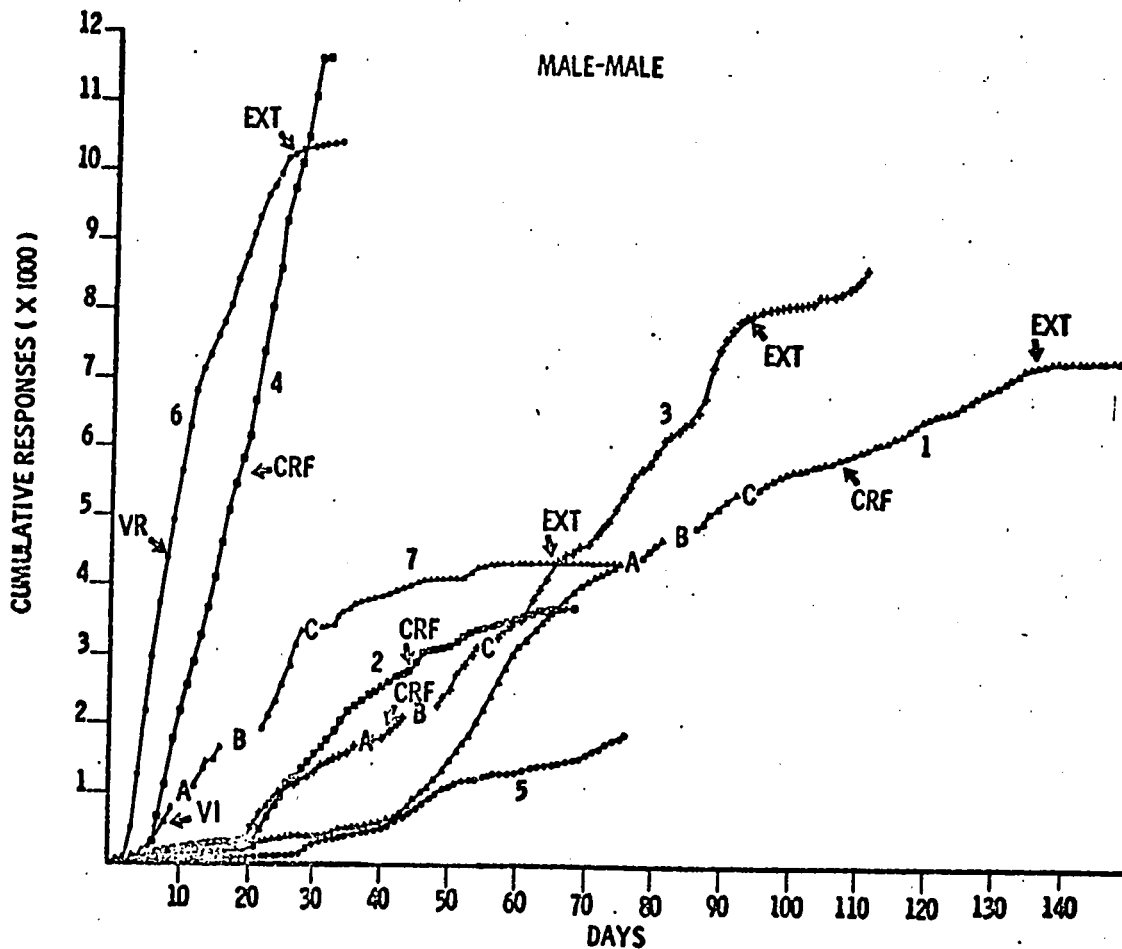


Fig. 3.7. Daily cumulative operant responding for male *Betta* reinforced by the presentation of another male. "A" and "B" are two and four day periods of deprivation and "C" is exposure to a female *Betta*. The record shows wide individual differences in the rate of responding.

immediately and lasts for about five days, during which time the rate falls to about 500 responses/day. The second decrement follows immediately after the first, in which a still lower rate of 240 responses/day is maintained thereafter until extinction. In the last week prior to extinction the fish averaged about 230 responses/day.

Subject 7 was switched to the VI schedule after two days of CRF acquisition and received only two days of VI training before the onset of the first treatment condition. Therefore, it is not possible to discuss long term VI responding in the MM situation since such responding is obviously confounded with treatments. The decision to implement treatments at the beginning of training rather than after a protracted period of prior conditioning was made on the basis of a statement of Morse (1966) who noted, "Deprivation is most important during the early stages of conditioning when strong conditioned behavior is not yet developed. A prolonged history of intermittent reinforcement attenuates the effects of deprivation so that it becomes less important for the maintenance of schedule-controlled behavior" (p. 79). The death of subject 2 which freed the VI test chamber, and the possibility of obtaining pronounced deprivation effects by testing early in training strongly argued in favour of observing the behavior of a new subject under these altered conditions. The effects of deprivation on schedule behavior will be considered shortly.

For the moment it is worth noting (see Table 3.3) that during the brief transition from CRF to VI there is a very slight rate increase in responding (an average of 174 responses/day during CRF and

183 responses/day during the two days of VI). While this is not a strikingly large difference, it is mentioned because the rate decrement obtained with the VR schedule did not occur on VI. Whether such a decrement would have developed under prolonged VI conditions is, of course, an open question since the attenuation which did occur was confounded with the exposure condition.

Deprivation: Subject 1 in the mirror CRF condition, subject 3 on CRF, and subject 7 on the VI schedule all received two deprivation conditions, the data for which are shown in Table 3.3. All three subjects showed rate increases after each deprivation period. These increases are seen when the data are analyzed 4 and 24h before and after deprivation.

These results are difficult to interpret because, besides being differentially nested within other conditions (e.g., light cycle), the increased rate after deprivation, in the case of the VI subject, the first and second deprivations, and the mirror CRF subject for the second deprivation, could well be a manifestation of a general incremental trend in responding.

Exposure: All the subjects that received the deprivation treatment were also exposed on a subsequent occasion to a female *Betta* for two days, during which time they could not gain access to the manipulandum or the reinforcer male.

For the two subjects on the CRF schedules (see Table 3.3) this treatment had a slight enhancement effect on responding when the 1-day before and after data are considered. However, because of within subject variability this meager effect is lost when the rate measures

in the 4h pre- and post-exposure conditions are considered. Thus the mirror subject shows a small increase while the remaining CRF subject shows a small decrease. The VI subject shows a drastic decline in performance after exposure, a decrement from which he never completely recovered.

Cyclicity: Figures 3.8, 3.9, and 3.10 are Esterline-Angus data records for three of the seven subjects in the MM condition. It is evident from these records that under LL a clear indication of a free-running periodicity does not emerge. These records show, however, that the fish respond continuously throughout the day.

The autocorrelograms of LL data did not show a periodicity for any of the subjects, but the Fourier transformation did suggest a peak at about 25h (see Fig. 3.11). It is only when a 25h periodicity is crosscorrelated with the original time series that the underlying circadian rhythm emerges (see Fig. 3.12). This figure also shows that neighbouring periodicities of 23 and 24h are also present in the data. Finally, Fig. 3.13 shows the daily performance under LL of two subjects in the MM condition. These records suggest the presence under LL of a short term cycle in operant responding of about 7 days.

Entrainment: Entrainment of the circadian rhythm is demonstrated by synchronization of responding with the LD cycle. Figures 3.8, 3.9, and 3.10 demonstrate such synchronization. Thus, it can be seen that during the twilight phase of the LD cycle, responding is greatly attenuated but not completely suppressed as, for example, in the case of the male-mirror condition. Moreover, only when the LD cycle is in operation does

MALE-MALE CRF

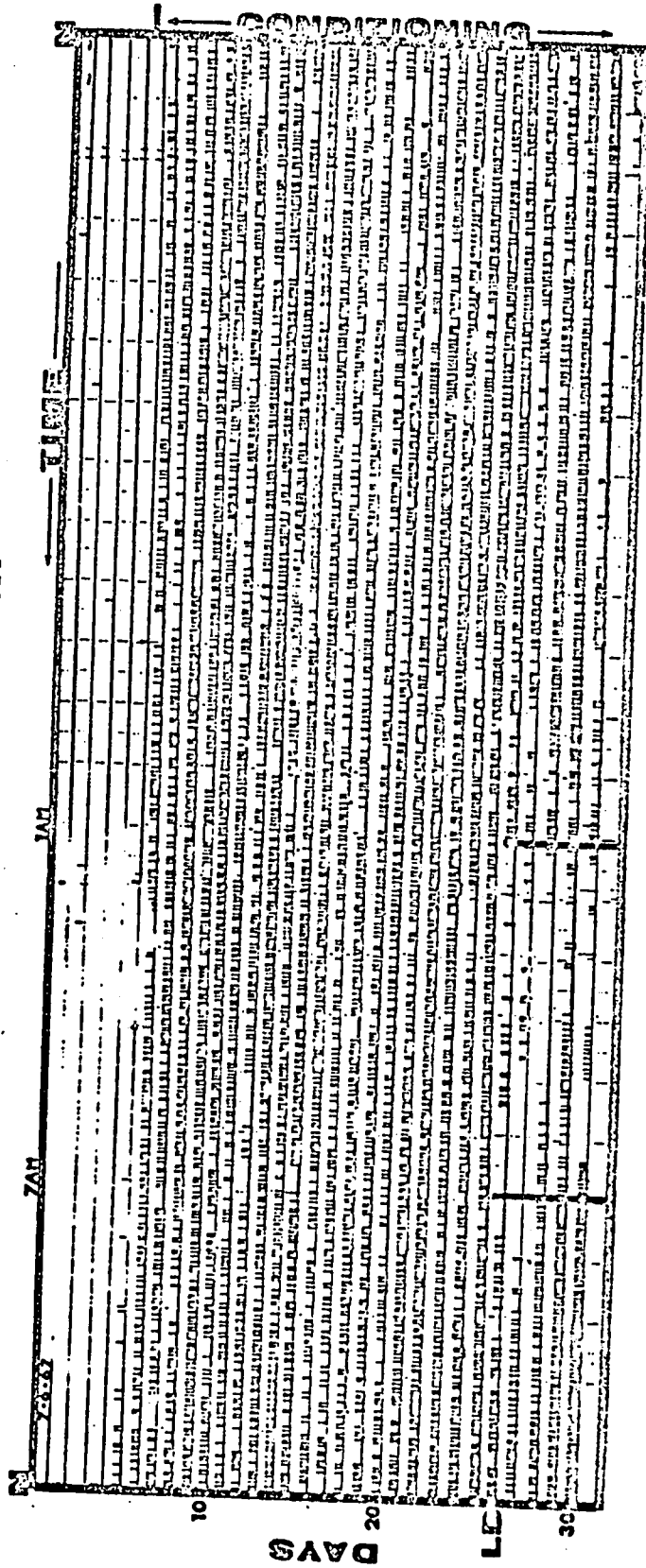


Fig. 3.8. Actogram for a CRF subject reinforced by the presentation of a male *Betta*. This subject showed a high response rate and the gradual formation of entrainment to the LD cycle.

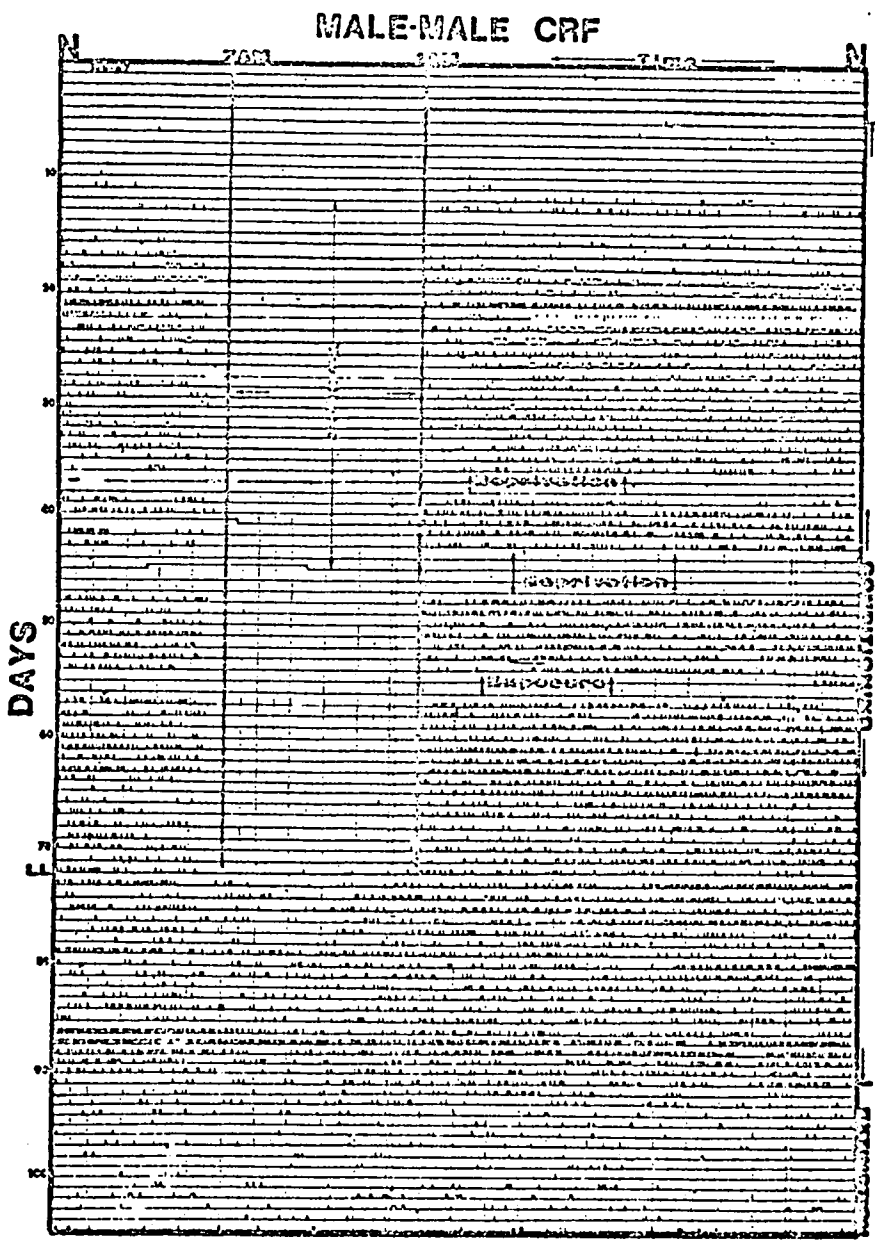


Fig. 3.9. CRF actogram for a male reinforced by another male. Unlike the subject in Fig. 3.8., this subject began the experiment under LD and shows evidence of more complete entrainment.

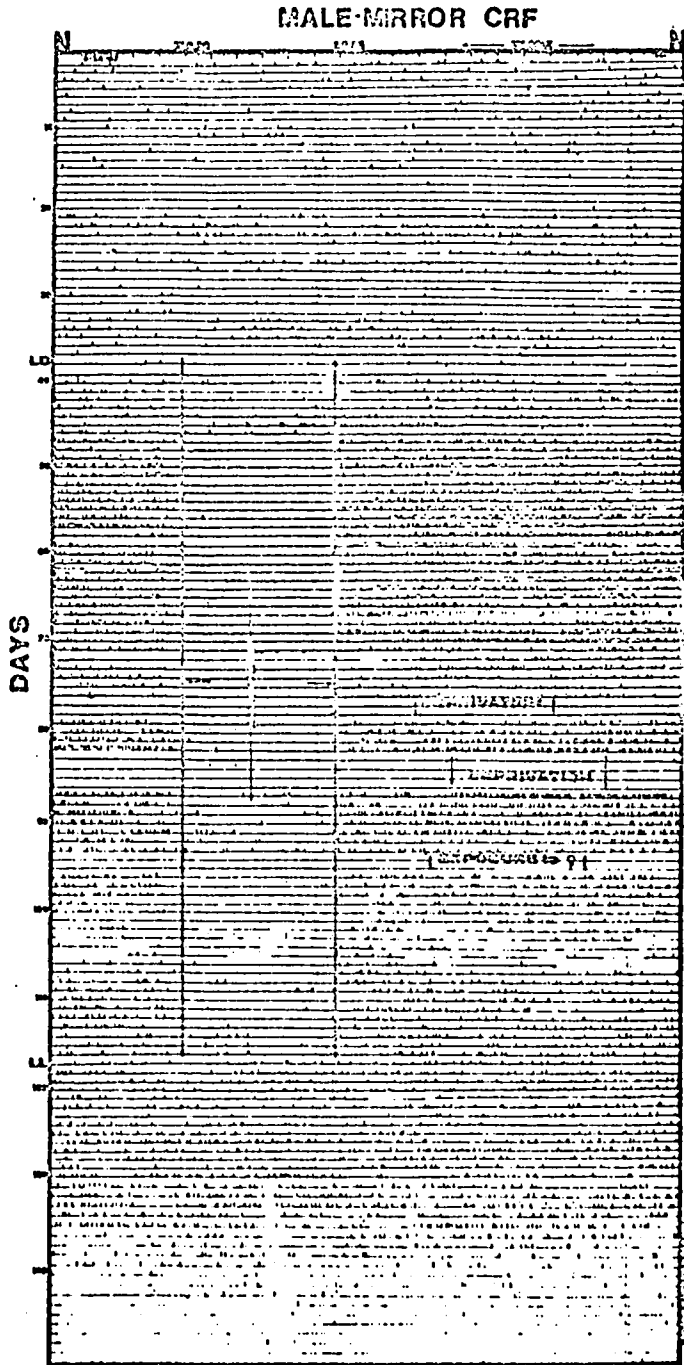


Fig. 3.10. CRF actogram for a male reinforced by his mirror image over a period of about 130 days.

CONTINUOUS ILLUMINATION
(LL)

LIGHT 12h - TWILIGHT 6h
(LD 18:6)

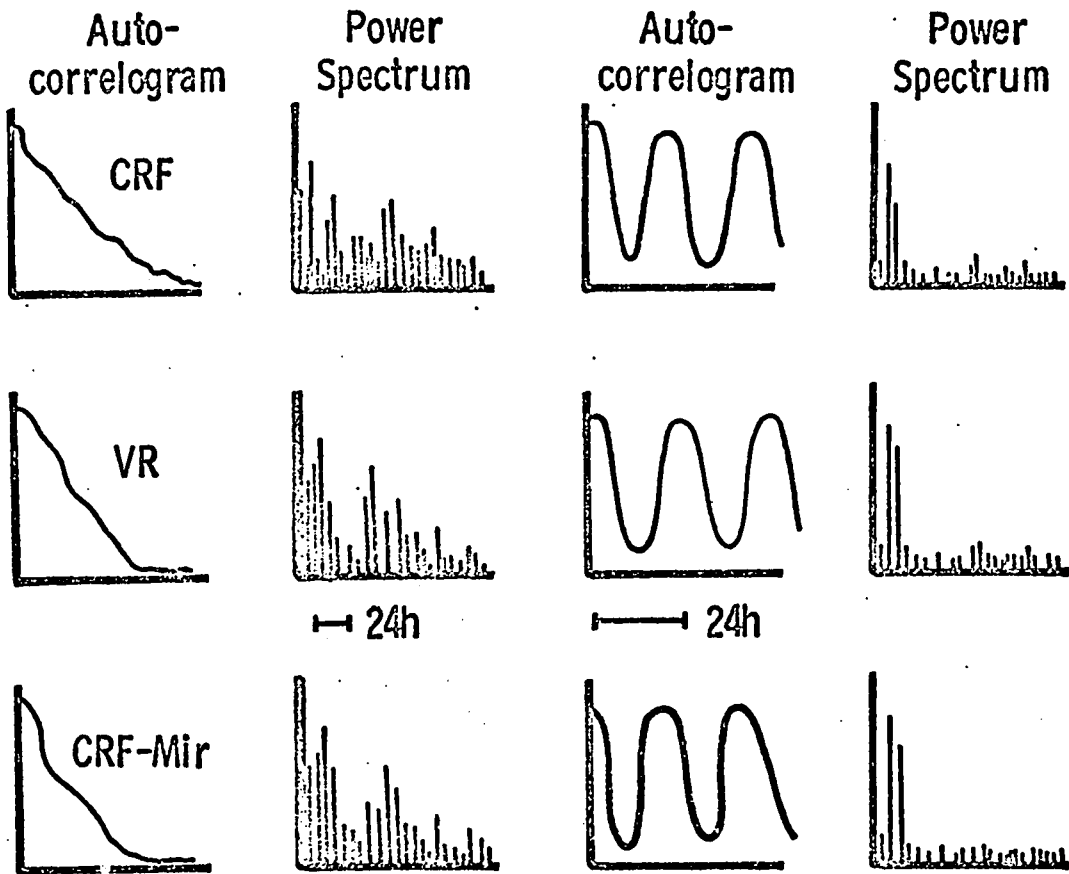


Fig. 3.11. Autocorrelograms and power spectra for representative ten day samples of operant responding in the male-male situation under various conditions of reinforcement and illumination. The figure shows a predominance of noise in LL and entrainment in LD 18:6.

CONTINUOUS ILLUMINATION

CROSSCORRELOGRAMS

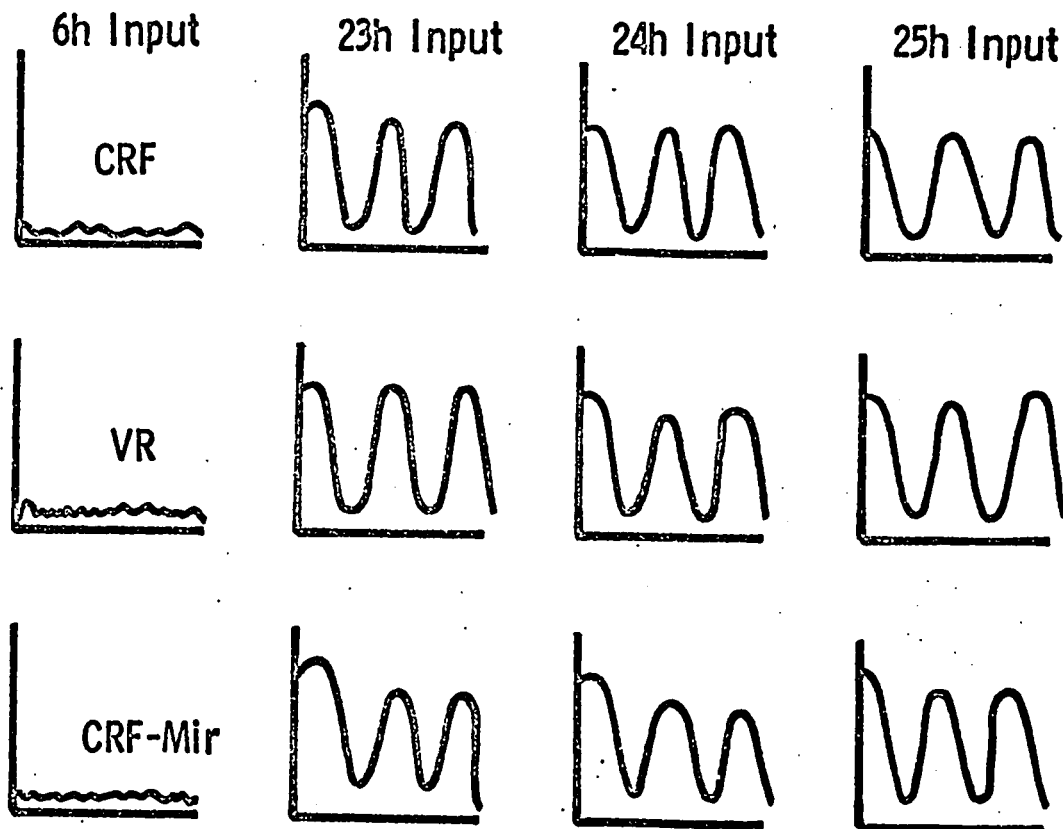


Fig. 3.12. Crosscorrelograms for representative ten day samples of operant responding maintained by a male reinforcer under various schedules and under LL. Strong 23 h, 24 h, and 25 h, components are evident.

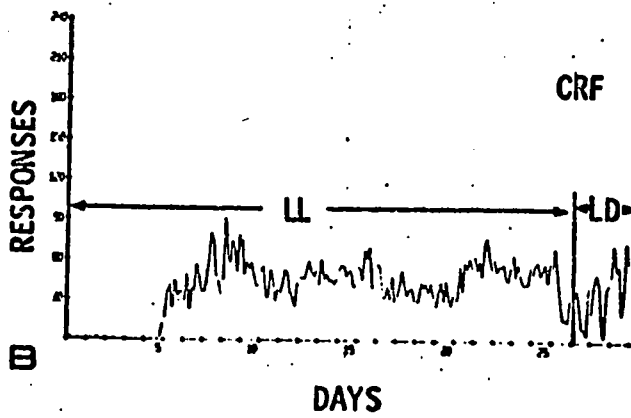
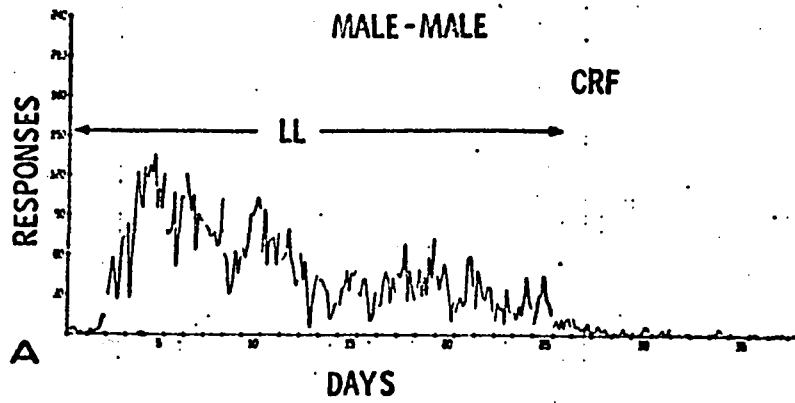


Fig. 3.13. Daily number of operant responses during successive 3 h periods for subjects maintained by CRF-VR 3 schedule and a CRF schedule. Note the attenuation of responding after transition to VR 3 and the beginning of synchronization to the LD cycle.

a clear indication of a 24h cycle emerge. Thus under LL the autocorrelogram cannot detect the periodicity because the signal is masked by "noise". However, under LD the rhythmicity in operant behavior is synchronized by the photic stimulus, and this is reflected in the autocorrelogram by the sinusoidal waveform obtained under LD (see Fig. 3.11). The effect holds for all fish tested under these conditions.

There is also a general tendency for the entrainment to be more compelling when the fish begins the study under LD than under LL. This is seen from an inspection of the actograms in Fig. 3.8 and 3.9. Thus, for the subject represented in Fig. 3.8 the LL to LD transition is associated with responding during the twilight phase of the LD cycle. Similarly, there is also a tendency for some subjects (e.g., Fig. 3.9) to show a temporary suppression of responding in the "subjective" twilight phase of the LL cycle. Other subjects (e.g., those represented in Fig. 3.10) do not show this effect.

Finally, perusal of the actograms suggests that within a LD cycle a second type of transitional phenomenon occurs. This is characterized by a delay in responding to the onset of light in the morning hours. A slight spilling over of responses into the twilight phase is also evident, though not nearly as compelling as in the MF condition.

Extinction: Examination of Fig. 3.7 shows that the onset of extinction produces a sharp decrease in the rate of responding for all subjects except #7. This latter subject, maintained on the VI schedule, never completely recovered the pre-exposure rate of responding and, in fact,

was actually at operant level for about 10 days prior to extinction. This fish, it should be mentioned, readily accepted food and was otherwise active during this protracted period of response inactivity.

The VR, CRF, and mirror CRF subjects all showed gradual reductions in responding and after about five days were all at operant level.

There was also a tendency for subject 3 (Fig. 3.7) to show a pronounced increase in rate after some 10 days of extinction level responding; an effect similar to the rate increase found in extinction for the CRF MF subject.

Finally, an unexpected but interesting finding emerged from the extinction data. Examination of Fig. 3.9 shows the presence of square wave-like excursions in the extinction part of the record. The horizontal excursion representing the top of the "wave" indicates the time spent in the photocell ring device or, in other words, response duration. A perusal of the record suggests that response duration increased during the extinction phase of the study. The effect, however, is most pronounced for this subject; the others show it slightly, or not at all.

Comparison and Synopsis

In the preceding section, results of treatments with the male as reinforcer and with the female as reinforcer were treated separately. In this section, attention is focused on these reinforcers

in an attempt to assess possible differential effects exerted upon operant behavior. At the same time, this policy of comparison will allow a synopsis of the foregoing results section.

Reinforcer: Perhaps the most compelling question to ask with regard to the male and female reinforcers is, which is the more potent of the two? This question can be answered in several ways and, to the extent that these agree, a decisive answer is possible. For example, it is possible to consider rates of responding under CRF, under intermittency, and during extinction as indicators of the strength of the reinforcer. On a common sense basis, and on the basis of some existing data (Hill & Wallace, 1967; Wilton & Strongman, 1967; Uhl & Grant, 1967) the more potent reinforcer would be expected to sustain the highest rates under each of the above mentioned conditions.

CRF: While there is a good deal of variability and overlap between rates sustained by the male and by the female reinforcer, the two highest rates were both observed when the male acted as reinforcer. These rates were observed for subjects 4 and 6 in Fig. 3.7 and the rates, which are close to 800 responses per day, are about twice as great as the highest female-maintained rates. Therefore, these data suggest that the male is the more potent reinforcer of the two.

Intermittency: In previous sections it was seen that the transition from CRF to intermittent reinforcement tended to maintain or increase the rate of responding when the female acted as reinforcer and to maintain or decrease the rate when the male acted as reinforcer.

This suggests that the female is probably the more potent of the two reinforcers.

Extinction: Discounting the aberrant extinction behavior exhibited by the CRF subject in the MF condition, the highest extinction rate is shown by the VI subject in the MF condition. However, the combined extinction rates for subjects in the MM condition was not significantly different than the combined MF extinction rate ($U = 230$, $n_2 = 21$, $p = .246$).

These comparisons, then suggest the awkward conclusion that the male is the more effective reinforcer if the magnitude of CRF rate is the index of effectiveness, that the female is the more effective reinforcer if response rate in transition to schedule is the index, and finally, that no difference exists if resistance to extinction is the index.

Deprivation: Under conditions in which the female acts as a reinforcer, deprivation from her does not seem to produce a consistently reliable effect on subsequent responding. On the other hand, when the male acts as a reinforcer, deprivation exerts a consistent effect in increasing subsequent responding, though it was pointed out that this may have been part of a general incremental trend.

Exposure: Exposing a subject from the MM condition to a mature female either has no effect or else the effect is indeterminate due to confounding with other conditions, On the other hand, exposing a MF subject to a "rival" was followed by an increase in subsequent

responding toward the female. However, because of the small number of subjects tested the results could easily be spurious.

Periodicity: Finally, subjects from both groups showed a very noisy circadian rhythm under conditions of LL which could only be detected by means of crosscorrelation. When, however, a photoperiod was introduced, a clear 24h rhythm emerged. In addition, subjects from both groups tended to restrict responding to the light phase of the LD cycle.

Heteroplanic Stimulation

Figure 3.14 shows the mean number of responses emitted each day for all subjects in the three groups tested. Panel A shows the performance of subjects initially maintained by exposure to the full mirror, the frontal mirror, and the lateral mirror, respectively. The second panel shows performance in each mirror condition after a switch from the previous first panel mirror condition. Thus, subjects in the B-full condition were previously in the A-lateral and A-frontal groups, while the subjects in the B-lateral and B-frontal groups were originally in the A-full group.

In determining which mirror condition most effectively supports operant behavior, attention is called to panel A. It can be seen that the frontal condition supports the lowest rate of responding and that the full and lateral mirrors do not differ systematically. This impression is confirmed by significance tests (Fu. vs. Fnt., $U = 1$,

$n_{1,2} = 7$, $p = .002$; Lat. vs. Fnt., $U = 5$, $n_{1,2} = 7$, $p = .012$; Fu. vs. Lat., $U = 23$, $n_{1,2} = 7$, $p = .902$).

The transition from one display condition to another provides an interesting test of the effectiveness of the mirror conditions in controlling behavior, since if operant behavior is really under the influence of the reinforcer, the stimulus should exert its effects regardless of previous experience (except perhaps for the transition). Panel B shows performance in the three mirror conditions largely overlap each other, minimizing the differences between groups. This suggests that previous experience does exert an effect on current responding. The panel, however, confounds subjects and treatments and it is difficult to see exactly how behavior changes. This is more readily seen from the cumulative plot of Fig. 3.15 which shows how the different subjects are affected by a change in mirror condition. It can be seen that in all but one instance transition to the new mirror condition did not appreciably alter the established rate of responding. The one case where it did is the full-lateral condition in which a sharp rate decrement occurred under lateral mirror stimulation.

Two additional points require comment. First, as in Experiment I, large individual differences between subjects emerged independently of the treatment condition. Thus it is of some significance that of the 16 subjects tested in this study, three showed very high rates (over 240 responses/4h), two showed intermediate rates (about 140 responses/4h), eight were intermediate-low (about 25 responses/4h), and three showed low rates (15 responses/4h).

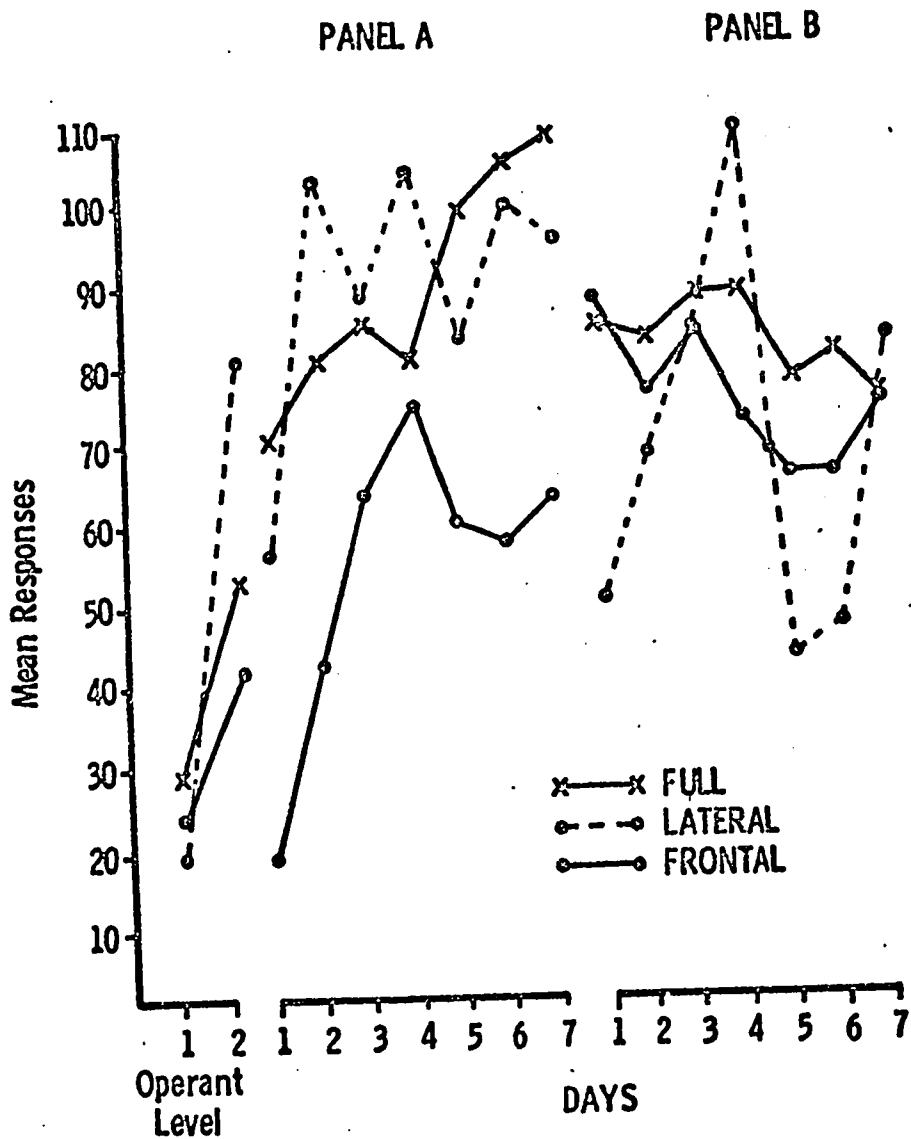


Fig. 3.14. Mean daily performance maintained by Full, Lateral, and Frontal mirrors. Panel B, which confounds subjects and treatments, shows performance after a switch from the panel "A" condition.

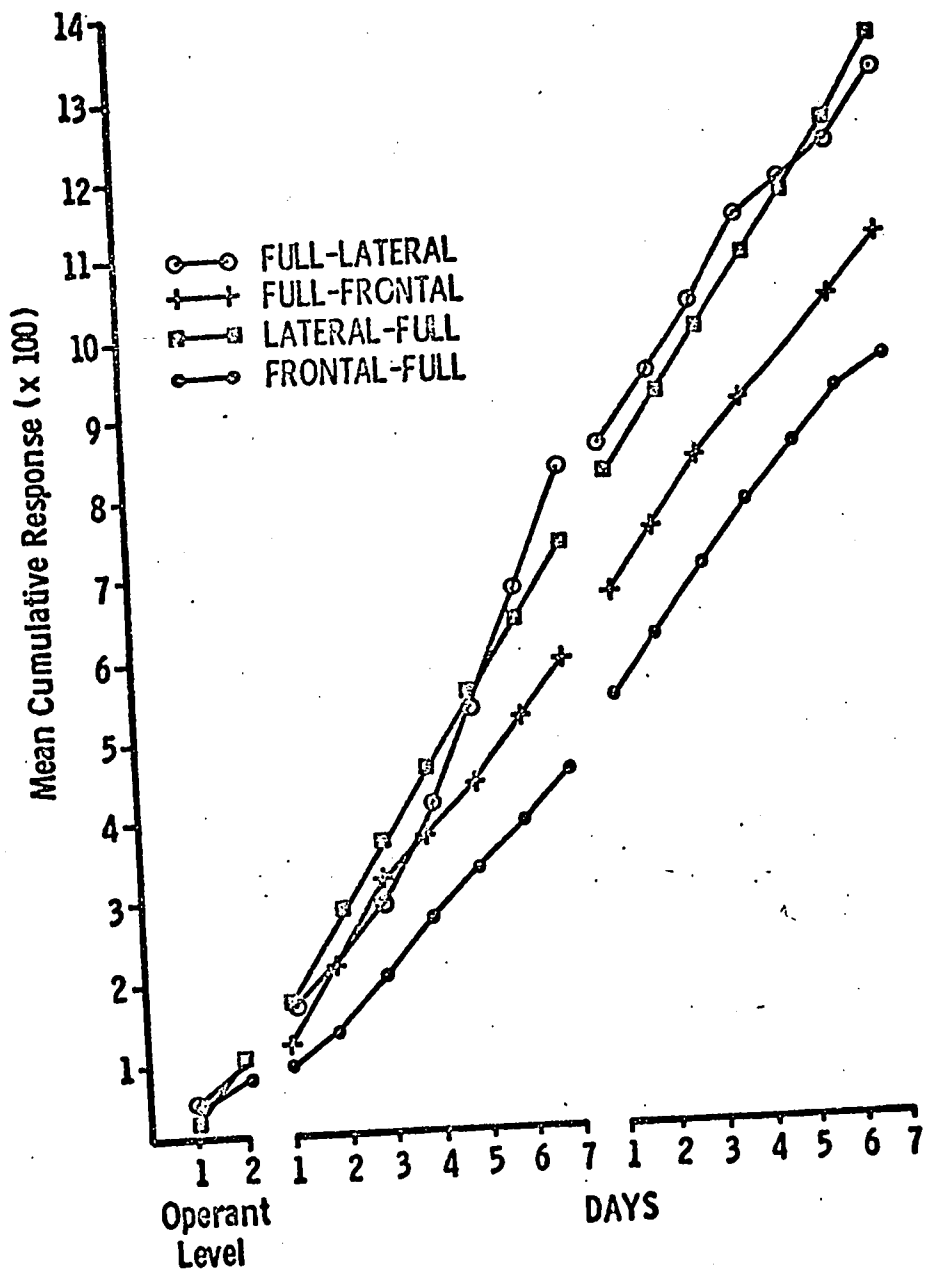


Fig. 3.15. Mean cumulative response for four groups maintained by various mirror conditions. Transition to the second mirror condition appears to affect only the Full-Lateral group.

The second point concerns the variability in operant levels observed for the subjects in this study. One subject actually emitted 248 responses during the second day of operant level determination, a performance which normally would be considered a very high conditioning score had the reinforcement contingency been in effect. Observation of this subject showed, however, that he was actively engaged in building a large bubble nest which was attached to the side of the manipulandum just in front of the ring opening. The concentration of this kind of activity in an area so close to the ring opening was particularly conducive to emission of a large number of "responses". This subject, as it turns out, also had the highest conditioning rate. On the other hand, a subject with the lowest operant rate had the fifth highest conditioning rate. In order, therefore, to determine whether a relationship existed between operant level and conditioning rate, a product moment correlation coefficient was computed and was found to be, $r = .60$ ($df = 14$, $p = .02$, two tailed). An r of $.60$ indicates that about a third of the variance in conditioning can be accounted for by the operant performance.

Operant Behavior and Fighting

Table 3.4 shows the outcome of six contests together with the mean operant rates under full mirror for both winners and losers. The table shows quite clearly that where large rate differences exist between combatants, the higher rate subject always

wins the contest. The prediction is also consistent with expectation when the difference between the operant measures is not as pronounced. In other words, within the limits of this study there is a perfect rank correlation between the operant rate and the outcome of a fight.

One subject was tested twice. In the first encounter with a high rate opponent, this fish did not counter-threat but instead adopted a head-up tail-down position. Shortly thereafter, as his opponent was going through the initial display maneuvers, this fish took a position in a lower corner of the tank and remained still there. After about 3 or 4 min it was decided that this was no contest and the fish were thus separated. On the following day, the loser of this contest was matched against another low rate subject. Both immediately showed intense display and subsequently fought a long (1h) battle in which the fish with the previous losing experience won the match.

Summary: In this chapter a parallel series of problems were stated with regard to the reinforcement properties of a male, and of a female *Betta*, for the operant behavior of another male. The problems were essentially concerned with CRF and schedule effects, deprivation effects, the effects of exposure to a fish of opposite sex to the reinforcer, the course of extinction, and the possible existence of periodicities. In a second study, attention was concentrated on determining whether Frontal, Lateral, and Full mirrors differentially sustained operant responding. A final study attempted to determine whether operant responding could predict the outcome of fighting contests. A simple operant conditioning technique was used to assess these problems in

Table 3.4. Victory and Defeat as a Function
of Mean Operant Rate

<u>Fight</u>	<u>Won</u>	<u>Lost</u>
1	300	30#
2	111	18
3	230	151
4	131	30
5	30#	27
6	34	15

Same Fish

which a fish swam through a ring and thereby gained access to the reinforcer for a period of 20 sec. Six basic findings emerged from this research:

(1) The female *Betta* is a potent reinforcer for the male *Betta*. Her effectiveness as a reinforcer varies considerably from male to male.

(2) Live male *Bettas* act as potent reinforcers for other males, again with considerable individual differences.

(3) For both the male and female reinforcers, under conditions of constant temperature and illumination, a noisy circadian rhythm containing 23, 24, and 25h components appears to control the gross temporal patterning of operant behavior.

(4) Entrainment of the circadian rhythm is established by synchronizing the operant behavior to an 18h light-6h twilight cycle. A marked suppression of responding occurs during the twilight phase of the LD cycle.

(5) Frontal display supports a lower rate of responding than either lateral or full displays.

(6) The CRF, full mirror operant rate predicts the outcome of fighting contests.

The remaining findings regarding schedule by reinforcer interactions, deprivation, and exposure must remain inconclusive because large within subject variability, small number of subjects, and confounding with other conditions, make clear cut interpretations impossible.

CHAPTER IV

D I S C U S S I O N A N D C O N C L U S I O N S

This chapter is devoted to an interpretative and methodological evaluation of the reported results. In particular, attention is focused on specific and general aspects of the reinforcement nature of the male and female *Betta*.

Male Reinforcer

In this study it was again demonstrated that visual stimuli comprising the male *Betta* can act as a positive reinforcer for another male. This is evident from a number of behavior changes associated with changes in experimental conditions.

One excellent way of determining whether a given stimulus has reinforcement properties is to observe the rate of response in both the absence and presence of the presumed reinforcer. Except in the case of some unique reinforcement schedules, response rates in the presence of reinforcement should be higher than in its absence.

Reinforcement is generally withheld under experimental conditions known as the operant level and under conditions of extinction. The data show clearly that the operant level is only a small fraction of the rate observed when the contingency is put into effect. For some subjects the change in rate from non-reinforcement to reinforcement is abrupt while for others it is much more gradual.

Some of this between subject variability may have resulted

from the fact that a "self" shaping as opposed to the more traditional shaping procedure was employed to effect acquisition. Thus acquisition could have been retarded in low rate subjects because very long inter-response times were reinforced as a result of a general level of inactivity, or because the very long intervals between reinforced responses retarded the formation of the relevant stimulus-response association necessary to obtain reinforcement. In either case the major increase in rate from operant level to acquisition level is in keeping with previous work demonstrating the reinforcement properties of male stimuli.

When, under conditions of extinction, the reinforcement arrangement is returned to operant like conditions, a reversibility in behavior follows. This change is characterized by a relatively smooth rate decrement commencing from as high as 500 daily responses and approaching a near zero operant level.

There are two exceptions to this smooth deceleration of response in the male-male condition. One Subject, #7, virtually stopped responding after being exposed to the female exposure fish and therefore did not come in contact with the extinction schedule. The other subject, #3, showed the expected decline in response rate upon introduction to extinction but then after some ten days began to exhibit an increased rate of responding. Since another subject in the male-female condition showed a similar effect, and since protracted extinction sessions of this nature are not common in the literature, it is difficult to say whether some sort of adventitious reinforcement was supporting the behavior, whether the fish showed an activity change sensed by the ring device, or

whether this form of response "bursting" is a bona fide effect of protracted extinction.

On the whole, however, it may be said that the basic rate changes observed from operant level to acquisition and from acquisition to extinction generally conform to those observed when traditional positive reinforcers are used to control behavior.

Another way of demonstrating the reinforcement properties of a stimulus is to observe behavior under different reinforcement schedules. The outcome of such manipulations indicate that behavior can be maintained by both VR and VI reinforcement. However, against this background of maintained behavior are data which show considerable day to day variability and a rate decrement in the schedule transition from which the fish never completely recovered. Though a total breakdown did not occur, the sluggish response rates may be taken as evidence of a "strained" schedule control of behavior.

While schedule strain constitutes a plausible explanation of the rate decrement on the variable schedules, it is not the only explanation and there are other considerations which may render it improbable. First, in the case of the VR schedule a very low response-to-reinforcement ratio, which should not have produced strain, was in effect. And second, though the same reinforcement schedules were utilized in the male-female condition, this same sort of strain did not emerge. This implies that the schedule may be sensitive to unique properties of the male and female reinforcer. On the other hand caution should be exercised in employing this interpretation since protracted sessions of ad lib

reinforcement generally prove to be detrimental to the generation of tight schedule-controlled behavior. Where such control has been demonstrated (Skinner and Morse, 1958) strict precautions were taken to prevent satiation. Under the present nondeprivation conditions with a constant 24h availability of reinforcement, the behavior could make a very cursory contact with the schedule and still be effective in obtaining reinforcement.

In a very recent paper, Hogan, Kleist, and Hutchings (1970) compared reinforcement properties of food and mirror image under FR schedules ranging from FR 1 to FR 6. With food reinforcement it was found that as the ratio size increased the reinforcement rate remained constant and the response rate increased. However, with mirror image reinforcement the response rate remained constant and the reinforcement rate decreased. The former effect is typical of FR behavior but the latter is not. A similar mirror-image schedule effect has recently been obtained by the present author. These results are in agreement with the data obtained with the live male reinforcer for the variable schedules.

In studies not mentioned by Hogan et al (1970), Thompson (1964, 1969) had on two earlier occasions studied mirror reinforced FR behavior in Fighting Cocks and Fighting Fish, respectively. In the first of these studies Thompson investigated the relative reinforcement properties of mirror, water, and food under fixed ratios ranging from 1 to 75. Thompson found the usual covariation between ratio size and response rate (up to a point) for all reinforcers, though when behavioral breakdowns occurred, they did so first with mirror reinforcement. In the

latter study, with Fighting Fish, Thompson also confirmed the failure of mirror image to support fixed ratios higher than about FR 6, though much higher stable ratio behavior was eventually established by the incorporation of secondary reinforcers into the operant chain. This may mean that the reinforcement decrement obtained with *Betta* may be class or species specific. It is more probable however, that the effect is due to an interaction between the topology of the operant and the nature of the reinforcer. Hogan et al simply interpret their results to mean that the mechanisms controlling food and mirror image reinforcement are different, though they do not suggest what this difference might be. We shall shortly have occasion to argue that mirror image is an ambivalent reinforcer containing both appetitive and aversive elements and it is this ambivalence factor which is responsible for its unusual operant effects.

Sometimes the reinforcement properties of a stimulus are investigated by the manipulations of conditions other than those involving the reinforcement schedule. One such is the deprivation condition. A condition of deprivation is created by withholding the reinforcer and the opportunity to respond for extended periods of time. Within limits, the typical effect of such deprivation is to potentiate responding to levels exceeding nondeprivation rates (Miller, 1957).

Food and water are the classic positive reinforcers and hunger and thirst are the deprivation states on which these substances presumably depend for their reinforcing properties. This, at least, is the traditional way of conceptualizing the matter and, to a large extent,

is still the prototype upon which much current thinking about positive reinforcers is based (see Kimble, 1961). It was in this tradition that an attempt was made to determine whether deprivation from the male reinforcer would engender rate increases when the opportunity to respond again became available. We have seen however that the deprivation data are inconclusive. This, however, is not the same as saying that a deprivation effect does not exist and in fact, such an effect is suggested by consistent increases in responding and by the disruption of LD control after the second deprivation for the mirror CRF subject. If further research establishes this phenomena, it must do so by controlling confounding factors as well as taking account of alternative explanations such as stimulus satiation (Glanzer, 1953) or frustration (Amsel, 1962).

By way of summary, it seems reasonable to conclude that the rate changes observed during the operant, contingent, schedule, and extinction conditions, together with the suggestive nature of the deprivation data, lend support to the contention that stimuli evoking aggressive behavior are positive reinforcers for conspecific males.

Female Reinforcer

Having considered the rationale behind the criteria for reinforcement assessment in the male-male condition, it is now possible to apply these same criteria to the evidence concerning the reinforcement status of the female *Betta*.

Consider first the case of operant and contingent rates. The data show, as in the case with the male reinforcer, that the rate of

responding during the operant level determination was only a very small fraction of that observed when the response-reinforcement contingency was instated. In addition, the same sort of between subject variability seen in the male reinforcer condition during transition from nonreinforcement to response contingent reinforcement was evident when the female acted as reinforcer. Presumably the individual differences in establishing contact with the reinforcement contingency may be attributed to the same factors suggested in the male-male condition; namely the reinforcement of long interresponse times, the failure of the formation of the relevant stimulus-response association due to the long intervals between reinforced responses, or (more nebulously but perhaps equally as valid), to individual differences in sexual motivation.

During acquisition different subjects reach different asymptotic rates of responding which range between about 125 responses a day to over 400 a day. Here again it is likely that asymptotic between subject variability can be attributed to those same factors which purportedly accounted for differences in transition to reinforcement. The ability to maintain behavior by making the presentation of a given stimulus contingent on behavior establishes that stimulus as a reinforcer, and it is on evidence of this sort that the female *Betta* is regarded as a reinforcer.

That the female *Betta* is a reinforcer is also evident from the behavior changes occurring during extinction. Here too, except in the case mentioned earlier, there is a steady decline in response rate approaching the operant level when the response reinforcement con-

tingency is ended. The same type of effect emerges with traditional positive reinforcers.

Finally, the reinforcement properties of the female *Betta* are evident from the fact that it is possible to maintain the operant under VR and VI schedules at rates above the CRF level. Thus, while there was a relatively brief decrement in transition to schedule the strained performance seen in the male-male condition did not emerge here. It is likely too, that had the experimental sessions been separated by 24h (for example) a more compelling picture of schedule controlled behavior in the form of higher, more stable, response rates might have been obtained.

When the male subject is deprived of visual access to the male reinforcer a suggestion of a deprivation effect emerged. When the male subject is deprived of visual access to the female reinforcer there was no indication that a deprivation effect emerged. The failure to find a deprivation effect with the female reinforcer is in keeping with the limited information available on other species. The available data indicate that within a day after copulation, increases in deprivation do not result in an increased tendency to mate (Warner, 1927; Beach & Jordan, 1956) though it is important to remember that the present situation differs from the ones cited in the important respect that physical contact between the pair was not permitted. Alternatively the failure to find an effect could be attributed to the high within subject variability and confounding referred to earlier.

The conclusion drawn from the above considerations is that

the female *Betta* is a positive reinforcer for the male *Betta*. By way of summary, this conclusion is based upon changes in behavior associated with the presence and absence of response contingent presentation of the female. That the female, and not simply access to an empty chamber, was the reinforcing event is suggested by the large rate differences between the operant level and the female contingent level. That the result was not due to an activation effect was not specifically controlled, though it has been suggested elsewhere (Goldstein, 1965) that there are grounds for considering a stimulus which produces an activation effect to be a reinforcer. Thus, if a reinforcer is considered to be any stimulus which increases the probability of responding, then both the conditioning effect and an activation effect would demonstrate the reinforcing properties of the stimulus in question. Beyond this, however, the area through which the fish could swim in order to procure reinforcement was deliberately made quite small in order to minimize the occurrence of "accidental" responses. The "ripeness" of the female, which may also have been a reinforcing factor, could not be systematically controlled, though an attempt was made to use only mature, apparently ripe females. Finally, it should be noted that the female-as-reinforcer demonstration does not differentiate between the female reinforcer as a social stimulus and the female as a sexual stimulus. In other words, it is possible to argue that the fish visits the female because it seeks visual contact with a conspecific rather than because it seeks to mate. Data from other species indicate that the opportunity to engage in visual contact with a conspecific can act as a reinforcer (Butler, 1957; Pinckney & Anderson,

1967). In partial answer to this, it may be said that casual observation of performing males revealed that subjects were displaying to and leading females in the same way as they would in a nonoperant situation, though more systematic work of the kind obtained for the male-male situation (Thompson & Sturm, 1965 b) must be done.

Discriminated Reinforcement

We have seen that both the male and female *Betta* can function as a positive reinforcer for a conspecific male. Now in the case of *Betta splendens* and indeed of all species depending upon behavioral dimorphism for sex recognition, a major interpretative difficulty in the operant situation arises. How does one differentiate between the possibility that the behavior is maintained by sexual tendencies on the one hand or aggressive tendencies on the other? Or to put this another way, how does one know that the experimental subject recognizes the sex of the reinforcer? The facts that both the female and male release such similar behavior patterns and that pseudofemale behavior and homosexual matings sometimes occur in this species (Forselius, 1957), make the position at least tenable that discrimination may not actually be taking place. Indeed, in psychological terms it is possible to maintain that the rate differences between male and female represent points along a generalization gradient much like the one obtained by Thompson (1963) using models and a mirror. While a within subject design would be desirable here, there are preliminary indications in the data suggesting that the fish does recognize the sex of the reinforcer.

The data in question are the rate differences observed under CRF and the subsequent effects observed during transition to intermittent reinforcement.

In the case of CRF it was seen that the highest rates of responding occurred when the male was the reinforcer. Thus, no subject in the male-female condition approached the CRF rates of two subjects in the male-male condition (subjects #4 and #6). This may be indicative of differential perception. One difficulty with this is that a good deal of overlap exists between the rates maintained by the two types of reinforcers. On the other hand, the ceiling rather than the overlap may be the more relevant dimension. In fact, male-male rates have been reported as high as 1200 (Goldstein, 1965) and 1400 (Hogan, 1967) responses in a day.

A second factor which may be taken as support for the idea of differential perception is that a permanent rate decrement tends to accompany transition from CRF to intermittent reinforcement in the male-male condition, an effect substantiated by Thompson (1968) and Hogan et al (1970), but does not occur when the female acts as reinforcer; if anything, the rate goes up. It should be emphasized, however, that the validity of these effects would have been strengthened by a return to CRF conditions. Provisionally, it may be suggested that this schedule-reinforcer interaction may be due to the ambivalent nature of the male-male situation, containing as it does both approach and withdrawal elements (Morris, 1954; Scott, 1958). This is potentially one of the most important findings in this study and for this reason needs to be

confirmed in future work. One hesitates to generalize on the basis of small numbers but if the effect is reliable it would mean that schedule performance is sensitive to sex differences.

Stimulus Factors

Three distinct classes of stimulus factors were investigated to determine what effect, if any, these would have on the operant behavior of Siamese Fighting Fish. The factors of interest were the potential differential effects of stimulus characteristics of the mirror reinforcer, the effects of exposure to stimulus fish of the opposite sex of the reinforcer and finally the effects of the light-dark cycle. Since the exposure data were inconclusive they will not be discussed here.

Heteroplastic Mirror Reinforcement

Several subjects in the male-male condition performed at rates appreciably lower than the 600 responses per day typically obtained in earlier work. It was to cover instances of this sort that a mirror reinforcement subject was employed to evaluate possible differential effects of mirror and live fish. The mirror subject, however, also responded at an atypically low rate (about 125 responses a day) over a period of five months. One implication of this was that in the present situation the live fish-mirror distinction was not a major factor in determining response rates though there is some evidence that in a choice situation *Bettas* will display more often to a mirror than a live male (Baenninger, 1968). If the mirror-live fish factor did not account for low rate responding it is necessary to look for other common features of

the experimental situation which may have differed from those used previously.

One of these factors is the strain of the fish. Strain differences could have accounted for low rate responding as many of the higher rate responders were of a different strain than their low rate counterparts. That strain differences could have affected response rates is supported by experimental work showing that the color of the *Betta* is associated with a unique response rate (Thompson & Sturm, 1965 b).

However, since the operant situation employed here represented a major departure from those used in earlier research, it was decided to ignore organismic factors and focus instead on possible situational variables which may have been in control of responding.

The factor which appeared most obvious was that of hetero-planic mirror reinforcement, or the area of reinforcement in different planes. Specifically, it was hypothesized that the horizontal extension of the reinforcement chamber was too narrow and discouraged the expression of lateral display. Accordingly, frontal, lateral, and full mirrors were used to investigate the possibility that response rate would vary with the type of mirror stimulation.

To recapitulate the results, it was found that frontal mirror supported a significantly lower rate of responding than either lateral or full which did not differ significantly from each other. The result confirmed the hypothesis under investigation: narrow width stimulus chambers discourage the expression of lateral display and when lateral display is impeded, response rate diminishes.

This is an indirect confirmation, however, since it proves only that such display factors could have been operative, not that they were. After all, in Study I, the area provided for visual control of lateral and frontal display was 3 in wide whereas in Study II, subject had only $\frac{1}{2}$ in for frontal display. Thus, if the frontal display area had been larger, differences between the three display groups might not have emerged. However, increasing the area of either the lateral or frontal conditions would probably have resulted in further confounding of display components.

This notwithstanding, it is clear that the opportunity to engage in different display behaviors affects the rate at which responding will occur. One possible reason why the lateral and full conditions did not differ systematically is that in the former case it was not possible to completely eliminate the opportunity to engage in a frontal display. Such a display usually emerged out of lateral display when the fish turned its head (rather than its entire body) towards the mirror with full gill cover erection. The occurrence of such surreptitious frontal display may also account for the day to day rate variability seen for the lateral condition.

Thus, the study of display components on operant responding suggests that both the absolute level, and day to day variability in responding, may be accounted for by display eliciting factors. At the same time, the same kinds of individual variability seen in previous work emerged.

As we have now seen, the research on heteroplastic stim-

ulation grew out of an attempt to locate situational factors as determiners of response rate. It turns out, however, to have significance beyond the limits of that particular situation. Thus, Thompson and Sturm (1965a) found in a classical conditioning study that frontal approach and gill cover erection were slow to condition relative to fin erection and undulations. The significance of this lies in the fact that frontal approach and gill cover erection were the consummatory behaviors in the frontal condition, while fin erection and undulating movements were the consummatory components of lateral and full mirrors.

In a very recent study on habituation in *Betta*, Peeke and Peeke (1970) found a differential waning of the components of display. One of the components, referred to as maximum aggressive display (MAD), appears from their description to coincide with what is generally regarded as frontal display. It was found that this component of display habituated more rapidly than a second component apparently equivalent to lateral display. Thus, the data emerging from these three different paradigms agree in showing that, relative to lateral display, frontal display is (1) slow to classically condition, (2) supports lower rates of operant responding, and (3) succumbs most readily to repeated stimulation. This congruence suggests that a common underlying mechanism controls the expression of aggressive behavior in these diverse situations. An insight into the nature of this mechanism may be forthcoming when the phylogeny and ontogeny of frontal and lateral display is analyzed.

Finally, before leaving the topic of mirror reinforcement,

a brief comment about Gallup's (1968) analysis of this phenomenon is in order. Gallup takes the position that the mirror reinforcement effect may be attributed to the novelty of the stimulus. This position, however, seems to be logically untenable as it is possible to maintain mirror reinforced behavior at very high rates, 24h a day, over relatively long periods of time. If stimulus novelty were the reinforcing event, it would be expected that the fish would stop responding in a day or so as this sort of protracted exposure would surely eliminate the novelty characteristics of the stimulus.

Gallup further contends that mirror-image stimulation has unique properties not present in a live conspecific and these unique properties render the mirror reinforcing. Therefore, a live male should not act as a reinforcer. The present study disproves this contention.

What is now needed are studies specifically designed to test the effectiveness of mirrors and live fish. It may be anticipated from such work that, in the long run, the mirror would sustain higher rates than the live fish. One reason for this, according to Peeke and Peeke (1970), is that the mirror situation represents one of "perfect positive feedback which will increase the rate of the elicited response at a steeply accelerated rate".

There is another reason for supposing that a mirror would be more effective than a live fish. In the live fish condition the reinforcer may be regarded as in either an habituation or in a simultaneous classical conditioning situation (depending upon collateral response-contingent events). In either case, the live male would be expected to

undergo a diminuation of (display) response (Kimmel, 1966; Peeke & Peeke, 1970) which presumably would make him a less effective reinforcer. If this happened in the present experiment it might help to explain the sluggish response rates obtained in the various schedule conditions. It might also help to explain the preference for mirrors over live fish observed by Baenninger (1968) in a nonoperant situation.

The effectiveness of the reinforcer is intimately tied to the problem of response variability. The possibility should now be considered that large within subject variability is an inherent characteristic of the present and related experimental arrangements. In addition to what has already been said, failure to achieve steady-state responding may be due to the facts that (1) subjects were run 24h/day over a period of several months possibly resulting in shifts in the effectiveness (i.e. magnitude) of the reinforcer (Carlton, 1962); (2) the visual reinforcer may be regarded as a species of sensory reinforcer which are known to maintain highly variable rates of responding (Kish, 1966); (3) the reinforcer releases a fixed action pattern (FAP) which is only partially under the control of the reinforcer (Moltz, 1965); and (4) there is no apparent "drive reduction" associated with the reinforcer in that the consummatory response of attack or mating does not occur.

Light-Twilight Cycle

The light-twilight cycle was the third major stimulus factor investigated. This was done by recording operant behavior under an 18:6 LD cycle and under conditions of constant illumination.

It will be recalled that a differential reinforcement

procedure was not used during the operation of LD. Yet, the results clearly demonstrate that the 18:6 LD successfully entrains, locks in or synchronizes the operant responding in both the male-male and male-female conditions. This light control of responding is characterized by an almost total inhibition of responding during twilight while responding is restricted to the light phase of the cycle. The significance of this is underscored by the fact that twilight, rather than total darkness, was used in the cycle.

As was pointed out earlier, it was determined by mechanically exposing the reinforcement chamber that the operator could see, and in fact would display to, the reinforcer fish. In a later study conducted at Dalhousie University, the author found that the probability of display was independent of the level of illumination in a range from 0.3 to 25 lux. This may mean that twilight does not specifically affect the motivational or reinforcement properties of the reinforcer but rather that it results in a general suppression of gross motor activity. Since activity was not independently measured, however, this interpretation must be accorded the status of a speculative inference. Forselius (1957), on the other hand, points out the male Anabantids typically engage in maintenance activities such as nest repair during the night rather than in courtship or aggressive behavior. Thus, twilight suppression of operant responding may also be interpreted as an alteration in motivation without in any way diminishing the releasing properties of the reinforcer.

However the effect is interpreted, the empirical fact remains that twilight suppresses operant responding. One consequence of

this for further operant responding with Siamese Fighting Fish is that an effective "time out" from reinforcement is now available which appears to be similar to the time out procedure used with pigeons (Ferster & Skinner, 1957).

The powerful control exerted by light over the operant behavior is seen when, instead of a light-twilight cycle, continuous illumination is employed. Under these conditions fish in both male-male and male-female conditions respond continuously around the clock.

The use of continuous illumination allows for the expression of a possible circadian rhythm. The circadian rhythms obtained here were quite noisy but appeared to contain dominant frequencies of 23, 24, and 25h. This held for both reinforcers and for the various reinforcement schedules. This suggests a schedule independence of circadian periodicity. Thus, while schedule parameters may determine the frequency of local responding, it appears that endogenous oscillations govern the gross temporal patterning of responding. A somewhat analogous finding was recently obtained by Terman and Terman (1970) using different magnitudes of reinforcement brain stimulation under CRF. A circadian pattern emerged independently of the reinforcer magnitude, though the absolute rate of response varied directly with magnitude.

Another point regarding operant behavior under monophasic conditions also warrants further attention. This concerns the nature of the free running periodicity and is most meaningfully understood in terms of the circadian rule as formulated by Aschoff (1960).

Aschoff's rule, as it has come to be called, is actually

a generalization from empirical data which states that under LL dark-active organisms will tend to show a lengthening of the period to about 25h while day-active animals will show a shortening or speeding up of the rhythm to about 23h. The converse effect holds for continuous darkness.

In the present study, it was shown that the autocorrelation function for LL was unable to detect any clear periodicity, but rather suggested a predominantly noisy "rhythm". Only after the more powerful cross-correlational analysis was applied to the data did the underlying circadian periodicity emerge. We saw that the period was spread over three elementary neighbouring bands of 23, 24, and 25h. In view of what is known about the daily occurrence of reproductive behavior in *Betta* and in view of Aschoff's rule, the failure to find a dominant periodicity is quite interesting. In particular, attention is called to the fact that *Bettas* are frequently observed to spawn in the morning hours and to engage in nest building, repair and perhaps transport during the night (Forselius, 1957). Therefore in a very real sense, as far as the reproductive cycle is concerned, *Betta* seems to show both diurnal and nocturnal tendencies. Apparently, both these tendencies are reflected in the free running rhythm. One way to view this, following Sollberger's (1965) approach, is that the endogenous control mechanism searches the input signal for rhythmic information with which to synchronize. Since it finds none, it oscillates between its dominant circadian frequencies. However, many other interpretations are possible, the one suggested being more illustrative than definitive.

Finally, to conclude this section on periodicities; some-

thing must be said about the death rate found among subjects that started this experiment. Of the original eight experimental subjects, only one survived the total time the experiment was in progress. All the others died within one month after the commencement of the study. In contrast to this, no subject that started this experiment in LD died. Thus, all but one of the deaths occurred under LL and the one that occurred under LD did so four days after LL-LD transition.

Against this background it may be mentioned that Pittendrigh (1960) and others have taken the position that aperiodicity may be detrimental to health. Pittendrigh cites a now classic study by Harker (1958) who found that in transplant experiments with the cockroach, tumors developed if the diurnal rhythm of the transplant organ (subesophageal ganglion) was out of phase with that of the host. There is also evidence to show that damage will occur in tomatoes grown in LL (Arthur & Howell, 1937) and that death occurs to arctic mice within a week after LL and constant temperature (see Pittendrigh, 1960). It is at least conceivable that the death of the experimental subjects in this study might be attributed to the aperiodicity of constant temperature and illumination. The fact that the autocorrelograms show noisy pictures under LL may indicate that constant illumination is stressful to *Betta*. Marshall's (1967) data on the disturbed breeding of the Anabantids, *Trichopsis pumilis* and *Trichopsis vittatus* under LL certainly suggests that this is the case. On the other hand, it can be seen from the various Esterline-Angus data records that under LL the fish do not take a decided "break" from responding during the "day". One subject (see Fig. 3.8) responded

at a high rate 24h/day for about 30 days. The stress, therefore, may be the result of overactivity or lack of rest rather than to the aperiodicity per se. While more work is needed, it seems clear that this area promises to provide important insights into the complexities of behavior exhibited by *Betta* and other organisms.

General Problems Regarding Reinforcing Effects

Perhaps the primary reason for concern with the reinforcing nature of aggression provoking stimuli is that the data lend themselves to the interpretation that aggression is reinforcing, and furthermore, since the display response is innate, that it is inherently so. This, to be sure, is a highly controversial notion and the general tendency, at least among North American behaviorists is to reject this interpretation (e.g. Scott, 1958). It is clear, however, that a greater understanding of this phenomenon must be achieved as the number of diverse species exhibiting it continues to grow (Thompson, 1963, *Betta*; 1964, Fighting Cocks; Sevenster, 1968, Sticklebacks; Roberts & Kiess, 1964, Cats; Tellegan, Horn & Legrand, 1969, Mice; Melvin & Arson, 1970, Paradise Fish).

There are two slightly different viewpoints regarding the inherent nature of the reinforcer. One is the position that natural selection has made aggressive behavior reinforcing, the other that the aggressive behavior is associated with an affective state of pleasure which renders the behavior positively reinforcing. These positions will shortly be considered.

Concern with the inherent nature of the reinforcer can be by-passed by viewing reinforcement as a novelty effect or by viewing it in terms of response prepotency. The novelty interpretation has already been considered and found to be wanting. Attention is now focused on reinforcement and prepotent behavior.

Premack (1958) noted that in virtually all operant conditioning situations the emission of a consummatory response was contingent upon the execution of an arbitrarily defined, and therefore usually low probability, response. From this basic notion, Premack generalized that the necessary condition of reinforcement was simply an initial rate differential between two responses; under the proper contingency the response with the higher initial rate would reinforce the low probability response, but the converse of this was not true--a low probability response could not reinforce a high probability response.

Thompson (1966) and Baenninger et al (1970) have tentatively aligned themselves with this position by suggesting that the visual image of a male is not inherently reinforcing but, rather, that the display response represents a more probable behavior than ringswimming.

There are several difficulties with this approach. First, in the absence of pre-existing contingencies, responses tend to be of high probability precisely because they are consummatory or are part of a consummatory response sequence. Second, the validity of rate or frequency measures as indices of response prepotency may also be questioned. Are 60 foraging responses per h equivalent to 60 airgulping responses per h?

The third difficulty involves the possible circularity or the argument. For even in Premackian terms knowing that two responses have a differential probability of occurrence says nothing about why this differential should exist in the first place. And this is precisely the question we seek to answer; why is fighting such a high probability event?

We will presently consider some possible answers to this question, but it is to be noted that these are, appearances to the contrary, unsatisfying, as they offer explanations at nonbehavioral levels of organization. The attractiveness of Premack's Law is that it provides psychologists with an explanation of behavioral events in purely behavioral terms.

Threat display and fighting may represent high probability events because they impart a selective advantage in reproducing to the winner of such a contest. Thus more aggressive fish pass on this trait to their progeny, the most aggressive of whom will likely reproduce, etc. Fight and display thus become high probability events. To this it may be noted that in nature a positive feedback system may be prevented from runaway, in which fish fight each other sight, by modulators such as the possession of territory, an attack-distance gradient, etc. One possible reason that domestic *Bettas* do fight on sight may be that aggression has been selected for by man and has not been subject to the restraining checks that exist in nature.

Reinforcers are frequently associated with affective states and emotional responses, a fact which led Thorndike (1949) to

incorporate the arousal of affective states in his definition of positive and negative reinforcers. That the stimulus of a male *Betta* may engender a strong emotional response in a conspecific perceiver is suggested by the intense color changes, the erection of fins and gill membranes, the dropping of boli, and the control exerted by adrenalin and noradrenalin (Marrone et al, 1966). Changes of this nature are known to be associated with inferred affective states in higher vertebrates (Young, 1952, 1959, 1966). Considering Thorndike's definition and considering the data on *Betta* one could conclude that the emotional response engendered by exposure to another male might be, at least in part, a "pleasurable" one. However, the predictive value of such thinking, particularly with regard to infrahuman species, is questionable.

If one takes the position that the activation of an emotional state is a necessary condition of reinforcement then the aggressive and sexually maintained operant behavior may be understood in these terms. Interestingly, since fecal boli are usually dropped during the initial display encounters it may also be possible, as was suggested earlier, to regard aggression provoking stimuli as ambivalent reinforcers containing both appetitive and aversive elements. This implies that it should be possible to demonstrate *negative* reinforcing properties of male *Bettas*.

In a very recent experiment Baenninger (1970) demonstrated that male *Bettas* would indeed learn to make an operant response to turn off their mirror image, though he apparently regards this as a matter of habituation. While these results are consistent with the view that

mirror image is an ambivalent reinforcer there are technical problems which make the result difficult to interpret. Specifically, Baenninger presents the results in the form of median ratios, obtained by dividing the operant level by the response-reinforcement level of responding on any given day. Therefore, it is not possible to assess the absolute level of avoidance responding achieved by the fish nor is it really possible to appreciate the relative rates of responding since vastly different rates may yield identical ratios (e.g. $100/10 = 10$; $20/2 = 10$). Analysis of the absolute rate of response would have been particularly interesting in view of the fact that in similar experiments conducted at both Alberta and Dalhousie, attempts to obtain appreciable rates of responding in a mirror-off situation met with little success. This should not, however, be taken to mean that mirror image cannot act as a negative reinforcer. Such an effect might be difficult to establish with a simple contingency since the fish must approach the source of aversive stimulation in order to avoid it. In instrumental conditioning situations employing shock reinforcement a great deal of difficulty is encountered in establishing avoidance when the warning stimulus is in the direction of the response that terminates shock (Biederman, D'Amato, & Keller, 1964; McAdam, 1964). A Sidman avoidance procedure, in which a fish could indefinitely postpone the occurrence of mirror, might be a more feasible and convincing way of demonstrating the negative reinforcement properties of mirror image.

Finally, it should be pointed out that the main difficulty with all theorizing about this and any other reinforcer is that for all

the available information we still do not know what makes a stimulus a reinforcer, or why making a certain response is reinforcing. At least part of the answer may come from work started by Olds (1958) and his coworkers who located "reward" and "punishment" centers in the brain of rats. This work has led to a recent synthesis by Glickman and Schiff (1967) in which they propose that the mechanism of reinforcement is an enhancement of activity in the neural pathways (believed to be located in the brain stem) that mediate species-specific consummatory acts. Presumably, it should then be possible to modulate the reinforcing effects of mirror image and fighting by appropriate manipulation of the crucial (as yet undefined) brain centers. The early work of Noble and Borne (1941) certainly fits this theoretical framework.

Territory

Most ethologists accept Noble's (1938) definition of territory as any defended area. Thus, on both common sense and intuitive grounds there is really little difficulty in comprehending why an organism might threaten and fight off intruders as they approach his territory. A successful outcome drives off the intruder and secures the breeding site, food resources, etc. But the operant conditioning situation, in which the male swims through a narrow ring in order to *produce* the intruder poses something of a problem. One would think that the best defended territory is the one never under attack.

There are at least two ways in which this problem may be handled. The first is to assume that the defence of territory is truly

a fortuitous byproduct of aggressive rather than territorial needs. The fish, so to speak, is "looking for a fight", and making the operant response constitutes the appropriate appetitive behavior to engender one.

The second way of handling this problem is to assume that the operandum, by virtue of being in physical and temporal proximity to reinforcement, acts as a conditioned stimulus or a "secondary releaser", and thus, in a sense, represents the intruder's presence in the tank. Making the response, therefore, provides the experimental subject with a chance to drive off the real intruder and this, at the end of the 20 sec reinforcement interval, is exactly what happens. In other words, the ring elicits the behavior. Support for this interpretation comes from the fact that fish in the operant conditioning situation are frequently seen to display in their approach to the ring before the mirror (or live male) has become available. Further, in earlier work in which a target striking response was used as the operant, fish would, after a few shaping trials, begin to display to and attack the target. These observations support the idea that the operandum acquires aggression-eliciting properties, a fact which might explain the apparent contradiction which the operant demonstration imposes on the concept of territoriality. On the other hand it should be noted that persistent behavior may be maintained because a decisive consummatory element is not present in either the MM or MF conditions. Thus the operator neither has a chance to attack nor mate with the reinforcer and hence does not receive the feedback that would normally modulate aggressive and sexual behavior.

Choice between these alternatives if, indeed, they are mutually exclusive, will require further investigation.

Validity of the Operant Technique

It was found that the operant measure predicts the outcome of fighting contests. The data therefore suggest that the operant measure is sensitive to differences in intensity of aggression.

In a recent study referred to earlier, Baenninger (1970) also demonstrated a relationship between the outcome of fighting contests and an operant response measure. His approach was opposite to the one used here. Naive subjects were first placed together in a combat situation and winners and losers determined. These were then placed in an operant situation. It was found that the response rates were significantly higher for winners than losers. This result led Baenninger to conclude that the outcome of an aggressive encounter is a factor in determining operant responding. However, as a cautionary note he stated, "A question which is not answered by the present experiments is whether an underlying characteristic of male *Bettas* determines both their operant performance for visual reinforcement and their relative dominance status in pair encounters". In view of the findings reported in this dissertation, it would appear that Baenninger's second interpretation is correct. Presumably, a similar relationship holds between the operant rate and the sexual tendency (or reproductive readiness), though this still remains to be determined.

The apparent validity of the operant technique as a

measure of aggression or as a predictor of fighting contests will likely prove valuable in future research. Specifically, it seems likely that this procedure will substitute for more direct, though less humane, approaches to the study of motivational variables. Beyond this, we can expect further attempts to understand the reinforcement nature of intra-specific aggression. For example, the role of shock in the maintenance of mirror image operant behavior has received some recent consideration (Melvin & Anson, 1969; Grabowski & Thompson, 1969) and it is to be expected that further salient stimulus characteristics of the reinforcer will be identified and analyzed. In addition, since *Bettas* have in the past been used in drug research (Abramson & Evans, 1954; Brand & Weibel, 1969; Walaszek & Abood, 1956) it is anticipated that research concerned with the effects of various drugs on aggression and sexual maintained operant behavior will be forthcoming. And finally, it is quite probable that we shall see a major analysis of operant behavior per se, with special attention directed at the interaction of schedule, reinforcer, and response factors. Such analysis may not only lead to a better understanding of operant behavior but may also, in the long run, offer unique insights into the understanding and control of aggressive behavior.

Summary

It was concluded, on the basis of rate changes observed during operant and contingent levels of responding, and during conditions of deprivation, that both live male and live female *Bettas* can reinforce behavior of conspecific males. These findings seriously weaken a recent

contention that the mirror-image reinforcer effect is due to stimulus novelty.

Concerning the nature of the reinforcers, it was suggested that aggression obtains its reinforcement value by naturalistic contingencies and by the likelihood that it engenders an emotional response. The ethological concept, agonistic behavior, was used as a basis for contending that the male reinforcer actually elicits both approach and withdrawal tendencies making it an ambivalent reinforcer. On the other hand, only approach tendencies were thought elicited by the female stimulus. These contentions may help explain rate differences in CRF and intermittency between male and female reinforcers.

It was also pointed out that the present operant demonstration calls the concept of territoriality into question since the experimental subject actually intrudes the opponent into his territory by emitting the response. It was suggested that either the concept of territoriality really does need to be modified or else the operandum acquires display-eliciting or display-priming properties.

The assumptions underlying the operant analysis of motivation were reviewed and the validity of the operant conditioning situation MM was established by showing that high rate males defeat their low rate opponents.

Low rates of responding were found on the basis of Study II to be, at least in principle, attributable to the type of display eliciting stimulus used as reinforcer. The findings that frontal display supports the lowest, and lateral and full display the highest operant

rates, is consistent with research in classical conditioning and habituation of display, suggesting that these phenomena may be affected in the same way by a common source of control.

Finally, under the heading of light control of behavior, it was seen that the operant behavior under both reinforcers showed noisy circadian rhythms, an effect interpreted in terms of Aschoff's rule and the normal diurnal behavior patterns of male *Bettas* during the reproductive season. When conditions shifted from continuous illumination to a night-twilight cycle the operant behavior entrained to the light cycle. This effect was consistent with virtually all other research in the area showing the powerful effect of the light cycle in controlling behavior. It was also suggested that twilight suppression of responding was analogous to time out procedures used in operant work with pigeons.

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