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TEMPORALLY DISCRIMINATED OPERANT RESPONDING IN FISH

by

PHILIP GEE

A thesis submitted to the University of Plymouth in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

Department of Psychology Faculty of Human Sciences

June 1995

Temporally Discriminated Operant Responding in Fish Philip Gee

ABSTRACT

In Experiment 1, groups of 10 goldfish and of 10 grey mullet were trained to press a lever for food under a fixed, daily, light cycle. The periods during which responses were reinforced were restricted to two, 1-hr periods in every 24 hrs. These periods occurred at the same time each day. Responses were coordinated with the temporal contingencies of the schedule, and this pattern persisted for a number of days when no responses were reinforced. Experiment 2 demonstrated that a fixed light cycle was not essential for the maintenance of temporal discrimination.

Experiment 3 followed a similar procedure to that of Experiment 1, except with individual goldfish and with only one, 1-hr feeding period in every 24. Experiment 4 produced evidence that temporal discrimination could develop under continuous illumination in individual goldfish.

In Experiment 5, individual goldfish under continuous illumination were exposed to schedules that reinforced lever presses with food during a 1-hr period each day. Training with simultaneous temporal and visual contingencies, where food was available only in the presence of a stimulus light and at the same time each day, did not attenuate control over responding by either contingency. Further, pretraining on the temporal contingency did not prevent the subsequent acquisition of control by a stimulus light that was presented during the feeding hour. Similarly, pretraining on a visual contingency in which food was available at a different time each day did not prevent the subsequent acquisition of control by the temporal contingency (established by fixing the time of food availability). In Experiment 6, pretraining on the visual contingency did attenuate the subsequent acquisition of control by a different visual stimulus, showing that the lack of interference in control observed in Experiment 5 was not simply due to the intertrial interval used. These findings suggest that concurrent temporal and visual contingencies may control behaviour in parallel rather than in a competitive manner.

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This thesis was supervised by Dr. David Stephenson. In addition to his endless patience, his skill and flair marks him out as a player in the supervisors' Premier League.

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AUTHORS DECLARATION

At no time during registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

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Relevant scientific seminars and conferences were attended and work was presented at each of these. Several papers were prepared for publication and one paper has been published.

Publications

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Conference presentations

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- Gee, P. (1992). Behavioural engineering with fish. Presentation to the Fish Research Group, University of Plymouth.
- Gee, P. (1993). Behavioural toxicology in fish. Poster presentation to the Royal Microscopical Society symposium on pollution and the environment (14-16 April 1993), University of Plymouth.
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- Gee, P., Stephenson, D., & Wright, D.E. (1994) Absence of blocking of operant responding to a temporal stimulus by a visual stimulus, and vice versa. Poster presentation to the Experimental Analysis of Behaviour Group's annual conference (13-15 April 1994), University College, London.

Signed Ht

Date 8 - June 1995

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1.0 GENERAL INTRODUCTION

The foundation for this thesis was an undergraduate project on a potential application of psychological techniques in the control of farmed fish (Gee, 1990). The focus gradually changed from this applied and specific goal to a more theoretical and general one. This introduction is an attempt to place the work in context by outlining the manner in which these changes occurred. To this end, it will be necessary to give brief details of some of the studies and arguments that are explored further in the chapters that follow.

The initial concern was with the problems caused by overcrowding of stock in conventional fish farms. Very high stocking densities are required in order for a farmer to offset operating and equipment costs. However, as in intensive farming on land, high density monoculture brings with it the risk of the entire stock being lost to disease. This risk is increased by the fact that at high densities fish will be more prone to physical damage from contact with netting and with other fish. As a consequence, fish farms have to allocate a large proportion of their resources to the control of parasites and to the prevention and cure of bacterial and fungal disease. The industry is also under pressure to reduce environmental damage caused by chemical treatments and by food waste.

One method that has been proposed for the alleviation of these problems is marine ranching (Fujiya, Sakaguchi, & Fukuhara, 1980). In this system, fish are not enclosed but are trained to return to a feeding station whenever a tone is played. It was hoped that this system would avoid most of the problems of overcrowding in intensive aquaculture, while providing superior control over stocks than is possible in conventional fisheries.

Unfortunately, ranching with conditioned stimuli has its own problems. One of these is the expense of the sound generating equipment (Bardach & Magnuson, 1980).

The project that formed the basis of this thesis explored the potential for avoiding the need for acoustic stimuli by exploiting temporal discrimination. Put simply, if fish could learn that food would be dispensed at a certain time, then a tone might not be necessary.

If a large lake stocked with large fish had been available for this study it would have been used. Instead the experiment was carried out on small fish in a small plastic tank in a small room. Nevertheless, the focus at this stage was firmly fixed on a practical problem for which it was hoped that psychology might provide a solution.

The experiment provided evidence of temporal discrimination, and the most interesting questions appeared to be methodological and practical ones. How could the recording of behaviour be improved? Would the phenomenon apply to other species? How might the technique be adapted to a commercial scale?

The first experiment in this thesis (Chapter 5) was an attempt to replicate the findings of the undergraduate project, but with an improved data recording technique. In the project, the subjects had been recorded on video tape and changes over time in the number of fish in the feeding area were analysed. This required long and tedious sessions reviewing fish videos, and it is not always possible to be sure whether there are 24 or only 22 fish in a particular location when they are all identical and all moving in three dimensions. Further, it was not possible to record behaviour in dim light. In view of this experience, it was decided to opt for analysis of the rate of a lever-press response. This was primarily because of the ease with which data could be recorded, but also because, unlike the video technique, it would allow continuous rather than "snapshot" monitoring, and data could be recorded regardless of ambient light levels.

Both the undergraduate project and Experiment 1 were carried out under a regular light cycle. Alternating periods of light and dark were used because previous laboratory experiments had suggested that a light cycle might provide the optimum conditions for temporal discrimination (Davis & Bardach, 1965). Experiment 1 was designed to examine whether operant temporal discriminations over long intervals

could even be formed, and at this early, exploratory stage, it was important to give the best chance for success. However, once operant temporal discrimination had been demonstrated it became possible to investigate the necessity of the light cycle in the coordination of responding. Experiment 2 studied the effect on response patterns of switching over to continuous lighting.

At this stage theoretical concerns began to balance the applied issues. The behaviour patterns observed in Experiments 1 and 2 were reminiscent of those in the literature on temporally structured schedules of reinforcement. The rationale for Experiments 1 and 2 had been to explore techniques of potential use in aquaculture. Bearing in mind this applied concern they were carried out on fish housed in groups, with all individuals within each group having access to the lever. This meant that the findings had more relevance to the conditions in which farmed fish were kept but made integration with data derived from individual subjects problematic. In order to overcome this Experiments 3 and 4 (Chapter 6) were run as replications of Experiments 1 and 2, but with only one fish having access to the response lever.

Analysis of individual subjects gave a less ambiguous picture of the behaviour of interest, and temporal discrimination was evident both with and without a light cycle. However, a demonstration that the light cycle was not necessary for temporal discrimination failed to answer some interesting questions about its role in discrimination when present. For example, chronobiological research has suggested that a regular light cycle is the most important influence in the coordination of behaviour under the control of circadian rhythms but has also shown that feeding opportunities that are scheduled at the same time each day can have a similar influence on behavioural rhythms in the absence of a light cycle (Aschoff, 1984). Experiments 5 and 6 (Chapter 7) were designed to explore the relationship between temporal contingency and exteroceptive visual stimuli in the control of behaviour. The key question was now one of the distribution of control over responding where both an immediate, exteroceptive, discriminative stimulus and a temporal regularity were both predictive of reinforcement. More specifically, the experiment set out to discover

whether temporal control would develop where responding was already under the control of a visual discriminative stimulus, and whether control by a visual stimulus would develop where responding was already under the control of a temporal contingency.

The sequence of experiments outlined above reflects a change in emphasis from applied to more general concerns. The methodology used throughout was similar, but was initially adopted for reasons of expediency. In the later stages, the behaviour analytic perspective, which originally promoted the study of operant behaviour as a psychological method, started to exert an influence on the interpretation of the data. The goal of behaviour analysis is the prediction and control of behaviour, but it also has a tradition of concern with the application of that science. This brings together the aims both of the early and the later work in this thesis. A science of behaviour could well have its uses in aquaculture, and if behaviour-analytic psychology has something to do with the price of fish, then so much the better.

2.0 AQUACULTURE

2.1

Introduction

The past 25 years have seen a massive, world-wide expansion in aquaculture. This has been due in part to a decline in the stocks that once supported conventional fisheries and, in part, to improved technology and husbandry procedures in the fish farming industry (Metcalfe, 1990). About 10% of the world fish harvest is now produced by aquaculture (Shepherd, 1988), with the species farmed ranging from shrimp through to leatherback turtle.

It is probable that techniques for farming terrestrial species have evolved over thousands of years. In contrast, it is only very recently that intensive aquaculture has undergone significant development. This may seem surprising given the extent and the productivity of the aquatic environment, but there was little need for sophisticated management of fish stocks until advances in technology and demand made traditional capture fisheries less viable (Beveridge, 1987).

A typical modern fish farm consists of large floating cages usually anchored in sheltered water to minimise the risk of weather damage and close inshore to allow access for feeding and maintenance. The stock is raised in shore based hatcheries, and only when the fish are large enough to withstand the harsher environmental conditions are they transferred to the cages. The cages are stocked at the high densities in order to obtain the best return on investment (Beveridge, 1987). The fish are fed pre-processed foods either by hand or by automated dispensers, and the cost of this food comprises up to 60% of the production costs of a farm (ADCP, 1983).

High density monoculture brings an inherent vulnerability to disease. Substantial resources must also be allocated to the prevention and control of parasites and of

bacterial and fungal infections. In addition, uneaten food and the waste produced by the fish can accumulate in the vicinity of the cages where it may promote the formation of algal blooms that can reduce the viability of the stock by depleting dissolved oxygen levels (Beveridge, 1987). Indeed, it is now common practice, following a logic similar to that behind crop rotation on land, for cages to be rotated from one site to another in order to allow a particular area to recover from the environmental stress produced by the farm and for local populations of harmful organisms to decline. The cages also require regular maintenance to remove marine growth which may clog up the netting and make the structure more vulnerable to tidal damage (Edwards, 1978).

A number of techniques for avoiding or reducing the problems outlined above are being explored. For example, low maintenance cage systems that are capable of withstanding off-shore conditions have been developed. These can be sited in areas where the tidal flow is sufficient to carry away and disperse the waste products but are far more expensive than conventional systems and may be inaccessible for considerable periods during rough weather (Beveridge, 1987). A technique that is being evaluated as a potential alternative to chemical treatment for certain parasites is the introduction of small "cleaner fish", usually goldsinny wrasse (Ctenolabrus rupestris), rock cook (Centrolabrus exoletus), or corkwing wrasse (Crenilabrus melops), to the cages. This appears to be effective to some extent, but collection of the fish from the wild may damage the environments they are taken from and increases the risk of other diseases being introduced to the fish farm. Further, if adopted on a large scale this method would require farming of the cleaner fish as well as of the stock (Darwall, Costello, Donnelly, & Lysaght, 1992). Population management based on the control of homing behaviour has also met with some success. Salmon use discrimination of olfactory stimuli in returning to a specific spawning ground, and fry that are exposed to a particular odour in the hatchery prior to release may later (following migration and maturation in open water) be lured back to a specific area by the imprinted odour (Donaldson & Allen, 1957). Unfortunately this technique is only applicable to certain species, and recapture rates are fairly low (Shepherd, 1988).

However, the techniques that are of most relevance to the subject of this thesis are those which involve the exploitation of learned behaviour in stock management. These practices might best be described as behavioural engineering.

2.2

Behavioural Engineering

Operant techniques have been explored for potential as a solution to some of the problems inherent in high density aquaculture in various field trials (see below), but an understanding of the variables affecting fish behaviour also requires consideration of data from experiments carried out under the more controlled conditions of the laboratory. Although a great deal of information on fish behaviour in general is available (for reviews see Bull, 1957; Hoar & Randall, 1971; Ingle, 1968; Keenleyside, 1979; Pitcher, 1993; Winn & Olla, 1972), the work outlined in this section will be restricted to studies of operant behaviour.

One of the earliest studies of operant conditioning in fish was that carried out by Triplett (1901). Perch (*Perca americana*) were housed in one side of an aquarium that was divided by a glass partition and minnows were placed in the other side for a 30 min period three times per week. During early trials, the perch would repeatedly crash into the glass in an attempt to get at the minnows. As the experiment progressed, these abortive attacks extinguished. After a month, the partition was removed and the minnows were able to swim with the perch unmolested. Indeed, Triplett observed that the perch was at first reluctant to cross the line where the partition had previously stood even when driven toward it.

Despite the charm of Triplett's (1901) demonstration, the most frequently studied class of operant has been the lever-press response. A number of variations on this have been devised. Most of have consisted of some type of pivoting rod that is activated by contact with the subject's mouth (e.g., Boujard & Leatherland, 1992; Gonzalez, Eskin, & Bitterman, 1962; Landless, 1976a), but other operants have included breaking a beam of light falling on a photo-electric cell (Van Sommers, 1962)

and the displacement of a small float (Takahashi, Murachi, Sekitani, Moriwaki, & Ogawa, 1981).

Both aversive and appetitive reinforcements have been used (Gleitman & Rozin, 1971). Food is the most commonly used positive reinforcer, although fish have also been conditioned to respond for adjustments in the temperature of their water (Rozin & Mayer, 1961) and for exposure to aerated water when oxygen deprived (Van Sommers, 1962). Studies involving aversive, negative reinforcement have almost exclusively used electric shock (Bull, 1957; Gleitman & Rozin, 1971).

With some exceptions (see Chapter 3, Section 3.3), variables which modulate rate of responding in other laboratory animals have generally been found to have a similar function in fish (Bull, 1957; Gleitman & Rozin, 1971; Salzinger, Freimark, Fairhurst, & Wolkoff, 1968). For example, Eskin and Bitterman (1960) have demonstrated that the duration of pre-trial food deprivation has a similar effect on rate of responding on a fixed-ratio schedule of reinforcement to that found in birds and mammals, and Rozin and Mayer (1961) have shown that the rate of a lever-press response can be controlled by the nutritional value of the food reinforcer. Variations along a range of stimulus dimensions, including temperature, salinity, touch, and smell have been shown to function effectively as discriminative stimuli (Bull, 1957), but the stimuli most frequently used in experiments with fish are either visual (e.g., Takahashi, Murachi, Moriwaki, & Ogawa, 1985; Tennant & Bitterman, 1975) or auditory (e.g., Tennant & Bitterman, 1975, Wright & Eastcott, 1982b).

The studies outlined above show that operant responses are easily established in fish. It is also clear that this behaviour may come under the control of a variety of classes of discriminative stimulus and types of reinforcement schedule. These findings have inspired a number of experiments for which the ultimate aim was to address applied rather than theoretical problems (e.g., Takahashi et al., 1981; Wright & Eastcott, 1982a). Food reinforced operant behaviour has been studied in the laboratory by several authors interested in aquacultural science (for reviews see Metcalfe, 1990; Talbot, 1985). Several authors have been interested in food demand

in fish over extended periods as a method for collecting data on how appetite in a particular species will be likely to change over time. This information is then used to devise recommendations to fish farmers as to the amounts and timing of feeds dispensed either by hand or by automatic feeder (e.g., Adron, Grant, & Cowey, 1973; Boujard & Luquet, 1990; Boujard & Leatherland, 1992; Boujard, Moreau, & Luquet, 1991; Takahashi, Murachi, Moriwaki, & Ogawa, 1984, 1985). Operant techniques based on the relative response rates on two or more levers providing different foods as reinforcement have also been used to study food preference (e.g., Boujard, Dugy, Genner, Gosset, & Grig, 1992; Hildago, Kentouri, & Divanch, 1988). This information is useful in the formulation of commercial fish diets. An area which shows potential but has yet to receive much attention is environmental monitoring through the analysis of changes in baseline rates of operant responding. For example, it has been suggested that the stable and extended baseline behaviour patterns that can be obtained using operant techniques might prove valuable in toxicological studies or in monitoring behaviourally significant environmental fluctuations on fish farms that use demand feeding systems (Anthouard & Wolf, 1988; Coble, Farabee, & Anderson, 1985; Marcucella & Abramson, 1978).

Field studies on the exploitation of learned behaviours in aquaculture have generally focussed on appetitive conditioning, although Balchen (1984) has described an underwater electrical barrier that uses a combination of light stimuli and shock to prevent farmed fish escaping from a bay in Norway. In programmes that do use appetitive conditioning, food has either been contingent on some form of lever press or has been available only at a particular location.

Aquacultural systems in which food is dispensed in response to a lever press are known as "demand feeders". These are in fairly widespread use in fish hatcheries and in pond aquaculture but have also been developed for sea-cage systems. The most commonly used design is the home-made "pendulum feeder". These consist of a food hopper made from a plastic drum and a funnel and a metal rod which extends from the tip of the funnel down to just below the water surface. When the rod is moved by a

fish, a disc attached to its upper end is tipped over and releases some food (Meriwether, 1986). At the other extreme of complexity are commercially produced systems which use electronic technology and computer control to measure the force with which a response lever is displaced and to precisely regulate the amount of food delivered by an automatic dispenser (Alanärä, 1992a). Several reports (Alanärä, 1992a; Alanärä, 1992b; Landless, 1976b; Meriwether, 1986; Powless, 1989) have shown that demand feeding can be effective in reducing mortality rates, increasing the efficiency of food use, and reducing the volume of waste products in aquaculture.

A behavioural technology that has yet to come into widespread use is "recall ranching". This is the general term given to techniques that use behavioural conditioning to attract fish to a stimulus source for feeding, monitoring and harvesting. Possibly due to commercial sensitivities, detailed information on the various programmes that have been implemented is often lacking. However, a number of reports are available. For example, Abbott (1972) reported that a population of rainbow trout (*Salmo gairdneri*) quickly learned to congregate near a hydrophone suspended beneath a float anchored in their pond. The fish formed a tight shoal whenever a 150 Hz tone was played, as this was always followed by the delivery of food to the vicinity of the stimulus source. A similar system has been successfully implemented with trout reared in a larger, natural body of water by Landless (1978).

Fujiya et al. (1980) reported an experiment in which red sea bream (*Pagrus major*) were trained to associate a 200 Hz tone with the operation of a food dispenser mounted in their sea cage. When the fish were released from the cage, the tone-food relationship was maintained, and after a period of 5 months, nearly half of the 10,000 fish still congregated near the dispenser whenever the tone was played. This experiment formed part of a re-stocking program that relied on the conditioned association to keep juvenile farmed fish within the confines of a sheltered bay (away from areas heavily fished by commercial fleets) until they reached a marketable size.

Balchen (1979) reported an elaboration on this technique in which the fish were ultimately lured into a processing plant's holding pen by the tones emitted from a string of underwater feeding stations that were activated in sequence. Marine recall ranching has also been reported by Midling, Kristiansen, Ona and Oeistad (1987). Juvenile Cod (*Gadus morhua*) kept in a rearing pond were conditioned to search for food when presented with a 160 Hz tone. The fish were then released into a fjord and fed at fixed times every day in the presence of the tone. A monitoring programme using echo-sounders, underwater video and ultrasonic transmission tags revealed that a majority of the subjects regularly returned to the stimulus location, and that some 'wild' cod had also adopted this behaviour.

Perhaps the most ambitious recall ranching programme is that in Saeki Bay, Japan. This was was set up under the Oita Prefecture of Japan's "Marinopolis" plan for the development of coastal fisheries and consists of a shore based hatchery and two sound-generating and feeding buoys sited in the bay. In the hatchery, red sea bream fry are fed several times a day following a series of 300 Hz pulses through an underwater loudspeaker. When released into the bay, the fish are fed, again following 300 Hz tones, by automatic food dispensers attached to the buoys. Radar, underwater cameras, and a range of sensors are used to monitor water temperature, salinity, currents, and fish movements. These data are relayed to a control station on shore and used in the management of the ranch (Hara, 1988).

2.3

Temporal Control

Recall ranching requires that the animals respond to some form of discriminative stimulus, but the practicality of using sound for this purpose has been questioned. The maximum range for projecting sound underwater that is non-directional, of the required frequency, and audible to fish over ambient noises is in the order of a 1- or 2-km radius (Bardach & Magnuson, 1980). In the Saeki Bay ranch, for example, fish more than 2 km from the loudspeakers fail to respond to the sound stimuli (Hara,

1988). Even where a range of 2 km is adequate, the cost of the equipment may prohibit its use in areas where state funding is not available. Suitable tone emitting apparatus that is durable, portable and inexpensive has yet to be developed (Bardach & Magnuson, 1980).

However, acoustic discriminative stimuli might not be necessary, if the behaviour of the fish could be brought under the control of a temporal contingency. In their natural environment, many species of fish coordinate their activity with diurnal rhythms such as the onset of dawn and dusk (Müller, 1978). Given that fish already show temporal discrimination between particular times during the day in their feeding behaviour, it seems reasonable to ask whether they will learn the time at which food will be dispensed.

There are indications in the literature on recall ranching that the temporal patterning of feeds may be important even where acoustic stimuli are used. As well as employing sound as a discriminative stimulus, Fujiya et al. (1980) used fixed and regular feeding times in their ranching programme. No reason was given for this in their report, and they did not analyse the contribution that the temporal aspect of the conditioning procedure may have had in the establishment and maintenance of the response. Abbott (1972) used less regular feeding times for the bulk of his experiment but noted that for sections where a fairly rigid feeding schedule was followed, the shoaling response was almost coincidental with the onset of the tone. Conversely, trials that were conducted later than they had been in preceding days resulted in a noticeable increase in the time taken to display the shoaling response. Abbott concluded that the regularity of the feeding times was instrumental in bringing the fish to the feeding area in anticipation of the delivery of food.

If temporal discrimination could be exploited in recall ranching by using "time of day" instead of an exteroceptive discriminative stimulus, the benefits might include the potential for recalling fish from greater ranges than is possible using acoustic conditioning and a reduction in equipment costs. Timer-controlled automatic food dispensers are already in widespread use (Beveridge, 1987), but even farmers who

can not afford these devices might be able to engage in recall ranching, if a reasonably accurate timepiece could substitute for the sophisticated sound generating equipment presently required. In Chapter 3 the literature on temporal control will be examined.

3.0 TEMPORAL CONTROL OF BEHAVIOUR

3.1

Introduction

Cyclic variations have been found in a wide range of behavioural and physiological measures (Armstrong, 1980). Systematic changes in some of these variables may become conditioned through the regular coincidence of a particular event with a particular period or moment in time (Aschoff, 1984).

The relationship between time and behaviour has generally been studied within one of two broad areas of research with little interdisciplinary collaboration (Lejeune, Richelle, & Mantanus, 1980). Chronobiologists have primarily studied changes in physiological variables and in unconditioned behaviour, whereas experimental psychologists have focused on temporal control of conditioned responses. As rhythms with a period approximating 24 hr appear to have a distinct status in biological systems, chronobiologists have paid particular attention to fluctuations which coincide with the solar cycle. Behavioural psychologists, on the other hand, have generally studied cycles with a period of only a few seconds or minutes.

In this Chapter, psychological literature on the behaviour of birds, mammals, and fish under a periodic schedule, the fixed-interval schedule of reinforcement, will be discussed. This will be followed by a review of some of the relevant findings in chronobiology, and finally by consideration of the relationship between chronobiological and psychological findings, and of some of the more general theoretical issues in timing.

Fixed-Interval Schedules in Birds and Mammals

On the fixed-interval schedule of reinforcement, the first response following a given interval, measured from the preceding reinforcement, is reinforced (Ferster & Skinner, 1957; Skinner, 1938). Responses made during the interval have no programmed consequences. The most frequently used subjects in experiments on fixed-interval schedules are rats and pigeons, although experiments have also been run using humans (e.g., Lowe, 1979; Lowe, Beasty, & Bentall, 1983), cats, wood mice, and turtle doves (Lejeune & Wearden, 1991). Data on fish will be discussed in Section 3.3, below.

Two main patterns of performance have been identified as characteristic of performance on fixed-interval schedules. Both feature a post-reinforcement pause in responding, but once responding has commenced it may exhibit either a positive acceleration through to the terminal rate, or it may assume a more or less stable high rate of responding that continues through until the time of reinforcement. The former pattern has been described as the "fixed-interval scallop" because of its appearance on a cumulative record (Dews, 1978; Ferster & Skinner 1957). The latter pattern has been described as "break-and-run" (Cumming & Schoenfeld, 1958; Schneider, 1969). The variables which control whether a subject produces one or the other of these patterns have yet to be demonstrated unequivocally. Schneider (1969) has suggested that the break-and-run pattern may be more common where the interreinforcement interval is short, and Dews (1978) has argued that break-and-run is more likely to develop after an extended history of exposure to fixed-interval schedules, possibly through the fortuitous association of a specific response rate with reinforcement.

Richelle, Lejeune, Mantanus, and Defays (1980) classify performance on fixedinterval schedules as an example of spontaneous temporal regulation. The regulation of responding is spontaneous in the sense that reinforcement is not contingent on the changes in rate produced by the subject. Nevertheless, the pattern of responses

characteristic of performance on a standard fixed-interval schedule is observed under a number of procedural variations. For example, the patterns remain whether each successive interval is contiguous, or whether sessions are divided into discrete trials by inserting signalled periods of time-out from reinforcement (Richelle et al., 1980). The longest fixed interval duration on which characteristic response patterns have been obtained was nearly 28 hr (Dews, 1965b). More typically, the interval duration will be a few minutes, but intervals of a few seconds (e.g., Schneider, 1969) have also been used. Indeed, the phenomenon is so robust that Sidman (1960) suggested that behavioural laboratories calibrate the adequacy of their control over reinforcement variables by attempting to maintain the characteristic pattern of fixed interval responding before going on to manipulate other experimental variables.

It is clear that temporal regularity is necessary for the maintenance of the patterns of responding typical of fixed-interval schedules. Ferster and Skinner (1957) have shown that a constant rate of responding emerges when a fixed-interval schedule is converted into a variable-interval schedule. However, the nature of the variables controlling response rates from moment to moment during the interval is less clear.

One possible source of temporal control is the after-effects of ingestion. Consumption of food reinforcers might initiate some progressive physiological change which in turn controls response rate. This explanation can not account for all the data on fixed interval responding, however. Other reinforcers, including escape from a stimulus associated with electric shock (e.g., Morse & Kelleher, 1966), appear to be equally effective in controlling the characteristic fixed-interval performance. Further, the pattern of responding on food reinforced schedules is not destroyed by the occasional omission of reinforcement at the end of an interval (Catania, 1970; Dews, 1966b).

Skinner (1938) suggested that the response pattern during an interval might be a consequence of imperfect discrimination. Responding accelerates up to the end of the interval, because conditions become more like those existing at the moment of the previous reinforcement. Sharp stimulus control is not achieved because the

discrimination between points on a gradually changing continuum is difficult. Ferster and Skinner (1957) proposed that, if this theory were correct, the provision of an external "clock" should enable more efficient responding. However, a series of experiments with external stimuli that varied systematically with time during the interval resulted in only moderate improvements in performance. Palva and his colleagues (Palya, 1985; Palya & Bevins, 1990; Palya & Pevey, 1987) also found that the provision of time correlated external stimuli does not eliminate responses during the interval. This suggests that the pattern of responding is not primarily a result of temporal confusion. Further evidence against the pattern of responding being due to poor discrimination has been provided by an experiment in which the ability of stimuli correlated with successive periods in the interval to support a response that produced or removed them was assessed. Palya (1993) found that the later stimuli functioned as positive reinforcers, and stimuli early in the interval functioned as negative reinforcers. If the increase in responding across an interval was due simply to increasing similarity with the moment of reinforcement, then stimuli associated with the earlier part of the interval might not be expected to acquire positive reinforcing properties, but neither would they be expected to become negative reinforcers.

Another possible explanation of fixed-interval responding is that the temporal properties of the response patterns result from the performance of a number or chain of mediating behaviours. This suggestion is given credence by the frequent finding of an association between the presence of stereotyped collateral behaviour with superior temporal regulation (see Greenwood & Richelle, 1980 for a review). In a chain of behaviour, every response serves as a discriminative stimulus for the next even though only the final segment is reinforced. In order to coordinate with temporal contingencies, the subject only needs the capacity to react to its own overt behaviour. However, the chaining or counting hypothesis has been called into question by the results of a series of experiments on the effect of presenting a negative discriminative stimulus on response patterns maintained by fixed-interval schedules (Dews, 1962, 1965a, 1965b, 1966a, 1966b). Response rates are suppressed during the negative discriminative stimulus, but the rate quickly returns to a level that would be expected

on an uninterrupted fixed interval at the offset of the stimulus, leaving the overall pattern of responding during the interval intact. A chaining or counting process would, presumably, have been disrupted by the effect on behaviour produced by the negative discriminative stimulus.

Dews (1970) favours an explanation of fixed interval responding based on the effect of delay to reinforcement. All responses emitted during the interval are reinforced, but responses early in the interval are reinforced following a longer delay than those emitted later in the interval. The longer the delay, the lower the rate of responding that the reinforcer will support. However, as Lejeune, Richelle, Mantanus, and Defays (1980) point out, this is not entirely satisfactory either. The delay to reinforcement within any interval can only be discriminated by reference to the start of the interval. Control by delay to reinforcement itself implies discrimination of the passage of time, and the problem of explaining this discrimination remains. Further, Palya's (1993) finding that stimuli associated with the earlier parts of the interval functioned as negative reinforcers is not consistent with the decay of a positive process at successively earlier times before the reinforcer.

As attempts to explain timing exclusively in terms of observables have not met with much success, more recent theories have assumed the existence of endogenous pacemakers or "clocks". It is proposed that these, in conjunction with some form of counter or accumulator system, underlie timing behaviour. The "Behavioral Theory of Timing" (Killeen & Fetterman, 1988, 1993) proposes that adjunctive behaviours may serve as a counter with the emission of specific classes of behaviour forming the basis for conditional discriminations of the passage of time. Pulses from the pacemaker are said to initiate sequential transitions from one internal state to another, and each state may be characterised by a particular class of behaviour. Killeen and Fetterman (1993) identify the states with propensities to respond rather than with responses themselves, thus avoiding the notion of response chains in which the emission of one response is necessary for the next.

The information processing analysis of timing developed from "Scalar Expectancy Theory" by Gibbon and his colleagues (Gibbon, 1977, 1991; Gibbon & Church, 1990; Gibbon, Church, & Meck, 1984) also assumes the existence of an endogenous pacemaker. Timing behaviour is explained with reference to a timing system that comprises a clock, a reference memory for duration, and comparison and decision processes. A response will be made if the number of pulses emitted by the pacemaker matches a value held in memory. Responses are emitted at times other than the target time because of variance in the pacemaker or in the storage, retrieval or comparator systems.

Both of these theories can account for a great deal of data on performance on fixed-interval schedules, but the Behavioral Theory may be preferable because of its lesser reliance on hypothetical constructs (Killeen & Fetterman, 1993).

3.3

Fixed-Interval Schedules in Fish

As most data on fixed-interval schedules have been obtained in experiments on birds and mammals, the extent to which these data will generalise to the behaviour of fish is largely unknown. However, comparative studies of performance on other schedules have concluded that, in most respects, fish behave in a similar fashion to other animals when tested under analogous conditions (Gleitman & Rozin, 1971). Nevertheless, before considering data on fixed-interval schedules, the two main qualitative differences between the performance of fish and of other phyla that have been identified will be briefly examined.

Firstly, it has been found that fish show little improvement in serial reversal tasks, whereas rats and pigeons rapidly learn to switch their responding under similar schedules (Bitterman, 1968). The second difference is in the effect of partial reinforcement where trials are widely spaced. Unlike rats and pigeons, fish responding on schedules in which only a proportion of trials are reinforced may be no more resistant to extinction than responding maintained by schedules in which all trials

are reinforced (Gonzalez, Behrend, & Bitterman, 1965; Longo & Bitterman, 1960; Schutz & Bitterman, 1969).

However, it should be noted that, in the examples above, conclusions on the differences between phyla are based on null effects. Aside from the possibility that positive effects might have been found under different conditions, there is the problem of generality within a phylum. Comparative work involving aquatic subjects has centred on the goldfish (*Carassius auratus*) and the African mouthbreeder (*Tilapia macrocephala*). It has yet to be established whether the differences between these species of teleost fish and other laboratory subjects are common to all fish, or whether the differences between species in the same phylum may be as great as they are across phyla (see Bitterman, 1968 for a review of comparative studies of learning in fish).

The available data on the performance of fish on fixed-interval schedules of reinforcement provide a mixed picture. An experiment carried out by Grailet (1983) is the only study involving fish cited in a recent review of the comparative psychology of fixed-interval responding (Lejeune & Wearden, 1991). In Grailet's study the responses of African mouthbreeders were reinforced on fixed-interval schedules with interval durations that ranged between 2 s and 120 s. Although all subjects responded at a higher rate towards the end of the interval compared to the beginning, only weak evidence of temporal regulation was found. Similarly, Gonzalez et al. (1962) reported that African mouthbreeders displayed temporal regulation when lever pressing on 1-, 2-, and 4-min fixed-interval schedules, but the scalloping typical of rats and pigeons under analogous conditions was absent.

In contrast, Wolf and Baer (1963) reported that a gourami (species unspecified) developed the characteristic fixed interval scallop on both 10- and 20-min fixed-interval schedules, and Rozin (1965) obtained well defined scallops in records of responding by goldfish on 1- and 2-min fixed-interval schedules.

Rozin's experiments provided particularly interesting data on the role of metabolic and behavioural variables in temporal regulation. Goldfish are poikilotherms, and so
their metabolic rate is dependent on ambient temperature. By manipulating the temperature of their water, Rozin was able to observe the effect of metabolic rate on timing. The fish displayed scalloping on a 1-min fixed-interval schedule both at 30 °C and at 20 °C, but the response rate at 30 °C was approximately double that at 20 °C. Despite this dramatic change in absolute rate, the relative distribution of responding through the interval was almost identical. This suggests that temporal control in the goldfish is not directly tied to metabolic rate as this is approximately halved by a temperature drop from 30 °C to 20 °C. A separate experiment was run in order to check that the correspondence of relative rates was not simply the result of the subjects rapidly learning what might effectively have been a "new" interval following a temperature change. Fish held at 25 °C were initially trained with an interval of 1 min and then transferred to an interval of 2 min. The performance of subjects under these conditions remained similar to that under a 1-min fixed interval for several days after the change to the 2-min schedule, whereas in the earlier experiments the temperature transitions had been made over a 6 hr period and were reversed every 2 days.

As well as providing evidence against the involvement of a simple metabolic "clock" in temporal regulation, Rozin's experiments also provide further evidence against behavioural pacing or counting as a source of temporal control. If behavioural pacing had been a controlling mechanism then the halving of the rate of ongoing behaviour caused by a transition from 20 °C to 30 °C would be expected to spread the process out in time and so disrupt temporal coordination. Rozin (1968), in a review of the use of poikilothermy in the analysis of behaviour, concluded that an endogenous temperature-independent physiological clock was used in the timing of short intervals in the goldfish, and that this timing ability may be related to the mechanism involved in circadian rhythms. In Section 3.4 some of the literature on circadian rhythms in general, and in fish in particular, will be examined.

Circadian Rhythms

In the fixed-interval schedules studied by experimental psychologists reinforcement is made available following a specific period. The behaviour of subjects usually comes to anticipate the time of reinforcement, even though the temporal structure of the schedule is imposed and arbitrary. The environment outside the laboratory is also temporally structured. The four main natural periodicities are: the seasons, the lunar cycle, the solar cycle, and the tides. These cycles repeat themselves at regular intervals and so are predictable. Just as the behaviour of laboratory subjects may anticipate a schedule of reinforcement, an organism in the natural environment may anticipate these external rhythms (Aschoff, 1984).

In the chronobiological tradition, it is assumed that many physiological and behavioural rhythms are coordinated by an endogenous "biological clock". There are said to be clocks that are synchronised with each of the four environmental cycles mentioned above (Aschoff, 1984), but the one which has received the most attention is that related to the solar cycle. As with the others, this is characterised as a selfsustaining oscillator. It is self sustaining in the sense that, under constant environmental conditions, the cyclic variations associated with the clock will persist, although with a frequency that deviates slightly from 24 hr. It is for this reason that the prefix "circa" is used to designate a circadian clock (Aschoff, 1984).

Under normal conditions, the biological clock is kept in synchrony with the actual periodicity of the environment through the action of "zeitgebers". A zeitgeber is an exogenous event against which the endogenous clock may be reset daily. The most powerful of these is the light cycle, and many circadian rhythms are said to be entrained by the temporal regularity of dawn and dusk. Entrainment establishes an identical period between the endogenous and exogenous oscillations, and in the absence of a zeitgeber, a rhythmic variable linked to a circadian clock will dissociate

3.4

from actual clock time and advance or recede in time by a small constant each day. A rhythm in this state is described as "free-running" (Aschoff, 1984).

Actually, chronobiologists suggest that there may be more than one circadian pacemaker. The evidence for this lies in the finding that, in a constant environment, the period of the fluctuation in one measure may eventually differ from the period of another (Aschoff, 1984). Of particular interest has been the phase dissociation between activity rhythms that appear to be entrained to the light cycle, and rhythms in activity and operant responding that appear to be entrained by the schedule of food availability. Free-running rhythms in the drinking behaviour and the locomotor activity of rats are eliminated by lesions of the suprachiasmatic nuclei (SCN). However, it has been shown that the response patterns of SCN lesioned rats on a feeding schedule where a lever press is only reinforced during a fixed 4-hr period continue to show accelerations that anticipate the feeding time. Further, when reinforcement is withdrawn entirely for five consecutive days the accelerations persist (Boulos, Rosenwasser, & Terman, 1980). This has been interpreted as evidence that, while the rhythms in locomotory and drinking behaviour are controlled by a lightentrainable circadian pacemaker that is mediated by the SCN, the pattern of leverpressing behaviour is under the control of a separate oscillatory system. Indeed, Aschoff (1984) suggests that the finding that (in intact animals) free-running rhythms in activity persist under a temporally structured feeding schedule (even though periods of activity that anticipate the feeding time also develop) shows that feeding schedules do not act as a true zeitgeber. Rather, restricted feeding schedules uncouple from the main circadian system a component of activity that has circadian-like characteristics. That is to say, the feeding schedule is not a zeitgeber, because only a component of behaviour is synchronised with it under otherwise constant conditions. Free-running rhythms in the same and in other behavioural and physiological measures persist, and it is these that are related to the "true" circadian system.

If rhythms in food related behaviour are not controlled by the same process as light-entrainable rhythms, then the question arises as to whether they are not simply a

result of a process similar to that controlling behaviour patterns under short fixedinterval schedules. The data most frequently cited against a common process (e.g., Aschoff, 1984; Boulos et al., 1980) is that reported by Bolles and his co-workers (Bolles & de Lorge, 1962; Bolles & Stokes, 1965). Because these studies have been so influential in distinguishing between conventional fixed-interval and circadian timing, they warrant detailed discussion.

In the first study (Bolles & de Lorge, 1962), wheel running activity in rats fed for 1 hr at 19-, 24- and 29-hr intervals was recorded. No attempt was made to eliminate potential temporal cues from the animals' environment. The experiment was run in a corner of an active laboratory, and the laboratory lights were switched on at 6:00 a.m. and off at 6:00 p.m. each day. Records of wheel running activity from the group on the 24-hr feeding schedule showed accelerations that anticipated feeding time, whereas the curves from the 19-hr group were fairly flat. The authors claimed that no anticipation was evident in 29-hr group, except for two subjects in which there was an acceleration in activity 23- or 24-hr after the last feed. However, as the data presented were averaged over five intervals it is possible that individual records may have created a different impression. Further, the data from the two subjects that did show accelerations in the averaged curves only differed from the 24-hr group in that there was a small drop in rate over the final 2 hr of the interval (Bolles & de Lorge, 1962, Fig. 2). Despite this, the authors concluded that anticipation would only emerge if subjects were fed at same time of day. They favoured an account in which a biological clock, rather than the interval between feeds per se, controlled the rate of wheel running behaviour.

However, in the introduction to the second study (Bolles & Stokes, 1965) it was acknowledged that both controlled and uncontrolled diurnal cues in the experimental environment may have interfered with discrimination in the (a-diurnal) 19- and 29-hr groups. In an attempt to equate conditions for all groups, subjects in the 19- and 29hr groups were bred, reared, and tested in isolation rooms. In these rooms the light cycle was set such that the light and dark phases would each occupy half of the inter-

food interval. Subjects in the 24-hr group were simply obtained from a standard supplier and housed in a normal laboratory prior to being tested in an isolation room. Half of the subjects in each group were used to study wheel running activity. The other half were placed in operant conditioning chambers where food was contingent on a bar press during a feeding period. Half of the subjects in each group were fed during the dark, and half fed during the light. The authors claimed that only the diurnal group showed clear anticipation in wheel running and bar pressing activity. Increases in these measures that were evident for both of the a-diurnal groups were said to result simply from reactions triggered by changes in illumination. Bolles and Stokes concluded that their results, while not showing conclusively that rats could never learn to anticipate a 19- or 29-hr feeding schedule, did show that, were such learning possible, it would be based upon a temporal discrimination which was difficult for the rat to make. It is this conclusion that has been cited as evidence that operant responding on short fixed-interval schedules is under the control of a process that is different from that controlling behaviour that anticipates 24-hr feeding schedules. The rationale for this distinction is that, in the 19- and 29-hr groups, temporal control was absent, or at least weaker than in the 24-hr group. It is assumed that this difference is due to the involvement of circadian timing in the performance of the diurnal group but not in the performance of the a-diurnal groups because, if circadian timing were not an important factor, then a similar degree of temporal control would be expected in all three groups.

However, given that in both sets of experiments (Bolles & de Lorge, 1962 and Bolles & Stokes, 1965) the subjects in the 24-hr groups had histories that differed from the other groups in more than the lighting regime and inter-food interval to which they were subjected, the weight that has been given to these data in the literature of temporal control may not be entirely appropriate. Although there were obvious qualitative and quantitative differences in the performance of the three groups, uncritical acceptance of the conclusion that responding on fixed-interval schedules with an interval of 24 hr is under the control of a process different to responding on schedules with shorter or longer intervals would be unwise. Examination of Figures 1

and 3 of Bolles and Stokes (1965) shows that, even in the 19- and 29-hr groups, accelerations in both wheel-running and bar-pressing commence *before* the transition in the light cycle in all groups except for 19-hr subjects fed during the dark phase. This pattern, in itself, suggests anticipation of the a-diurnal light cycles. Further, Dews (1965b) has obtained scallops in pigeon key pecking (under constant conditions) that are nearly identical in form over interval values that range from 500 s to nearly 28 hr. This finding that relative temporal control at 28 hr was equivalent to that at 500 s does not argue for different controlling processes. It could be, for example, that the data produced by the 19- and 29-hr groups run by Bolles and Stokes gave the impression of less acute temporal control primarily because those subjects had been reared in environments less rich in temporal cues than that of the 24-hr group.

3.5

Circadian Rhythms in Fish

Fish inhabit an environment that is, perhaps, even more overtly affected by natural environmental rhythms than the terrestrial one. Further, unlike birds and mammals, the metabolism of fish is directly influenced by changes in temperature that may themselves be a consequence of the solar cycle. As activities such as feeding, avoiding predation and reproducing all take place within a world governed by the regular action of the tides and the light cycle, it might be expected that evolutionary pressures would favour individuals with the ability to discriminate time intervals. This expectation is supported in a number of studies. A few early experiments, such as those of Spencer (1939) and Spoor (1946) revealed diurnal rhythms in the activity of fresh-water fish under natural light. More recently there has been an enormous increase in the volume of research on rhythmicity in fish. For example, Spieler and Kendall (1984) reported that a search of the biological literature published between 1978 and 1983 found approximately 1200 papers on circadian and other periodic rhythms in fishes.

Some of the most influential data on the control of behaviour under artificial light cycles was reported in three papers by Davis and his colleagues (Davis, 1962; Davis, 1963; Davis & Bardach, 1965). The first of these (Davis, 1962) examined cyclic variations in the duration of a "light-shock reaction" in bluegill sunfish (Lepomis m. *macrochirus*). The fish were maintained under a light cycle composed of alternating periods of complete darkness (12 hr 10 min) and moderate light (400 lx, 11 hr 50 min). Feeding and maintenance of the aquariums was carried out shortly after the start of the photophase. Once per day, over a 63-day test period, the fish were exposed to 5- or 10-min of very bright light (1000 lx) at a randomly selected point in the scotophase. This treatment produced a pronounced reaction in the subjects. Davis measured the time taken between the onset of the bright light and the resumption of a normal posture. He found that this duration varied systematically across the scotophase. Early on recovery was relatively fast, later the durations increased, but then decreased again towards "dawn". This function was taken as evidence of some internal anticipatory or "time measuring" system. However, it was not clear whether the rhythm in recovery time was under the control of the light cycle or of the feeding time.

Davis (1963) reported a series of experiments on the effect of changes in the time of the onset and offset of the photophase, and one experiment in which the relationship between the light cycle and the feeding time was shifted. Rather than the duration of a light-shock reaction, the dependent measure in these experiments was "general" activity, as indexed by a movement detector. Davis found that, when subjects were fed at light onset under a 12-hr light, 12-hr dark illumination cycle, peaks in the rate of activity would develop during the final 1 to 3 hr of the scotophase after between 10 and 20 days. When the onset of light and the feeding time were shifted forward or backward by 6 hr to a later or an earlier time of day the peak in activity shifted by a small amount each day until the original relationship to the schedule was restored. Shifts in the time of light offset or in the feeding time did not affect the timing of the pre-dawn peak. Further, a peak in activity that corresponded to the pre-dawn peak persisted for the first 2 days of a 6-day period of constant darkness

without feeding. When the light and feeding schedules were reinstated the pre-dawn peak reappeared in 1 to 2 days. On the basis of these findings, Davis suggested that the pre-dawn peak in activity was endogenously regulated by a rhythm which was itself coordinated by the daily change from dark to light.

However, data from experiments carried out by Davis and Bardach (1965) suggested that, contrary to the findings reported by Davis (1963), the time of feeding may also be a critical variable in the control of the patterning of activity. Using apparatus similar to that used in the earlier experiment, they found that peaks in activity would develop both prior to light onset and prior to a feeding time that was scheduled in the middle of the photophase. The timing of the pre-feeding peak was influenced by shifts in the timing of the light cycle and by shifts in the feeding time. These schedule adjustments resulted in equivalent shifts in the time of the pre-feeding peak in activity over 1 to 3 days. Even under constant light, peaks in activity that anticipated a fixed feeding time would develop in 5 to 10 days. Davis and Bardach (1965) concluded that the pre-feeding peaks in activity were controlled by a conditioning process in which the act of feeding became associated with an endogenous cue. The endogenous cue was, in turn, coordinated by the regularity of the light cycle and feeding schedule. That is to say, that the light cycle and feeding schedules acted as zeitgebers for some endogenous rhythm, and that the rhythm was responsible for the coordination of activity.

Davis and Bardach's (1965) findings on the relationship between rhythms in activity and light and feeding schedules have been replicated in goldfish by Spieler and Noeske (1984). When held under a fixed light cycle and fed at the same time each day, the activity of the fish came to anticipate the feeding time. This activity cycle persisted through between 3 and 10 days of a test period of starvation under the light cycle and for at least 3 days under constant light or constant dark. In addition to general activity, Spieler and Noeske also measured concentrations of serum-cortisol and serum-thyroxin during the test periods. Although there were diurnal variations in both of these measures, only serum-cortisol concentrations appeared to be coordinated

with the feeding schedule. Serum-thyroxin concentrations were more heavily influenced by the light cycle. Because these two endocrine rhythms appeared to be entrained by different zeitgebers, it was concluded that the daily integration of these rhythms with their environment involved a multioscillatory system in goldfish.

This multioscillatory model of the control of rhythmicity in fish is consistent with Aschoff's contention (see above) that feeding schedules entrain only a subset of behavioural and physiological variables. Aschoff's position was largely based on the finding that, in rats, free-running rhythms in activity persisted even where activity that anticipated a fixed feeding time was present. However, a recent report by Spieler and Clougherty (1989) suggests that this dissociation in rhythms of activity may not occur in goldfish. The fish were held under a fixed light cycle and fed at the same time each day for 46 days, prior to a test period of 5 days without food under either constant light or constant dark. Different groups of fish had been fed at a different point in the light cycle. The activity rhythm remained entrained to the approximate time of feeding throughout the test period with no apparent splitting related to the constant lighting conditions. Spieler and Clougherty argued that if the activity rhythm had been entrained to the light cycle, or if feeding induced rhythms had been masking an endogenously controlled activity rhythm, then at least a component of the rhythm would have become free-running during the test period. This may not be particularly conclusive evidence, however. Free-running rhythms are usually only clearly apparent under constant light over periods much longer than 5 days.

However, Spieler and Clougherty's suggestion that, in goldfish, accelerations in activity that anticipate a fixed feeding time appeared to be solely under the control of the feeding schedule again raises the question of whether the control of behaviour on fixed-interval schedules of reinforcement is of a different nature to the control of food anticipatory behaviour attributed to circadian timing. This question will be discussed further in the following section along with a discussion of the similarities and differences between the chronobiologist's zeitgeber and the psychologist's

discriminative stimulus and the particular theoretical problems involved in the concept of temporal control.

3.6

Theoretical Issues

Groos and Daan (1985) argue that the control of responding by non-circadian fixed-interval schedules implies recognition of the lapse of time, whereas control by endogenous oscillators that are phase locked with the light cycle implies only the recognition of local time. In principle, however, a circadian clock could provide the basis for interval estimation. In Section 3.4 the evidence most frequently cited in favour of separate mechanisms was discussed. This was the finding that response patterns under long-interval schedules that depart significantly from 24 hr are qualitatively different (Bolles & Stokes, 1965). Although, it was argued that these data may have been accorded an undue weight, it would be unwise to discount the strong probability that schedules that approximate the solar cycle have a particular status in the control of behaviour. Rather, the key question is whether the process whereby circadian rhythms become entrained is qualitatively different from the process whereby non-circadian intervals come to control behaviour.

Precise 24-hr periodicity in circadian rhythms is dependent on the availability of a zeitgeber to re-set it each day and check the tendency to free-run. The zeitgeber most commonly provided in the laboratory is a regular cycle of alternating periods of light and dark. However, Rosenwasser (1980, cited in Terman, 1983) has shown that a full light cycle is not necessary for the maintenance of circadian rhythmicity in drinking and operant feeding patterns in rats. Subjects held under otherwise constant dim light, but exposed to a 15-min pulse of bright light at the same time each day, maintained patterns in these behaviours that had been established under a conventional light cycle. When the pulses were discontinued these rhythms began to free-run. The finding that this "skeleton photoperiod" was sufficient to function as a zeitgeber

suggests that in the circadian domain, as in fixed-interval schedules, relatively discrete events may control temporal coordination.

In behavioural psychology, an event that sets the occasion on which a response may be followed by reinforcing consequences is termed a discriminative stimulus. For example, responses may be differentially reinforced in the presence of or following a discretely presented light or tone. Indeed, in a behavioural chain a particular response may function as a discriminative stimulus for the performance of another response (see Section 3.2). Clearly, a zeitgeber is not a conventional discriminative stimulus where it controls rhythms in behavioural and physiological variables that are not themselves under the control of reinforcement contingencies. However, a zeitgeber might be regarded as a form of discriminative stimulus if its function is to coordinate, or set the occasion for, the initiation of a timing process that regulated the emission reinforced behaviour. In this view, the timing process itself is regarded as a class of behaviour that may be susceptible to stimulus control. Just as the first unreinforced response on a fixed-interval schedule might serve as a discriminative stimulus for the initiation of a timing process that is reinforced at the end of the interval, the presentation of a zeitgeber where reinforcement is scheduled according to a 24-hr cycle might serve as a discriminative stimulus for, if not the initiation of a timing process, the placing of reinforcer-related behaviour under the control of timing processes that pre-exist for the specialised control of other behavioural and physiological variables. Indeed, the differences that have been identified in chronobiological studies between food-related and other types of circadian rhythms might result from a process in which a fixed-interval like time estimation develops from a pre-existing internal circadian timing component. As the foodanticipatory component is reinforced directly it might remain under the control of a fixed feeding schedule even where the light cycle that controlled other circadian rhythms is removed and those less directly reinforced patterns start to free-run.

A problem with suggesting that zeitgebers might function as discriminative stimuli is that they are effective in the coordination of behaviour even though they may occur

at a point temporally remote from the moment or period during which that behaviour is reinforced. This is the same problem that was raised in the discussion of theories of fixed-interval responding in Section 3.2. There are no obvious events in the intervening interval that might have local control over the systematic changes in behaviour that constitute a circadian rhythm. The solution to this problem of "filling in" the interval on periodic schedules that has been adopted in some theories of fixed interval control is to assume the existence of temporally coordinated patterns of endogenous stimuli that fulfil the discriminative function (e.g., Church, 1984; Gibbon, 1977). Indeed, psychological theories based on this assumption usually justified it by reference to evidence of physiological pacemakers derived in chronobiology (e.g., Killeen & Fetterman, 1988). A zeitgeber might regulate the relationship of such stimuli to the phase of the solar cycle in the same way that discriminative stimuli associated with reinforcement (or that signal the start of an interval) might regulate the temporal relationship between the endogenous stimuli presumed to underlie fixed interval performance and the temporal parameters of the schedule. This view of the control of endogenous stimuli by external cycles does not imply any major distinction between zeitgebers and discriminative stimuli or between temporal regulation with periodicities of any particular value. It may well be that there are rhythms in endogenous stimuli which are inherently circadian, but even these require a process of entrainment in order to keep pace with the external cycles experienced by an organism. The plasticity evident in the timing processes studied in chronobiology could be taken as an indication that circadian timing may simply represent a more specialised and less flexible subset of a more general timing process that is evident in fixed-interval performance. Furthermore, an assumption that temporal control is mediated by endogenous stimuli does not necessarily imply an assumption that the function of these internal stimuli would be exactly equivalent to that of exogenous stimuli. Indeed, in Chapter 7 there will be a discussion of the possibility that the interaction in control between a temporal contingency and a concurrent exogenous discriminative stimulus may differ from interactions in control between two or more exogenous stimuli.

Finally, a brief discussion of the concept of temporal discrimination is required. All events take place in time and have a particular duration. Duration itself is not a stimulus, however. Rather it is a quality or dimension of stimuli. This point was emphasised by Skinner. Although an organism may respond differentially at a particular temporal point in the course of a continuous stimulus if that point is reliably associated with reinforcement, in no way "does 'time' or 'an interval of time' enter with the status of a stimulus. Time appears as the single property of duration, comparable with intensity, wavelength, and so on" (1938, p. 269).

Temporal discrimination, then, may be discrimination of a stimulus in terms of its duration. However, in many of the experiments on temporal control reviewed in this Chapter, efforts were made to exclude external stimuli correlated with the schedule. Temporal discrimination developed even though the external stimulus situation was identical throughout. Because there is no obvious duration receptor, it is tempting to appeal to the discrimination of temporally configured endogenous stimuli. In the present thesis references to "temporal stimuli" will be made because it is assumed that the behaviour under investigation is, at some level, directly under the control of stimuli. Insofar as behaviour is temporally coordinated in the absence of identifiable temporally coordinated public stimuli, the controlling stimuli are likely to be private. It is assumed that these hypothetical private stimuli derive their control over behaviour through their relationship to reinforcement on schedules with temporally defined contingencies. Nevertheless, references to hypothetical internal timing processes do not serve as explanations in the experimental analysis of behaviour. Instead interest is focused on the conditions under which temporal discriminations are acquired and maintained (Harzem, 1969). Acknowledging that an analysis that is dependent on hypothetical states may be of dubious value, the central concern in the present thesis will be with the relationship between the experimental environment and the behaviour of the subjects.

4.0 METHODOLOGY

4.1

Introduction

This Chapter will address issues from three main areas in the methodology used in the experimental sections of this thesis. The first area concerns the nature of the subjects. In Chapters 2 and 3 data on fish were discussed separately. Fish are not frequently used as subjects in investigations where the point of interest is the discovery of general behavioural principles rather than in the behaviour of a particular species. In more general work, especially in psychology, the laboratory rat and pigeon have been the most common subjects. In Section 4.2 some further findings relevant to experimental work on the behaviour fish species will be considered. The second area concerns the particular technical issues related to the carrying out of the experiments, and these will be considered in Section 4.3. The third area (Section 4.4) involves the general approach adopted in the analysis and interpretation of data.

4.2

Fish Behaviour and Laboratory Studies

As with all subjects, fish come to the behaviour laboratory with particular qualities that have, presumably, been shaped by the contingencies of their natural environment. In designing experiments, the behaviour of the investigator must, in turn, be shaped by the qualities of the subject. One of the qualities that is of particular significance in the behaviour of many species of fish is their complex social organisation. It is the group behaviour of fish that will be the main subject of the discussion which follows.

A significant portion of ethological research has been directed at the inter- and intra-specific behaviour patterns displayed by communities of fish. A wide range of symbiotic relationships and intricate social hierarchies have been described, and

investigators have attempted to delineate the factors which control these behaviours in natural environments (for reviews see Bull, 1957; Hoar & Randall, 1971; Ingle, 1968; Keenleyside, 1979; Pitcher, 1993; Winn & Olla, 1972). Here the emphasis will be on reviewing laboratory studies of group behaviour, with particular regard to learned responses.

In a seminal paper on group behaviour in fish, Welty (1934) reported a series of laboratory experiments in which the subjects (mostly goldfish) were required to swim through a gate into a partitioned-off area of their aquarium whenever a red light was shown. If they performed this task correctly they were given food. By testing fish in groups of various sizes he was able to examine the effect that this variable had on the performance of the task. The most striking result was that when fish kept either individually or in groups of two, four, or eight were compared, there was a marked trend towards faster acquisition in the larger groups.

In a further experiment, Welty found that placing trained fish in with naive ones reduced the time taken by the naive fish to learn the task by more than half. This was shown to be due to more than just a simple "lure" effect. Even if a naive fish was left in the feeding area as an encouragement for other naive fish to cross through the gate, the rate of acquisition was far slower than when a pre-trained "leader" was included in a group. Welty also found evidence of a group cohesion effect. The variability of reaction times for isolated fish was greater than for fish housed in groups. Other, less conclusive, experiments indicated that the retention of learned responses is superior in grouped fishes, that fish in groups tend to eat more, and that fish will learn to run a simple maze more rapidly after having observed another fish perform the same task (Welty, 1934).

A possible source of the group superiority effect observed in Welty's experiments could be the higher activity levels of fish in groups. The more active a fish is, the greater the chance that it will find the gate and swim through it. Another effect observed was that isolated fishes are more prone to display fright reactions, with the consequence that fish in groups spend more time engaged in exploratory behaviour.

However, despite problems in interpretation of the processes involved, the number of replications and variations of design used by Welty suggest that learning in fish is more efficient in groups than in individuals.

Another aspect of group behaviour in fish has been reported by O'Connell (1960). In an experiment using delay conditioning with a light as the conditioned stimulus and with food as the unconditioned stimulus, he found that it was possible to simultaneously condition the behaviour of all 21 members of a group of Pacific sardines (Sardinops caerulea). A conditioned response in which the school turned towards a feeding area and instantly reacted to the food developed after only a few trials. A particularly interesting effect was observed when members of the school that had died were replaced with naive fish. These replacements acted in unison with the school on the very first conditioning trial to which they were exposed. This shows that schooling fish will imitate the learned behaviour of conspecifics, and suggests that, where behavioural conditioning is required in aquacultural settings, the use of pre-trained "seed" fish may be an effective technique for speeding up acquisition in untrained fish. Indeed, Yamagishi and Nakamura (1978) cite work published in Russian by Gerashimov (1962; 1967; 1971) which suggests that schooling fish quickly establish conditioned responses where a pre-trained fish is available as a "model", whereas for non-schooling species the opportunity to observe a pre-trained fish before being given the same task produced no increase in performance.

Evidence of a group superiority effect in acquisition has been also been provided by Munson, McCormick and Collins (1980). They trained juvenile rainbow trout, housed in a large tank (0.6 m wide by 2.4 m long by 0.45 m deep), to swim from one end to the other in order to receive food. Groups of 20 fish required about one half as many training sessions to reach a criterion as did individuals.

Experiments performed by Olla and Samet (1974) indicate that the visual pathway plays an important role in the co-ordination of group behaviour. The sight of other fish engaging in group activities can influence the type of behaviour exhibited by individuals. They found that isolated striped mullet (*Mugil cephalus*) spent a

significantly higher proportion of their time in the proximity of the glass wall of their aquarium that was adjacent to an aquarium containing a group of other fish. This happened even if the fish were of another species. They also found that visual contact with feeding groups of conspecifics significantly decreased the latency and increased the duration of the feeding response of isolated fish. Furthermore, the sight of a nonfeeding group had a significant inhibitory effect.

However, not all experiments on group learning in fish have shown a straightforward group superiority effect. Gleason, Weber, and Weber (1977) found that the relationship between group size and performance may be more complex. In training zebra fish (Brachydanio rerio) on a two-way shuttle avoidance task, they found that a group of five did show superior rates of acquisition and performance in comparison with single fish, but scores lower than those of single fish were produced by fish tested in pairs. One explanation for the difference between the single and the paired fish might be that shock induced aggression that was directed at the other fish and so conflicted with the avoidance response. This explanation would not account for the superior performance of the larger group however. The performance of the larger group might be enhanced because it would be more likely to contain faster learners, but if this was the only pertinent factor, then the pairs would be expected to be superior to individuals. Gleason et al. advanced two hypotheses that might account for their results. The first was that pairs of fish may be subject to conflict inhibition. Even if one of the fish was a fast learner, it would have to choose between avoiding the shock and the tendency to shoal when threatened. They argued that the conflict would be less in a larger group as there would be a variety of responses available for imitation. Their second hypothesis draws on work showing that the behavioural response of a rat to an aversive stimulus depends on the environment (Antelman & Szechtman, 1975; Caggiula, 1972). When in pairs, fish might interpret the shock and the agitation of their companion as aggression. This misinterpretation would interfere with learning of the avoidance response. When the fish are in a larger group, the agitation of other members of the shoal would be likely to be interpreted as a signal for

escape rather than attack, and thus learning of the avoidance response would be enhanced. No evidence was presented in support of either of these hypotheses.

Yamagishi and Nakamura (1978) found that the position of a fish in the social hierarchy of a shoal can have a dramatic effect on performance measures of learning. They used acoustic conditioning to train a group of four swordtails (Xiphophorus *helleri*) to enter a small chamber in their aquarium in order to be fed. Only one of the fish (the dominant one) reliably displayed the target behaviour. This response was temporarily extinguished if the fish was defeated in a fight, and recovered when the fish regained its dominant position. Because the dominant fish would often start to attack the others as soon as the conditioned stimulus was applied, there were few opportunities for these subordinates to develop the association between the tone and food. When subordinate fish were tested in isolation, the level of performance of the conditioned response was generally low, with the more stable performances coming from fish which had been higher in the hierarchy. However, these isolation tests were only carried out for one day, and so it is unclear whether the lower performance was due to a lack of ability or to a conflict between the food reward and an inhibitory association between the conditioned stimulus and the probability of attack by another fish. Nevertheless, Tateda, Nakazono, and Tsukahara (1985) have also found that the presence of a dominant fish in a group of seven young red sea bream disrupted the conditioned feeding response of other group members by interfering with their movement.

In a replication with goldfish of their earlier swordtail experiment (Yamagishi & Nakamura, 1978), Yamagishi and Nakamura (1981) found evidence to support the theory that inhibition through aggression had prevented subordinates from performing the target behaviour. Although goldfish form dominance hierarchies and will attempt to defend territories, they are less effective at inhibiting the responses of subordinates, and consequently all fish in a group will perform the task at a stable rate. Interestingly, when tested in isolation the performance of the less dominant fish dropped markedly, suggesting that they may have been relying on imitation in the

group tests rather than learning the task themselves. Another feature of the isolation tests was that, for all subjects, inter-trial responses were emitted at a lower rate than in the group situation. This could be related to the reduced general activity in isolated fish that was described by Welty (1934).

The superiority of groups in acquisition and retention could be attributable to what social psychologists might call "pseudo group effects" rather than any "true group effects" on individual performances. For example, Welty's (1934) subjects were both trained and tested in groups. It is possible that many of them may have simply imitated more adept group members. Warren, Bryant, Petty, and Byrne (1975) attempted to overcome this problem by individually testing fish that had been trained in groups. The groups consisted of subjects from a central pool of 396 goldfish brought together either in pairs, or in groups of 5, 10, or 15 for training. In this way, it was possible to ensure that no fish was trained in the company of the same fish for more than one trial, although each fish was always trained in the same sized group. The task used was of the dark avoidance shuttle type with shock as the reinforcer. Even though all the fish were tested individually, fish that had been trained in all of the group sizes showed faster acquisition and superior retention when compared with individually trained fish. While it is unlikely that this group superiority could be due to imitation, it remains possible that it was a consequence of effects related to the mere presence of other fish, or to fish responding to some form of cue associated with others behaving in a more adaptive manner.

It seems clear from the studies of group effects in fish cited above that isolated fish may well behave differently to grouped fish. This presents a major methodological problem in the type of experimental work contained in this thesis. On one level, a decision must be made as to whether the phenomenon being studied should be investigated in grouped or in individual subjects where resources are not available for work on both. Here the question of the aim of the work becomes particularly important. If the rationale for the experiment is to evaluate behavioural processes which might ultimately be of relevance to aquaculture, then the collection of data from

grouped subjects is likely to be preferable because any applied developments will be used in the management of groups of fish. If, on the other hand, the aim is to examine more general behavioural principles, then it is preferable that data should, at least initially, be collected from individual subjects. This is because data relating to such principles is likely to be of limited value unless attempts are made, as far as possible, to equate the conditions to those under which the data reported in the existing literature were obtained. The overwhelming majority of work on general behavioural principles has been carried out on isolated subjects in order to maximise control over the subject's environment. Although social interactions are likely to affect the behaviour of all species, these interactions have not usually been a variable of primary interest in the study, for example, of the effects of different schedules of reinforcement. The general approach has been to attempt to determine the role of variables involved in the control of an individual's behaviour in a relatively simple experimental context. A variable that would increase the complexity of the experimental environment would be the presence of other individuals, but such experiments as still rare in experimental psychology. Perhaps, when the processes determining the behaviour of an individual in a simple environment are well understood it will be possible to examine more complex environments.

On another level, there are practical and ethical considerations surrounding the use of isolated subjects. The ethical consideration is whether the distress that may be caused by the isolation of a social organism can be justified. This issue is discussed in Section 4 (d) of the "Guidelines for the use of animals in research" published by the Association for the Study of Animal Behaviour and the Animal Behavior Society (1991). Here it states that isolation may be extremely stressful, but that the degree of stress caused may vary with a number of factors. These include the species, the social status, and the previous social experience of the individuals concerned. It is recommended that these factors are considered, and that stressful situations are avoided as far as possible. Essentially, the decision appears to rely on the subjective judgement of the experimenter in the first instance, but it is increasingly common for the editorial boards of academic journals to direct reviewers to satisfy themselves that

subjects have been treated in an "ethical" manner before recommending a particular manuscript for publication. Consequently, animal experiments during which, in the judgement of peers, the subjects were unduly stressed, are unlikely to be published. An experiment that remains unpublished will be of limited scientific value.

The definition and assessment of "stress" has formed a substantial area of psychological research in itself. Unfortunately, there are no published guidelines concerning behavioural indicators of stress in fish. However, fish held in isolation are generally less active, eat less, and are more likely to display vigorous escape behaviour when disturbed than are grouped fish (McMahon, personal communication; Welty, 1934). If these factors are accepted as indications of stress, then as the majority of fish species are social animals, it seems reasonable to assume that longterm isolation should be avoided where alternative procedures are available. Further, from a practical perspective, a subject that is not particularly active, that is easily disturbed, and that is unlikely to eat much even when food is freely available would not be ideal in a study of appetative behaviour.

Taking account of the practical and ethical considerations outlined above, none of the experimental work reported in the present thesis was carried out on isolated subjects. In the early experiments, where the aims were more closely related to applied concerns, the fish were housed and tested in groups. In the later experiments, where the aims were more focused on general behavioural principles, a method was developed whereby the behaviour of a single fish could be recorded, but some social contact with a conspecific was maintained (see Chapter 6, Section 6.2.1.4).

4.3

Technical Aspects

In this section the equipment used in the experiments reported in this thesis will be described and commented upon.

As the work was an investigation of operant behaviour, the basic requirements were that there should be some device that was sensitive to a response or class of responses, and some method of supplying a reinforcer when a response was registered. Response levers and food dispensers that had been developed for experiments on operant conditioning in fish by Wright and Eastcott (1982a; 1982b) were available and appeared to be suitable.

Wright and Eastcott's levers consisted of a 20 cm length of welding rod with a circular piece of white plastic (0.1 cm thick, 2 cm diameter) attached at its lower end, and with the other end attached to the arm of a standard mechanical microswitch (RS catalogue number 338-298). The switch was bolted to a section of plastic card, and this in turn, was clamped to a retort stand. By adjusting the position of the retort stand and clamp, the lever assembly could be placed so that the lower end projected approximately 2 cm below the surface of the water in the subject's aquarium. Any part of the rod that was likely to make contact with the water was sleeved in a silicone rubber tube to prevent contamination of the aquarium. The rod was held at an angle of approximately 20° from vertical. In Wright and Eastcott's experiments this lever apparatus had proved generally effective, although the contacts of the microswitch did occasionally require attention due to corrosion in the moist atmosphere above an aquarium (Wright, personal communication). Unfortunately the lever proved entirely inappropriate to the slightly smaller subjects used in the present work. This became apparent during one of many sessions in which the experimenter fruitlessly attempted to shape the lever-pressing response both by the method of successive approximation (see Experiment 1, Chapter 5, Section 5.1.2.4) and, finally, by attaching food to the lever tip. At one point three subjects were observed vigorously attacking the baited lever in unison, and still no response was registered. On the basis of this evidence, the old levers were abandoned, and a complete re-design of the mannipulandum was undertaken before the experiment was restarted.

The design that was finally employed throughout all the subsequent experiments was based on an opto-electrical rather than mechanical switch. The lever consisted of

a stainless steel rod (20 cm long, 0.3 cm diameter) with the lower tip sleeved with thick walled silicone rubber tubing (0.4 cm diameter). This projected approximately 0.5 cm below the water surface, 8 cm to the side of the point where food was dispensed. The rod was held in a near-vertical position and was pivoted at a point 7 cm from its lower tip. When the lower end was moved, the upper end passed through an opto-electrical sensor that was connected to the control equipment (see below). The fish activated the lever by pushing the lower tip 0.75 cm forward with their mouths. In order to reactivate the lever it had to be released, at which point gravity returned it to its resting position. A force of at least 0.0004 N was required to activate the lever. This was sufficient to prevent activation by water movement, but not to prevent activation by small fish. In addition to greater sensitivity, this lever had the advantage that with no moving parts in the switch assembly it was less likely to malfunction due to wear or corrosion.

Two distinct lever pressing techniques have been observed with this apparatus. Fish either made a single press by swimming up to the lever, pushing it, releasing it, and then swimming around in an arc to consume any food that has been dispensed or to prepare for the next activation, or they held station in front of the lever and made repeated activations using their pectoral fins to move forward and backward the required distance.

The dispensers were of a design based on that of Adron (1972). They were actuated by a 0.5-s pulse of power to a 22-V solenoid. This moved a sliding plate away from an aperture in the base of a food hopper. The plate was returned to its resting position by means of a steel spring. The size of the aperture was adjustable, and for all experiments reported in this thesis, it was set to dispense approximately 0.05 g food on each activation. The need for a 0.5-s pulse of power to activate the dispensers meant that the maximum rate at which reinforcement could be delivered was restricted to 120 per minute. In practice, the rate of responding never approached this figure. The dispenser assembly was positioned so that food was delivered to a point 12 cm inward from the centre of one end of the aquarium.

Extensive experience with these dispensers has shown that, while they are generally very reliable, care must be taken to ensure that moisture does not form on the underside, and that splashes of water do not enter the food hopper. If this does happen, the food will become damp and the dispenser mechanism will jam. In order to prevent this, the dispensers were mounted on pillars that raised the main body 10 cm above the upper edge of the aquariums. A further problem with this design is that, for smaller subjects, it might be preferable to dispense less food on each activation. However, attempts to set a smaller aperture resulted in inconsistencies in delivery. The setting which produced 0.05 g was the lowest to give a consistent amount. Finally, a solenoid-operated design may not be the most suitable for behavioural studies. Most subjects appear to habituate to the rather loud and sudden noise produced eventually, but casual observation suggests that during acquisition there may be considerable inhibition of any food directed behaviour. The reaction of most subjects on their first experience of dispenser operation appears to be directed more towards escape than towards the examination and consumption of the food.

It is likely that more rapid acquisition of the lever press response and greater control over behaviour would be gained by using a design of dispenser similar to the motor driven type commonly used in commercially produced operant conditioning chambers. In these designs, food pellets are collected in suitably sized holes drilled into the circumference of a disc that is rotated by an electric motor. When a pellet passes over a hole drilled in the floor of the unit, it falls through to a pipe or chute that leads down to a food cup. These dispensers are very quiet in operation, and because the holes in the disc can be drilled to suit any size of pellet, they permit very precise control over food delivery. A modified version of this design, suitable for use in experiments with fish, has been described by Beach, Baker, and Roberts (1986). A similar system has been under development in the workshop of the Department of Psychology at the University of Plymouth since 1991 (when the shortcomings of the solenoid driven dispensers became apparent). Unfortunately, due to various changes in personnel and to other factors, this project has yet to be completed. Further designs for fish food dispensers are available in Ames (1967), Haralson and Bitterman (1952),

Haralson and Ralph (1966), Holmes and Bitterman (1969), Mark (1967), and Woodard and Bitterman (1974).

The control and recording systems consisted of a microcomputer and an interface device. In Experiments 1 to 4 the computer was a BBC Model B with a $5^{1}/4^{"}$ disc drive. This was adequate, but in Experiments 5 and 6 it was replaced by an Acorn Archimedes 410/1. The Archimedes was better in a number of respects. Firstly, unlike the BBC, it could be set to re-load the controlling programme automatically following any interruption in its power supply. Secondly, the Archimedes had an integral $3^{1}/2^{"}$ disc drive that could hold many more data files than the drive used with the BBC. This was an advantage because data held in RAM could be saved more regularly before a disc became full. A full disc would prevent further data collection, but files had to be saved at regularly in order to reduce the potential for loss through power failure. In all of the experiments data was saved automatically after 1000 lever presses had been recorded. The use of $3^{1/2}$ " discs also simplified the final processing of data because these could, with the aid of a simple conversion programme, be read by the Macintosh computers that were used in data analysis. Processing data from the $5^{1}/4^{"}$ discs used with the BBC took considerably longer because it first had to be copied onto $3^{1/2}$ " discs. Finally, the additional processing speed and memory available on the Archimedes was needed to cope with the additional load required for the control of extra equipment (stimulus lights) in Experiments 5 and 6.

The programme used to control the experiments was developed in collaboration with technicians from the Psychology Department workshop. The programme's main functions were to record the time and source of all lever activations, and to activate the appropriate food dispenser only if the current time fell within certain parameters. These parameters were the start and finish of the feeding times that had been set by the experimenter for each aquarium. If a lever in a particular aquarium was pressed either before or after the feeding time, then the response would be recorded, but no food would be dispensed. In Experiments 5 and 6 a similar piece of code was used to control the times at which stimulus lights were turned on and off.

The inputs from and outputs to the equipment in the aquariums passed through a custom-built interface device. Essentially, this consisted of two main elements. Firstly there was circuitry which converted pulses from each of the opto-electrical switches used in the lever apparatus to signals that could be read by the computer. Secondly, there were relays which used the low voltage supply from the computer to switch on the higher voltage supply that was required to activate the solenoids on each of the food dispensers. This higher voltage was drawn from a separate regulated power supply unit. A further set of relays was used to switch the supply from this power unit to the stimulus lights in Experiments 5 and 6.

Once data were collected, they required analysis. As mentioned above, the basic datum recorded was the time at which the lever in a particular aquarium had been activated. These data were recorded continuously and so were collected in chronological order. The first step in analysis was to group the records so that responses from each successive 24-hr period were held on a single page of a spreadsheet programme (Microsoft® Excel®). Next these records of responding over a 24-hr period were sorted by aquarium number such that all responses from Aquarium 1 would appear in sequence, then the responses from Aquarium 2, and so on. In order to gain a measure of rate, the responses from each aquarium were then grouped into successive 15-min time bins. That is, a tally of the responses during successive 15-min periods over the 24-hr sample was made. The tally during each 15min bin was independent of the tally during other bins. It was this measure of responses per 15 min that was used in all further analyses. Each day the rate of lever pressing per 15 min over the 24 hrs immediately preceding the previous midnight was calculated and plotted (using Computer Associates[®] Cricket Graph[®]) for each aquarium.

In all of the experiments reported in this thesis, there were stages where during one or two 1-hr periods per day a lever press would normally result in food being dispensed. Food would not be dispensed in response to a lever press during other periods. In Experiments 5 and 6, some of the feeding periods were signalled by the

presence of a stimulus light that was on during (and only during) the time when food was available. All of the experiments were run in order to assess the extent to which the responses of the subjects were controlled by temporal contingencies or by visual stimuli. Where the question is simply whether control is present or not, the inspection of plots of responding over time might be sufficient. For example, temporal control may be deduced from characteristic patterns of responding (see Chapter 3, Section 3.2), and control by a discriminative stimulus may be deduced from systematic and reliable changes in rate in the presence of the stimulus. However, where there is a need for comparisons in the degree of control, some quantitative characterisation may be necessary.

In Experiments 5 and 6, discriminative control by stimulus lights was quantified in the form of a discrimination ratio (see Chapter 7, Section 7.2.2 for details of the method of calculation used). Discrimination ratios are a conventional index of stimulus control in studies where the discriminative stimulus is a discrete exteroceptive event. The ratio is a measure of the rate of responding in the presence of a stimulus as a function of the rate of responding in its absence. As such, it provides a convenient indication of the change in rate, above or below a baseline level, that occurs when the stimulus is present. A ratio value of 0.5 indicates that response rates were equal in the presence and in the absence of the discriminative stimulus whereas values between 0.5 and 1.0 indicate higher rates during the stimulus, and values between 0.5 and 0.0 indicate lower rates during the stimulus.

An important consideration in the use of discrimination ratios is the selection of the parts of a record that are to represent behaviour in the presence and absence of the stimulus. In the present case, the ratio of the sum of responses emitted during a particular hour-long presentation of a stimulus light as a function of the sum of responses emitted during the immediately preceding hour was calculated. However, it should be noted that alternative methods could have been used. For example, the baseline level could have been taken as the average rate during all periods where the stimulus light was absent, or some form of randomisation procedure could have been

used to select a particular 1-hr period in the record and this could have been taken to represent the baseline rate. Two factors influenced the decision to compare rates during consecutive 1-hr periods. Firstly, as an index of behavioural change the transition in rate over consecutive periods seemed more representative of the process than would comparing temporally remote periods. Secondly, under some of the experimental conditions, there was a concurrent temporal contingency. This contingency controlled response rates at points in the record that were temporally remote from the point at which the stimulus lights were presented on test trials. Any procedure (such as averaging or random selection) which included responses under the control of the temporal contingency in the calculation of the discrimination ratio would bias the results. Further, even if response rates under the control of a stimulus light presented at a point on the record where responding under the control of the temporal contingency was absent were, for example, subject to some suppressive effect of the temporal discrimination, this effect might be expected to be more similar during the hour immediately preceding the light presentation than at other times. That is, the greater similarity of "background" conditions during consecutive hours makes the adopted procedure preferable to alternative methods for calculating a relative index.

The assessment of temporal control can be more complex than is the case for control by discrete stimuli. Some of the methods available will be considered below, but a convention has yet to be firmly established.

In chronobiology, analysis of time-series data is most commonly carried out using a modification of the periodogram technique (Williams & Naylor, 1978). The periodogram is a plot of the degree of fit of a number of form-estimates with the actual data. Where the period of the form-estimate is similar to a period in the data, the degree of fit will be high. Where a form-estimate is unlike any period in the data, the fit will be low. This procedure typically results in a plot of the degree of fit that has several peaks of varying size. Procedures for assessing the statistical significance of these peaks are used to distinguish "true" peaks from "random fluctuations" (Williams & Naylor, 1978). A "true" peak indicates the period of a rhythm in the time-series

data. The method has the advantage that it does not involve modelling the period of a rhythm that is suspected *a priori* and, therefore, may reveal rhythms in the data with any period (whether previously suspected or not). However, for the present purpose it is not satisfactory. Principally, this is because it would only provide information on whether statistically significant rhythms were present over several days. As the rhythm of primary interest is that of operant responding in relation to temporally-fixed feeding times, the periodogram would simply show whether the imposed 24-hr reinforcement cycle was reflected in the data. It would not give information on the form of any accelerations in response rate associated with feeding times.

Measures of the form of accelerations are more commonly used in work on responding under fixed-interval schedules of reinforcement. Several methods have been developed for producing quantitative estimates of temporal regulation on fixedinterval schedules (see Richelle et al., 1980 for a review). All of these methods are based on the assumption that temporal control will result in the rate of responding being higher towards an interval's end when compared with rates earlier in the interval. Simply calculating the overall or average response rate, as is common for other types of reinforcement schedule, would be inappropriate for fixed-interval performances, as it would disregard the differential distribution of responses over the interval.

As performances on fixed-interval schedules are often characterised by a postreinforcement pause (see Chapter 3, Section 3.2), one approach would be to use the duration of this pause as the quantifier. The simplest way of doing this would be to measure the elapsed time between the start and the first response of the interval. However, Schneider (1969) has criticised this technique on the grounds that the time of the first response is not always the point at which the transition between low and high rates of responding is most rapid. Even where break-and-run patterns predominate, one or more responses may occur in a seemingly random fashion before the rate accelerates to its terminal value. This problem may be avoided to some extent by measuring the time to, for example, the fourth response, but the most appropriate

value will still depend on the performance of each subject on each interval, and so the worth of the measure as a standard index will be limited.

Schneider (1969) developed an analysis suited to the break-and-run pattern. With break-and-run there is a rapid transition between high and low response rates. Schneider's method uses an iterative, least-squares procedure to find the best fit for two lines on a cumulative record of responding within an interval. One line is fitted to responses during the later part of the interval and another line fitted to the early part of the record. Where the two lines intersect is termed the "breakpoint" and represents an estimate of the point of transition between the pause and the active phase. This procedure has the advantage of providing a separate analysis of the two behavioural states but assumes a constant rate in each and so is not well suited to "scalloped" performances.

The quarter-life measure developed by Herrnstein and Morse (1957) provides an index which is also less heavily influenced by the characteristics of a particular performance than is the time elapsed to a particular response, but which is more appropriate for scalloped records. The quarter life (Q) is the time elapsed until one-fourth of the total number of responses in an interval has been emitted. The value may be expressed in units of time or as a percentage of the interval. In comparing measures of responding on fixed-interval schedules, Dukich and Lee (1973), and Gollub (1964) have found the quarter-life measure to be highly correlated with the length of the post-reinforcement pause and with the time elapsed to the fourth (Dukich & Lee, 1973), fifth, or tenth (Gollub, 1964) response, but that it was not very sensitive to the absolute rate of responding. For example, an interval containing 1000 responses might give rise to the same quarter life as an interval containing 10 if the relative distribution of those responses were identical.

Another index which reflects the characteristics of the whole interval, and which is suitable for scalloped records, is the index of curvature or FKC index developed by Fry, Kelleher, and Cook (1960). This works on the principle that responding which continued at a constant rate throughout an interval would appear on a cumulative

record as a straight, diagonal, line. The index represents the direction and the extent to which the actual record deviates from a straight line that has its origin at the start of the interval and which terminates at the final response in the interval. In order to calculate the index the interval is subdivided into a number of successive temporal divisions of equal duration (for example, a 60-s interval might be divided into six 10-s divisions, starting with 0 to 9 s, then 10 to 19 s and so on). The area that is occupied in each of these divisions under the curve of the cumulative record is then summed, and this figure is subtracted from the total area under a triangle formed by the straight line. The maximum and minimum values which the index can take depends on the number of temporal divisions used. Values closer to the positive maximal value represent better temporal regulation. However, the index can be misleading when the number of responses in an interval is low (Fry et al., 1960), and it is not possible to compare performance on intervals where the index has been computed using different numbers of divisions (Richelle et al., 1980).

In choosing between measures, consideration should be given not only to how well the index appears to reflect the response pattern to which it is applied, but also to convention and to how easily it may be comprehended. All other things being equal, a widely used measure is preferable to an obscure one. Further, the more complex and difficult to follow the calculation of an index is, the more likely that mistakes will not be noticed. Of the measures reviewed above, the guarter-life and the FKC indices appear to reflect the distribution of responses under fixed-interval schedules most adequately (except where break-and-run predominates, in which case the breakpoint may be more appropriate). The FKC index and Q are highly correlated with each other (Gollub, 1964; Richelle et al., 1980), but neither measure provides an indication of response rate. However, Q has been found to be highly correlated with other measures of response distribution (see above), and the median value of a frequency distribution produced from the quarter-lives of individual intervals has been found to correspond reasonably well with the quarter-life of an mean average response distribution constructed from those intervals (Baron & Leinenweber, 1994). Given the simplicity and more widespread use (e.g., Zeiler & Powell, 1994) of the quarter-

life in comparison with the FKC index, together with the high correlation between the measures, the quarter-life appears to be preferable. However, while its insensitivity to the absolute rate of responding during an interval may be an advantage for some purposes (see Chapter 7, Section 7.4), some indication of rate should also be made available for inspection.

In Experiment 5 of the present Thesis (where there was a need to compare temporal discrimination under different conditions) a modification of the quarter-life method was used as a quantitative measure (see Chapter 7, Section 7.2.2). In earlier experiments, where the question was simply whether temporal discrimination was present or not, an even simpler analysis was adequate. In Experiments 1, 2, 3, and 4, the presence of temporal discrimination was inferred primarily by the inspection of plots of response rate over time, but a reasonably effective indication of discrimination was also available from comparisons of response rate during the period immediately preceding the time at which reinforcement was usually available with the response rate during a period of the same duration that occurred at a time that was remote from any scheduled events (see Chapter 5, Sections 5.1.1 and 5.1.2.4).

4.4

Perspective

Chapter 1 outlined the alteration in the aims of the work carried out in this thesis from rather applied and specific to more theoretical and general. In this Section some of the factors responsible for this change will be elaborated. The reason for including this discussion in a chapter on methodology is that the change occurred not only in the nature of the questions that were addressed, but also in the way in which these were addressed and in the type of analysis that was considered appropriate to those questions.

The most important change in focus was brought about after the data from Experiments 1 and 2 had been analysed. In the literature on temporal discrimination, there were so many references to the work of Ferster and Skinner (1957) that I eventually decided to obtain a copy of "Schedules of Reinforcement" on inter-library loan. Initially, I was very disappointed to find that it contained little more than a collection of cumulative records of the responses of a handful of pigeons. No great theories were proposed, and there was very little speculation on anything. I struggled through it, trying to find why the book was included in the reference list of almost every subsequent paper on temporal discrimination. Only after a great deal of head scratching did it dawn on me that I was supposed to be interested in behaviour and that this book was crammed full of it. The cumulative records indexed the actual responses of actual subjects to their environment. No theory, other than that which proposes that behaviour is modified by its consequences, was necessary. Indeed, a theory that attempted to integrate all of the data would, at best, have been premature, and at worst, might have constrained the search for orderly relations between the variables under investigation. What "Schedules of Reinforcement" showed was what happened to behaviour under certain conditions. Behaviour was presented as an interesting topic in itself, and the lack of a complex unifying theory was no distraction from this.

A further influence that shaped the adoption of a behaviour analytic perspective in reporting the experiments in this Thesis was the positive reinforcement provided by the editor and reviewers of a journal to which I had submitted an account of Experiments 3 and 4 (Chapter 6). When looking for a place to publish this study I had gone to the library and read through the most recent editorials and statements of purpose in all of the journals that dealt with work on animal behaviour. The editorial in one of these, the Journal of the Experimental Analysis of Behavior (JEAB), seemed to stand out from the rest. Branch (1992) argued that what distinguished JEAB from others was its "... view that behavior is worthy of study in its own right and is not a mere reflection or index of processes occurring at some hypothetical level" (p1). What was more astonishing was his seemingly outrageous claim that direct demonstrations

of reliability and generality set higher standards than "mere" statistical significance. In JEAB, the results of statistical significance tests would remain as ancillary information.

To me, having had statistical significance set up as the central concern of research over the whole of my psychological career, having spent hours in discussion with statisticians searching for an appropriate test for my data and weeks subjecting data to test that were not really appropriate but were the closest we could get to appropriateness, this casual attitude to statistical significance was staggering. In fact, I didn't really believe it. When the manuscript was submitted, the statistics were left in. Indeed, even when, in provisionally accepting it for publication, the editor suggested that the statistics could, if I chose, be left out, I suspected some kind of trap. The statistics were left in and have been published (Gee, Stephenson, & Wright, 1994).

However, more important than the editor's peculiar ambivalence towards statistical information was his and the reviewers insistence on the inclusion of other types of information. They were not satisfied with the group means that had been given, but wanted data on individual subjects. They wanted plots showing the development of discrimination rather than rather than just of performance at asymptote. In essence, they wanted to see what subjects had actually done, not some distillation of behaviour that could never be traced back to the original data.

There are no inferential statistics in the chapters that follow. Almost as much work has gone into removing them as went into creating them in the first place. This is because I was forced into a more detailed examination of the responses of individual subjects on individual days rather than relying primarily on data that were averaged across subjects and across days. Averaged data are still present where appropriate, but a greater emphasis on original rather than derived data has highlighted the richness of the behaviour of the subjects, and uncovered effects that had previously been hidden.

5.0 EXPERIMENTS 1 AND 2

TEMPORAL DISCRIMINATION LEARNING OF OPERANT FEEDING IN GROUPS OF THICK-LIPPED GREY MULLET AND IN GROUPS OF GOLDFISH

5.1 EXPERIMENT 1

5.1.1

Introduction

In Chapter 2 it was suggested that recall ranching techniques might provide a solution to some of the problems faced in modern aquaculture. Reports by Abbott (1972), Balchen (1979), Fujiya et al. (1980), Hara (1988), Landless (1978), and Midling et al. (1987) show that recall ranching programs can be successful in controlling fish behaviour in the field, but there are certain disadvantages in the use sound stimuli (Bardach & Magnuson, 1980).

It was proposed that a method involving control by temporal contingencies might provide an alternative to reliance on acoustic cues. This proposal was derived from findings in three areas of research. Firstly, it has been shown that the behaviour of fish species in the wild is coordinated with regular environmental cycles such as the onset of dawn and dusk (Chapter 2, Section 2.3). Secondly, it has been shown that operant behaviour in fish may come under the control of fixed-interval schedules of reinforcement (Chapter 3, Section 3.3). And thirdly, it has been shown that rhythms of activity in fish may come under the control of light cycles and feeding schedules which have a period close to that of the solar cycle (Chapter 3, Section 3.5).

In Chapter 3, the possibility that schedules in which events recur with a 24-hr periodicity may have a particular status in the control of behaviour was discussed. Although it was suggested that evidence cited in support of separate processes may have been accorded too much weight, it seems reasonable to assume that an attempt to use temporally structured schedules in a field setting would be more likely to succeed if the schedule was in phase with the periodicity of the natural environment. In order for a ranching method that relied on the coordination of behaviour with the provision of food at particular times to bring the advantages of non-intensive culture, the intervals between feeds would have to be long enough to prevent the fish from simply remaining in the close vicinity of the food source. If feeds were reasonably widely spaced it is likely that fish would disperse and forage on naturally occurring food during the inter-food interval. This implies intervals of several hours. If these intervals were such that each day the food was available at different points in the 24-hr cycle (as would be the case with, for example, a 5-hr interval), then the discriminative task might be more difficult. Although the learning of a 5-hr interval might be possible, the only exogenous discriminative cue available would be the previous feed. If, on the other hand, the schedule was such that feeds occurred at the same time every day then each period of food availability would not only be predictable on the basis of its 24-hr periodicity, but also in relation to the light cycle, the tidal cycle, and with any other environmental or internal rhythms under the control of these. However, it should be noted that the above is pure speculation. It is not at all clear that control mediated by a range of stimuli would be any more effective than control mediated by a single stimulus class. More specifically, there is no empirical evidence that a schedule with a circadian period would be any more or less effective in the control of behaviour under field conditions.

Nevertheless, the chronobiological data collected under laboratory conditions suggest that rhythms of general activity in fish will come to anticipate regularly scheduled feeds, and the psychological data suggest that patterns of food reinforced operant responding in fish will show similar characteristics. What has yet to be determined is whether patterns of food reinforced operant responding will come to
anticipate the parameters of a schedule where the reinforcers are only available at times which recur at the same point in each successive 24-hr period. That is, whether the rhythms in general activity reported for fish maintained on a schedule where food is presented at a fixed time each day (e.g., Davis & Bardach, 1965) would be produced in the patterning of behaviour on which food was contingent. In the context of recall ranching, demonstrations that the level of general activity is sensitive to imposed temporal regularity would not be sufficient. Ranched fish would have to engage in behaviour specifically directed at obtaining food. Where the fish are dispersed, the food-directed behaviour required would be movement towards the location of the food dispenser. As food would be contingent on geographical position, this movement might be regarded as a class of operant. The question, then, is will the temporal coordination of general activity that has been reported in previous experiments generalise to the coordination of an operant?

In the experiments reported here, aquarium-housed mullet and goldfish were required to press a lever for food. In Experiment 1, a stage in which patterns of responding were recorded on a schedule where every press was reinforced was followed by stages in which the food dispenser was operational only at certain fixed times. The only predictive external cues programmed were the temporal regularity of the light cycle and feeding schedules. If the lever-press response came under the control of the temporal contingency then it would be expected that the rate during the period immediately preceding feeding periods would be higher than at other times. Further, if conditions at the time of a feeding period became positive discriminative stimuli then conditions at times distant from feeding periods would be expected to become negative discriminative stimuli. This negative property could be apparent in a comparison between the rate of responding during periods in the 24-hr cycle distant from the feeding times on the restricted feeding stages with equivalent periods on the stages where each lever press was reinforced.

5.1.2

Method

5.1.2.1 - Subjects. Four groups of ten fish were studied. Two groups consisted of thick-lipped grey mullet (*Chelon labrosus*, mean standard length 6.7 cm, *SD* 0.47 cm) obtained by netting from St. John lake, Cornwall. The other two groups consisted of goldfish (*Carassius auratus*, mean standard length 6.8 cm, *SD* 0.61) obtained from J & K Aquatics Ltd., Wellington, Somerset. Prior to these experiments the fish were not kept on any fixed feeding regime or used in any other experiments.

Goldfish are an ornamental cultivar of the cyprinid family. Feral populations usually inhabit shallow, densely vegetated pools with muddy bottoms and diversified shorelines (Lelek, 1987) and feed on a broad range of food types including plants, insect larvae, and plankton (Wheeler, 1978). As goldfish have no stomach, their capacity for storing food is limited. When food is continually available, they tend to feed for extended periods rather than taking distinct meals (Rozin & Mayer, 1961). Studies of the relation between the light cycle and the pattern of free feeding (Rozin & Mayer, 1961) and activity (Spoor, 1946) in goldfish have shown a measure of variability between individual subjects. Most are predominantly diurnal, but some display patterns that are predominantly nocturnal, while others show no fixed pattern at all.

Thick-lipped grey mullet are found in salt and brackish water on the coasts of Europe, the Mediterranean, and parts of North Africa. There is a commercial fishery for grey mullet in Northern Europe and in the Mediterranean, and they are particularly common close inshore in harbours, sandy bays, and estuaries. They feed either on the sea bed, where they sift mud and sand for organic matter, or on plankton at the surface. As an adaptation to this relatively poor diet, they have a thick-walled stomach and a very long intestine (Wheeler, 1978). There are no data available on general activity cycles in grey mullet, and the only report of response patterns under the continuous food-reinforcement of an operant found that, under natural light, rates

were highest in the late afternoon and early evening and lowest between midnight and dawn (Wright & Eastcott, 1982a).

5.1.2.2 - Apparatus. The experiment was housed in a laboratory that was isolated from main corridors and rarely used by other workers. The windows were covered with foil to block light from outside.

Each group of fish was housed in one of four glass aquariums (90 cm by 30 cm by 38 cm). The aquariums were screened off from each other with opaque plastic sheeting. The water was maintained at 20 °C and aerated and filtered using standard laboratory equipment. Cleaning of the aquariums took about 10 min and was carried out approximately once every 3 days, between 9:00 a.m. and 12:30 p.m. or 2:30 p.m. and 7:00 p.m. The precise time (within these limits) was varied.

Aquariums 1 and 2 contained goldfish, and Aquariums 3 and 4 contained mullet. The mullet were fed Ewos[®] Salmon Crumble (No. 4), and the goldfish were fed Hikari[®] staple fish diet (a floating fish food) in the "baby" pellet size.

A food dispenser controlled by a fish-activated lever was mounted at one end of each aquarium. One additional dispenser was mounted in a narrow space between the rows of aquariums. This additional dispenser was under the direct control of the computer system (see below), and operated in randomly spaced bursts of between 5 and 20 activations. This "decoy" dispenser was used to reduce the potential for any temporal regularity in the sound of dispensers operating in adjacent aquariums acquiring discriminative control. No food was provided by the decoy dispenser.

The control and recording system consisted of a BBC Model B microcomputer and an interface device. This allowed the designation of times during which activation of the lever would result in food being dispensed, and it recorded the time of occurrence of all lever activations. There was also a manual override facility to allow remote activation of the dispensers.

The layout of major items of equipment is shown in Figure 5.1.



Fig. 5.1. Schematic plan view of the major components of the apparatus. 1, 2, 3, and 4 - Aquariums, A - BBC Micro, B - Interface, C - Dispensers, D - Decoy dispenser

Lighting was provided by two, 15-W, fluorescent bulbs mounted directly above the aquariums. These were operated by a time switch that turned the lights on at 8:30 a.m. and off at 5:30 p.m. each day. In addition, an 11-W, incandescent bulb was sited between the fluorescent bulbs. This was left on continuously, providing lowlevel illumination even when the main lighting was off. A fixed daily light cycle was used in this experiment because Davis and Bardach (1965) suggest that this provides optimum conditions for the development temporally coordinated prefeeding behaviour. Light intensity at the water surface was 302 lx when the fluorescent bulbs were switched on and 12 lx when they were off.

5.1.2.3 - Design. The main components of the design were as follows. There was an initial baseline stage in which response patterns with no temporal reinforcement contingencies were recorded. Next there was a restricted feeding stage in which responses were reinforced only during specific periods, which occurred at the same times each day. There followed an extinction stage in which no responses were reinforced. This served two purposes: Reinforcement itself provides a discriminative stimulus for further reinforcement of lever pressing. Consequently, the

first trial in extinction shows the pattern of non-reinforced responding during the periods in which responses had been reinforced on the restricted feeding stage. The second function of the extinction stage was to monitor the persistence of any temporal discrimination over days in the absence of reinforcement. In the second restricted feeding stage, responses were again reinforced only during specific periods, but, in order to check that no uncontrolled factor had influenced responding associated with the periods chosen in the first restricted feeding stage, different feeding periods were used. A second extinction stage was then implemented for the same reasons as the first extinction stage. Finally, there was a second baseline stage in which the temporal contingencies were again removed in order to assess any persistent effects of exposure to the contingencies of the preceding stages. The full design is represented in Figure 5.2, and the procedure for each Stage is described below.



Fig. 5.2. A representation of the design and variations in the schedule of reinforcement over each Stage of Experiment 1. Baseline - continuous reinforcement of responses; A & a, B & b, C & c, D & d - fixed times in each 24-hr cycle (two 1-hr periods) during which either responses were continuously reinforced (Feed at:), or during which data were collected for comparison with feeding times, but responses were not reinforced (No-feed at:); Extinction - no responses reinforced. 5.1.2.4 - Procedure. The specific procedures used over each stage of Experiment 1 are described below.

Stage 1 - Lever training: In this Stage, the fish were trained to operate the lever by the method of successive approximation. The apparatus was set so that lever presses would activate the dispenser at any time, and twice per day, there was a 15min training session during which the experimenter operated the dispenser through the remote control. Whenever a subject fulfilled a criterion of proximity to the lever, a portion of food was dispensed. The criterion became gradually more stringent with each session. Initially, the dispenser was operated if any fish swam to within a few centimetres of the lever, but eventually only actual physical contact resulted in food. These sessions were run at times during the day that had been selected using a table of random numbers. The training stage continued until at least one fish in each of the aquariums was regularly activating the lever (4 weeks).

Stage 2 - First Baseline: In this stage of the experiment baseline response rates (with no temporal restrictions) were monitored for 6 weeks. Each lever press produced food at any time.

Stage 3 - First Restricted: Stage 3 involved restricting the time during which a lever press would be reinforced to only two, 1-hr periods in each 24 hrs. These periods were set at least 4 hr apart, at times when baseline response rates had been approximately equal and close to the daily mean for the preceding week. They were also chosen so as not to be coincident with the start of any peaks in baseline rates, and so that one "feeding" time occurred during photophase and the other during the scotophase. Two similar periods were also designated "non-feeding" times. These were to be used for comparison with the feeding times in assessing the effect of restricted feeding (see Chapter 4, Section 4.3), but did not have any programmed consequences for the subjects. The dispensers in Aquariums 1 and 3 were active during the same periods. The dispensers in Aquariums 2 and 4 were also active simultaneously, but at times different to those used for Aquariums 1 and 3. The times used are shown in Table 5.1.

Aquarium	Feeding times	Non-feeding times
1 & 3	2:30-3:30 & 11:45-12:45	15:00-16:00 & 22:45-23:45
2 & 4	5:45-6:45 & 15:15-16:15	2:15-3:15 & 12:00-13:00

Table 5.1Feeding and non-feeding times used in Experiment 1.

This stage continued for 17 weeks, by which time visual inspection of plots of responding suggested that all four aquariums had produced a stable pattern over several weeks.

Stage 4 - First Extinction: To obtain a record of lever pressing in the absence of reinforcement, the dispensers were disabled for 6 consecutive days.

Stage 5 - Second Restricted: The fifth stage involved the same procedure as the First Restricted feeding Stage, except that the times of feeding were exchanged. The two previous feeding times became non-feeding times, and the previous non-feeding times became feeding times. This was an additional control for the possibility that regular external events might become discriminative stimuli. This stage ran for 10 weeks.

Stage 6 - Second Extinction: This stage entailed another 6 day disablement of the dispensers.

Stage 7 - Third Restricted: In this stage the feeding schedule used in the Second Restricted Stage was reinstated until response patterns and rates were re-established (4 weeks).

Stage 8 - Second Baseline: The eighth stage involved a return to continuous reinforcement. The goldfish were maintained on this schedule for 4 weeks, and the mullet for 6 days. This stage was used to monitor any persistent effects of experience with temporal restrictions on responding under continuous reinforcement.

Data were collected continuously, but a measure of response rate was calculated by grouping these data into consecutive 15 min time bins. This measure of rate was used as a basis for all subsequent analysis.

During the experiment an error in the programme controlling the times during which the dispensers reinforced a lever press was discovered. The effect of this error was to alter the schedule on Stage 3 (First Restricted) such that the probability of reinforcement being delivered during each feeding time was as shown in Table 5.2.

Table 5.2.

Probability of responses being reinforced during feeding times on the First Restricted Stage.

Aquarium	Feeding time	Probability of reinforcement
1 & 3	2:30-3:30	1 in 4
1 & 3	11:45-12:45	3 in 4
2 & 4	5:45-6:45	2 in 4
2 & 4	15:15-16:15	4 in 4

This was a considerable deviation from the original design, but its effect was to reduce the number of trials and so make temporal discrimination more difficult. With this in view, a decision was made to continue the experiment with the error uncorrected. In order to maintain the balance of the design, and to determine the extent to which the greater variation in response rates across days associated with the lower probability feeding times (see Section 5.1.3) was a consequence of their occurring exclusively during the scotophase, the programme was modified for the Second Restricted Stage. The same overall probabilities were used, but the higher probability periods were those that occurred during scotophase. The altered probabilities are shown in Table 5.3.

Table 5.3

Aquarium	Feeding time	Probability of reinforcement
1 & 3	15:00-16:00	l in 4
1 & 3	22:45-23:45	3 in 4
2 & 4	12:00-13:00	2 in 4
2 & 4	2:15-3:15	4 in 4

Probability of responses being reinforced during feeding times on the Second Restricted Stage.

5.1.3

Results and Discussion

The results are presented and discussed for each of the aquariums in turn. For the goldfish, the data analysed are taken from the final 12 days on each of the baseline and restricted stages, and from the 6 days on the extinction stages. For the mullet, the data are taken from the final 12 days on the First Baseline and on both Restricted Stages, and from the 6 days on the Second Baseline and both Extinction Stages. In the tables of results that follow, the four daily time periods are referred to (in chronological order) as T1, T2, T3 and T4 regardless of their actual time of occurrence or of their status as feeding or non-feeding times. Summary plots of rate over successive 24-hr periods, averaged over each analysed day on each stage, as well as plots taken from each day that contributed to the summary plots, are given.

5.1.3.1

Aquarium 1 (goldfish).

The response rate over 24 hrs, averaged over 12 days on the Baseline and Restricted Stages, and over 6 days on the Extinction Stages, is shown in Figure 5.3.



Fig. 5.3. Aquarium 1. Mean and standard deviation of lever presses per 15 min. The data are averaged over 12 days on the two Baseline and two Restricted Stages, and over 6 days on the two Extinction Stages. The vertical bars (F) indicate feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

The number of responses in the 30 min prior to the feeding and non-feeding times over each stage of Experiment 1 are presented in Table 5.4.

Table 5.4

		Time (Probability of reinforcement when a feeding time)				
Stage		T1 (1 in 4)	T2 (3 in 4)	T3 (1 in 4)	T4 (3 in 4)	
First Baseline	М	25.4	31.4	26.6	23.7	
	SD	27.2	25.5	24.9	21.9	
First Restricted	М	33.3	149.2	11.1	10.8	
	SD	24.0	54.8	24.0	24.3	
First Extinction	М	19.5	99.5	3.8	6.3	
	SD	30.8	47.9	4.5	9.3	
Second Restricted	М	8.8	13.2	38.5	79.9	
	SD	15.7	10.2	18.9	18.1	
Second Extinction	М	0.7	18.2	25.2	49.0	
	SD	0.5	38.7	38.3	38.0	
Second Baseline	М	33.8	17.7	48.6	37.5	
	SD	12.2	19.1	23.1	12.6	

Aquarium 1. Number of responses in the 30 min prior to the feeding (figures underlined) and non-feeding times over each stage of Experiment 1.

Note. Values averaged over the last 12 days of First Baseline, First Restricted, Second Restricted, and Second Baseline Stages, and over the 6 days of First Extinction and Second Extinction Stages. The response rates over each day that contributed to the averaged response rates of Figure 5.3 and Table 5.4 are shown in Figures 5.4 to 5.9.



Fig. 5.4. Aquarium 1. Lever presses per 15 min over each of the last 12 days on the First Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.5. Aquarium 1. Lever presses per 15 min over each of the last 12 days on the First Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.6. Aquarium 1. Lever presses per 15 min over each of the 6 days on the First Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.7. Aquarium 1. Lever presses per 15 min over each of the last 12 days on the Second Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.8. Aquarium 1. Lever presses per 15 min over each of the 6 days on the Second Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.9. Aquarium 1. Lever presses per 15 min over each of the last 12 days on the Second Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

Figure 5.3 shows that, when averaged over the 12 days of the First Baseline Stage, there was a fairly flat distribution of lever pressing activity over the 24-hr cycle. This is reflected in the similarity of the response rates prior to T1, T2, T3 and T4 given in Table 5.4. However, Figure 5.4 shows that, on each of the days that contributed to the average rates shown in Figure 5.3, periods with little or no responding were interspersed with bouts or extended periods of variable response rates. No systematic temporal patterning, either in relation to the light cycle, or across days, is discernible.

The averaged rates on the First Restricted Stage (Figure 5.3) show a higher rate of responding prior to the feeding times (T1 and T2) than prior to the non-feeding times (T3 and T4). This was particularly evident prior to T2 (a feeding time with a probability of reinforcement of 3 in 4), but an acceleration in responding is also apparent prior to T1 (a feeding time with a probability of reinforcement of only 1 in 4). The sharp acceleration in rate that preceded T2 is coincident with the start of the photophase. Response rates rose slightly during the feeding times, and fell to a level similar to that observed on the First Baseline Stage within 2 hr of their end. The daily plots of responding on this stage (Figure 5.5) show a fairly constant pattern associated with feeding time T2, but a measure of variability at other times in the 24-hr cycle. At most times on days 3, 4, and 10, the response rate was higher than on the other days. Particularly noteworthy on these days are the accelerations associated with feeding time T1, and the continuation in responding past feeding time T2. It is likely that much of the variability across days is related to whether or not lever presses were reinforced during particular feeding times. Unfortunately, due to the error in the controlling programme, information on whether food was dispensed during specific feeding times is not available.

There was an increase in response rate between about 3:00 p.m. and 4:30 p.m. on day 3 of the Second Restricted Stage (Figure 5.7). 3:15 p.m. to 4:15 p.m. was a feeding time (T4) for Aquarium 2 on this stage. It is possible that the subjects learned to associate the sound of the dispenser in their own aquarium with food and that,

despite the use of the decoy dispenser (see Section 5.1.2.2), this association may have generalised to the sound of a dispenser operating in an adjacent aquarium.

There was no evidence for this effect operating at any other time for any of the aquariums on any other stage. In some cases (e.g., feeding time T4, Aquarium 2, First Restricted Stage, Figure 5.10), any control by the sound of a dispenser in an adjacent aquarium may have been masked by an increase in response rate that continued through to a feeding time. However, in other instances the rate in an aquarium remained low and constant despite considerable dispenser activity in an adjacent aquarium. For example, feeding time T1 was between 2:30 a.m. and 3:30 a.m. in Aquarium 2 on the Second Restricted Stage, but in Aquarium 1 there was a slight decrease in the average response rate at this time (Figure 5.3). It is possible that the sound of adjacent dispensers was only effective as an eliciting stimulus when presented within a few hours of a feeding time.

In Figure 5.3, the pattern of responding associated with T2 (the more frequently reinforced feeding time on the preceding stage) on the First Extinction Stage was similar to that on the First Restricted Stage. The main differences are a reduction in rate of about one third, an increase in variability, and that there is no evidence of responding persisting in the complete absence of reinforcement at T1. The averaged plot is a fair representation of the data from its constituent days (Figure 5.6), although from these it can be seen that the reduction in rate was a function of a decline over days which commenced only on day 4.

The most striking feature of responding over this stage was the rapidity with which it ceased following the end of what had been feeding time T2 on the previous stage. On the Restricted Stages, the end of a feeding time could be discriminated by the failure of responses to result in the noise associated with the delivery of food, and in the cessation of the delivery of food itself. On the extinction stages the fall in rate occurred in the absence of any such changes.

When the feeding and non-feeding times were interchanged on the Second Restricted Stage, the pattern of responding again showed higher rates prior to feeding times T3 and T4 than prior to non-feeding times T1 and T2. Figure 5.3 shows that the averaged rate associated with the more frequently reinforced feeding time (T4) was higher than that associated with the less frequently reinforced feeding time (T3). The plots of responding on individual days during this stage (Figure 5.7) are smoother than their equivalents for the First Restricted Stage (Figure 5.5). Although the accelerations in rate preceding the more frequently reinforced feeding time commence at about the same relative point (around 4 hr in advance), the accelerations are more gradual and do not attain the same terminal rate as on the First Restricted Stage. There are clear accelerations in advance of the less frequently reinforced feeding time (T3) on days 5, 10, 11, and 12. These are followed by sharp decelerations at the end of T3. On days where there was a peak in responding during T3 (days 1, 5, 9, 10, 11, and 12), there follows a period with very low rates before an acceleration in advance of T4. On most of the other days there appears to be a moderate increase in rate in advance of T3 that carries on through to T4. Again, this variability across days is probably a function of the availability of reinforcement at specific feeding times, but this can not be verified in the absence of data on which specific periods were reinforced and which were not.

There is a suggestion of the persistence of temporally coordinated responses on the Second Extinction Stage in Figure 5.3, but the patterns of responding are not particularly pronounced. The picture is clarified by the plots of responding on individual days given in Figure 5.8. There was a substantial rate of responding that had built up prior to the preceding stage's less frequently reinforced feeding time (T3) on day 1. This responding continued through to the time of the offset of the photophase, at which point there was a sharp decline in rate, followed by a gradual acceleration the continued through to the time that had been feeding time T4. There was little responding past this point (early on day 2), and on all the other days of this stage there was little responding associated with T3. There were moderate

accelerations in rate associated with T4 that declined over days 2, 3, and 4. There were few responses at any time on days 5 and 6.

When the restrictions on food availability were removed (Second Baseline Stage) the differences between the four time periods was attenuated (Table 5.4), and the averaged pattern and rate of responding (Figure 5.3) were similar to those of the First Baseline Stage. There was no evidence of exposure to restricted feeding regimes altering the averaged free-feeding response patterns of the group, but the daily plots for the Second Baseline Stage (Figure 5.9) show that, in comparison to the First Baseline Stage (Figure 5.4), responding was spread slightly more evenly over the 24-hr cycle.

Taken as a whole, the results for this group are consistent with the establishment of an temporally discriminated operant. The baseline stages produced relatively undifferentiated averaged rates of responding over the 24-hr cycle. The two stages that imposed temporal contingencies produced accelerations in rate prior to the feeding times, and there were instances of these patterns persisting in the extinction stages.

The effect of the limits on feeding opportunities imposed during the restricted stages was an acceleration in rate, not only during feeding times, but for a period of several hours before them. This effect was most robust at the feeding time with the higher probability of reward. These accelerations are reminiscent of the performance goldfish (Rozin, 1965) and other species (e.g. Dews, 1965a, 1978; Ferster & Skinner, 1957; Lejeune, Richelle, Mantanus, & Defays, 1980) on fixed-interval schedules of reinforcement. On cumulative response records these accelerations would appear as scallops.

There was little evidence of non-feeding times acquiring the function of negative discriminative stimuli. During the restricted stages, rates at points in the 24-hr cycle that were distant from feeding times did fall below the rates emitted during the baseline stages, and in each case the rate of responding prior to non-feeding times on the restricted stages was lower than during the equivalent time period on the baseline

stages. These differences were not large, however. Perhaps, because the baseline rates were themselves rather low, a "floor effect" may have operated. That is, the rates on baseline were so low that it would be difficult for them to drop significantly.

A factor that might have worked against finding differences between the feeding and the designated non-feeding times is evident in the panel of Figure 5.3 that shows responses rates on the Second Restricted Stage. In some cases, the feeding and nonfeeding times may have been too close together. For example, the long acceleration that preceded feeding time T3 commenced before non-feeding time T2. This will have increased the mean rate for T2. Despite the possibility that the rate during non-feeding times may have been contaminated with responses under the control of the contingency of an impending feeding time, the figures in Table 5.4 are consistently higher for feeding times than for non-feeding times.

In the averaged plots (Figure 5.3) for both restricted stages, the averaged response rate prior a feeding time appeared to be a function of the probability of reinforcement. Higher rates preceded higher probability feeding times. However, the plots of responding on the individual days that were combined in the averaged plots show that this was largely due to greater variability in response rate across days associated with the less frequently reinforced feeding times (see General Discussion, Section 5.3). Despite this variability, discrimination of the less frequently reinforced feeding times is apparent. It is noteworthy that the subjects learned to discriminate these feeding times at all, given the probability that responses during these times would be reinforced was only 1 in 4.

There was little evidence of responding under the control of the lower probability feeding time on the extinction stages. In rats and in pigeons, responding on schedules where only a proportion of trials are reinforced, control by the discriminative stimulus is usually found to be more resistant to extinction than on schedules where all trials are reinforced (Bitterman & Schoel, 1970). This "partial reinforcement effect" (PRE) does not seem to have occurred in the present case. There may be several reasons for this. The schedule for the less frequently reinforced feeding time may have been

"stretched" too far to maintain responding in extinction. Experiments on the PRE have usually involved schedules where at least half the trials are reinforced (Bitterman & Schoel, 1970). Even if the present schedule had been rich enough to support the PRE, it may be that the reinforced response rate was so low that a slight fall during extinction resulted in masking by a non-timed, background rate of responding. Alternatively, the lack of a PRE may be a consequence of the species and the trial spacing used. Experiments on operant conditioning in the African mouthbreeder (*Tilapia macrocephala*) (Gonzalez, Behrend, & Bitterman, 1965; Longo & Bitterman, 1960) and in goldfish (Schutz & Bitterman, 1969), suggest that fish may not be subject to the PRE when trials are widely spaced.

Despite the limited amount of responding associated with the lower probability feeding times, the key feature of the pattern of responding on both extinction stages was that, although the magnitude of the response reduced over days, the temporal pattern remained relatively fixed. On each of the first 5 days of the First Extinction Stage, and on each of the first 4 days of the Second Extinction Stage, accelerations in response rates associated with the period that had been the more frequently reinforced feeding time commenced at approximately the time that they had commenced on the preceding restricted stage. Further, these elevated response rates started to fall at, or just before, the end of what had been the preceding stage's feeding time. Once the rate had started to fall it dropped close to zero within 2 hr. In itself, this pattern suggests temporal discrimination, and its persistence in the absence of food over several days suggests that the coordination of responding was not entirely dependent on any simple homoeostatic or metabolic process such as increasing hunger or the emptying rate of the gut.

The acceleration in rate that preceded T2 on the First Restricted and First Extinction Stages commenced at the onset of the photophase. An accelerating, rather than constant, rate suggests temporal discrimination, but it is not possible to determine which features of the light and/or feeding schedules were controlling this behaviour. This problem will be explored further in Experiment 2.

5.1.3.2

Aquarium 2 (goldfish).

The response rate over 24 hrs, averaged over 12 days on the Baseline and Restricted Stages, and over 6 days on the Extinction Stages, is shown in Figure 5.10.



Fig. 5.10. Aquarium 2. Mean and standard deviation of lever presses per 15 min. The data are averaged over 12 days on the two Baseline and two Restricted Stages, and over 6 days on the two Extinction Stages. The vertical bars (F) indicate feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

The number of responses in the 30 min prior to the feeding and non-feeding times over each stage of Experiment 1 is presented in Table 5.5.

Table 5.5

		Time (Probability of reinforcement when a feeding time)				
Stage		T1 (4 in 4)	T2 (2 in 4)	T3 (2 in 4)	T4 (4 in 4)	
First Baseline	М	38.7	19.2	25.1	45.7	
	SD	29.6	23.4	25.3	31.2	
First Restricted	М	21.2	105.1	20.6	162.6	
	SD	28.2	32.4	20.0	39.2	
First Extinction	М	11.8	25.3	2.7	67.3	
	SD	29.0	60.1	3.6	62.9	
Second Restricted	М	111.8	6.3	<u>59.3</u>	6.4	
	SD	24.0	5.8	33.8	6.7	
Second Extinction	М	22.7	16.3	20.2	0.0	
	SD	30.8	40.0	31.5	0.0	
Second Baseline	М	43.5	28.7	20.9	39.6	
	SD	13.5	20.5	27.7	25.1	

Aquarium 2. Number of responses in the 30 min prior to the feeding (figures underlined) and non-feeding times over each stage of Experiment 1.

Note. Values averaged over the last 12 days of First Baseline, First Restricted, Second Restricted, and Second Baseline Stages, and over the 6 days of First Extinction and Second Extinction Stages. The response rates over each day that contributed to the averaged response rates of Figure 5.10 and Table 5.5 are shown in Figures 5.11 to 5.16.



Fig. 5.11. Aquarium 2. Lever presses per 15 min over each of the last 12 days on the First Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.12. Aquarium 2. Lever presses per 15 min over each of the last 12 days on the First Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.13. Aquarium 2. Lever presses per 15 min over each of the 6 days on the First Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.14. Aquarium 2. Lever presses per 15 min over each of the last 12 days on the Second Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.15. Aquarium 2. Lever presses per 15 min over each of the 6 days on the Second Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.16. Aquarium 2. Lever presses per 15 min over each of the last 12 days on the Second Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

Figure 5.10 and Table 5.5 show that the averaged response patterns from Aquarium 2 were similar to those from Aquarium 1 on each stage of the experiment. The average rate of responding on the First Baseline Stage assumed a more or less constant low value, and this pattern was resumed during Second Baseline Stage. The feeding schedule imposed during the restricted stages altered the pattern of responding, and (at least for T4 on the First Extinction Stage) these altered patterns persisted in the absence of reinforcers.

Response patterns on the individual days that were used in constructing the averaged plots were also similar to those from Aquarium 1. Figures 5.11 and 5.16 (which show responding on the 12 days of the First and Second Baseline Stages respectively) are almost identical to their equivalents for Aquarium 1 (Figures 5.4 and 5.9). Figure 5.12 (First Restricted) shows that the start of accelerations in response rate prior to feeding times were not coincident with changes in the light cycle. The patterns of responding associated with the lower probability feeding time (T2) were similar to those associated with the consistently reinforced feeding time (T4). The only difference was the slightly sharper accelerations in rate that preceded the latter, and the more variable duration of the elevated rate of responding that followed the end of T2. On days 6, 7, and 9, the response rate fell considerably within an hour of the end of the feeding period, whereas on days 1, 2, 4, and 10 the rate fell more gradually (over 3 or 4 hr). It is likely that these differences were related to particular instances of the reinforcement (or lack of it) of this feeding time, but data are not available to evaluate this hypothesis. However, there were no instances of elevated rates of responding continuing through to the second daily feeding time (T4). The schedule was such that on half of the days shown there will have been no reinforcement at T2, and the finding that feeding times were separated by a period of little or no responding suggests that even under these conditions, the feeding time was discriminated.

Figure 5.13 (First Extinction) also shows a similar pattern to its equivalent from Aquarium 1, with responses associated with the lower probability feeding time extinguishing rapidly. There was some responding in advance of this feeding time on

day 2, but little on subsequent days. For the consistently reinforced feeding time there was evidence of temporally coordinated responding on days 1, 2, 3, and 5, but very few responses were emitted at any time on days 4 and 6.

The daily plots for the Second Restricted Stage (Figure 5.14) are similar to those for the First Restricted Stage (Figure 5.12), although responding associated with the less frequently reinforced feeding time on the Second Restricted Stage attained a slightly lower rate than for the equivalent feeding time on the First Restricted Stage. There is no obvious reason for this, but it maybe related to the fact that, on the Second Restricted Stage, the acceleration in rate that preceded this feeding time commenced at the onset of the photophase. If the transition in the light cycle functioned as a direct discriminative cue, it may have interfered with the rate of responding under the control of the temporal contingency. This possibility is discussed in detail in Chapter 7.

In the Second Extinction Stage (Figure 5.15), there was responding associated with what had been the preceding stage's consistently reinforced feeding time (T1) on days 1, 2, and 4, but the pattern of these responses was less distinct than for the equivalent time on the First Extinction Stage. The response patterns on day 4 are particularly interesting, as there was a sharp acceleration in rate that terminated at the precise time that had been the start of feeding time T1 on the preceding stage. Responding continued at a relatively constant rate until 6:00 a.m. At this time there was a sharp reduction in rate, and very few responses were then emitted until approximately 10:00 a.m. (1.5 hr after the onset of the photophase). At this time the rate of responding started a gradual acceleration that peaked at a time that was coincident with what was the start of the less frequently reinforced feeding time (T3) on the preceding stage. This rate was sustained at a more or less constant level for a further 105 min, then returned to zero for the rest of the day. This pattern suggests that temporal discrimination had persisted over the preceding 3 days of the stage, even though the performance of the subjects produced no evidence for the discrimination of T1 on day 3, or of T3 on any of the 3 preceding days. This highlights the problem of

distinguishing between performance and capacity in discrimination experiments, and will be discussed further in Chapter 8.

The maximum response rates on the Second Extinction Stage were lower than those on the First Extinction Stage. A similar, but less acute, difference between the First and Second Extinction Stages was evident in Aquarium 1. It is possible that the subjects learned more rapidly that lever pressing would not be reinforced following their experience on the First Extinction Stage.

As with Aquarium 1, the proximity of the feeding and non-feeding times may have attenuated any differences between them on the First Restricted Stage. The acceleration in rate prior to feeding times T2 and T4 commenced before the nonfeeding times T1 and T3. This problem does not seem to have occurred on the Second Restricted Stage.

5.1.3.3

Aquarium 3 (mullet).

The response rate over 24 hrs, averaged over 12 days on the First Baseline and the two Restricted Stages, and over 6 days on the Second Baseline and the two Extinction Stages, is shown in Figure 5.17.

The number of responses in the 30 min prior to the feeding and non-feeding times over each stage of Experiment 1 is presented in Table 5.6.



Fig. 5.17. Aquarium 3. Mean and standard deviation of lever presses per 15 min. The data are averaged over 12 days on the two Restricted Stages and on the First Baseline Stage, and over 6 days on the two Extinction Stages and on the Second Baseline Stage. The vertical bars (F) indicate feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

Table 5.6

		Time (Probability of reinforcement when a feeding time)				
Stage	(1	T1 (1 in 4)	T2 (3 in 4)	T3 (1 in 4)	T4 (3 in 4)	
First Baseline	М	0.1	0.3	0.0	36.0	
	SD	0.3	0.6	0.0	36.2	
First Restricted	М	0.0	8.8	0.2	0.0	
	SD	0.0	6.5	0.4	0.0	
First Extinction	М	1.0	1.5	0.0	0.0	
	SD	1.3	1.2	0.0	0.0	
Second Restricted	М	0.8	0.3	0.0	4.0	
	SD	2.1	0.5	0.0	4.1	
Second Extinction	М	0.0	0.0	0.0	4.0	
	SD	0.0	0.0	0.0	7.9	
Second Baseline	М	0.2	0.7	30.7	20.5	
	SD	0.4	0.5	35.1	42.0	

Aquarium 3. Number of responses in the 30 min prior to the feeding (figures underlined) and non-feeding times over each stage of Experiment 1.

Note. Values averaged over the last 12 days of First Baseline, First Restricted, and Second Restricted Stages, and over the 6 days of Second Baseline, First Extinction, and Second Extinction Stages.
The response rates over each day that contributed to the averaged response rates of Figure 5.17 and Table 5.6 are shown in Figures 5.18 to 5.23.



Fig. 5.18. Aquarium 3. Lever presses per 15 min over each of the last 12 days on the First Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.19. Aquarium 3. Lever presses per 15 min over each of the last 12 days on the First Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.20. Aquarium 3. Lever presses per 15 min over each of the 6 days on the First Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.21. Aquarium 3. Lever presses per 15 min over each of the last 12 days on the Second Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.22. Aquarium 3. Lever presses per 15 min over each of the 6 days on the Second Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.23. Aquarium 3. Lever presses per 15 min over each of the 6 days on the Second Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

Figure 5.17 and Figure 5.18 show that, in contrast to the largely undifferentiated patterns produced by the goldfish, this group responded almost exclusively during the scotophase on the First Baseline Stage. Responding commenced at, or just in advance of, the start of the lights off period. On most days responding rapidly reached a peak rate that continued for 1 or 2 hr. There usually followed a period of little or no responding, and then a second (smaller) period of activity. Responding ceased soon after midnight, and remained virtually absent for the next 16 hr. This pattern is reflected in Table 5.6, with responding recorded at T4 only.

On the First Restricted Stage (Figure 5.19) the pattern of responding altered markedly, with nearly all responses emitted during the photophase. There was no responding associated with the less frequently reinforced feeding time (T1, probability 1 in 4), or with either of the non-feeding times. Indeed, there were few responses emitted at any time other than during the 2 hr immediately preceding the more frequently reinforced feeding time (T2, probability 3 in 4), and during feeding hour itself. The rate increased sharply during T2, and fell back to near zero within 1 hr of its offset.

On the Second Restricted Stage (Figure 5.21) the pattern of responding was similar to that on the First Restricted Stage, with a small increase in rate that commenced about 2 hr in advance of the more frequently reinforced feeding time (T4). On day 5 there was a second peak in response rate during the less frequently reinforced feeding time (T3), but there were no responses immediately preceding this feeding time, and no responding associated with T3 on any other day. Although there were high response rates during the more frequently reinforced feeding times, the rates immediately prior to the feeding times were low compared with the goldfish. These low rates of nonreinforced responding could be interpreted as showing poorer temporal discrimination. Certainly, responding that anticipates feeding times was far more obvious in the goldfish. However, the relationship between absolute response rate and discrimination is far from clear. Discrimination is usually indexed by relative response rates. That is, a subject is said to discriminate a stimulus when response

rates in its presence are different to those when it is not present. Rather than reflecting poor temporal discrimination, the lack of lever pressing at times other than immediately preceding a feeding time might be an indication of superior discrimination. The ambiguity inherent in the use of performance measures as indices of discriminative capacity is discussed further in the General Discussion (Section 5.3) and in Chapter 8.

There was a near absence of responding during the lower probability feeding times. This may have been because the mullet grouped responses into distinct periods, even when food was continuously available on the First Baseline Stage. When the temporal contingency was introduced they may have failed to respond during the lower probability feeding times because these periods were outside of their normal feeding period. If no responses were emitted during these feeding times, no responses would be reinforced. This problem will have been compounded by the fact that there was only a 1 in 4 probability that responses would be reinforced on any particular day. Shaping of the temporal discrimination was not carried out in this experiment. Another possibility, also suggested by their performance on the First Baseline Stage, is that they were satiated by a single daily feeding period. The majority of responses on the First Baseline Stage were emitted over a 2-hr period. On the restricted stages, reinforcement was only available during 1-hr periods, but the rate of responding during the more frequently reinforced feeding times was higher than the peak rate on the First Baseline Stage.

On the extinction stages there was very little responding at any time. However, Figures 5.20 and 5.22 show that most of the responses that were recorded occurred close to the time that had been the more frequently reinforced feeding time on the preceding stage. It is not possible to determine whether this indicates poorer temporal discrimination, or greater sensitivity to the schedule. For example, on the first day of the Second Extinction Stage (Figure 5.22) there was an acceleration in response rate that immediately preceded what would have been the more frequently reinforced feeding time on the preceding stage. The rate then dropped back to near zero within

15 min of what would have been the start of the feeding time. On the one hand, this could be taken as evidence of very precise temporal control. On the other hand, the low rate of responding might be taken to suggest that the temporal contingency was only weakly conditioned. However, the notion of "strength of conditioning" is necessarily relative, and is usually used within subjects to compare control associated with two or more stimuli, or with one stimulus under different conditions. In the present case, the rate of nonreinforced responding was low in comparison with the rate of reinforced responding on the preceding stage, and in comparison with the performance of goldfish on a similar schedule. To compare rates of reinforced with nonreinforced responding, and to compare the absolute response rate of mullet with that of goldfish, would not be meaningful in this context. Due to these problems, at least two contradictory interpretations of the performance of the mullet are possible. The first is that temporal control was only weakly established, and that this resulted in low response rates and rapid extinction. The second is that the responses of the mullet were under close control of the schedule, with very little generalised control acquired by times preceding the feeding period, and low response rates when responding was no longer reinforced. It is not possible to choose between these alternatives on the basis of the present data.

The pattern of responding on the Second Baseline Stage (Figure 5.23) was different to that on the First Baseline Stage (Figure 5.18). On each day there were several peaks in response rate that were separated by variable intervals with no responding. As on the First Baseline, most responses were made during the first half of the scotophase. Unlike the First Baseline however, there were also peaks in activity during the photophase. These occurred on all except the first day. It might be that this increase in activity during the lights-on period resulted from experience of daytime feeding on the restricted stages. This experience may have modified a preintervention bias towards responding only during the dark period. Presumably mullet are more vulnerable to predation by birds when feeding at the surface in daylight. Phylogenetic and ontogenetic (these subjects were obtained from the wild) contingencies may have shaped avoidance of daylight surface feeding. This avoidance

may have extinguished over the course of the experiment, as daylight feeding was reinforced on the restricted stages, and birds were excluded from the laboratory. Alternatively, the possibility of a maturational change in feeding patterns can not be ruled out.

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5.1.3.4

Aquarium 4 (mullet).

The response rate over 24 hrs, averaged over 12 days on the First Baseline and the two Restricted Stages, and over 6 days on the Second Baseline and the two Extinction Stages, is shown in Figure 5.24.



Fig. 5.24. Aquarium 4. Mean and standard deviation of lever presses per 15 min. The data are averaged over 12 days on the two Restricted Stages and on the First Baseline Stage, and over 6 days on the two Extinction Stages and on the Second Baseline Stage. The vertical bars (F) indicate feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

The number of responses in the 30 min prior to the feeding and non-feeding times over each stage of Experiment 1 is presented in Table 5.7.

Table 5.7

Aquarium 4. Number of responses in the 30 min prior to the feeding (figures underlined) and non-feeding times over each stage of Experiment 1.

		(Probabili	Tin ty of reinforcen	me nent when a fee	ding time)
Stage		T1 (4 in 4)	T2 (2 in 4)	T3 (2 in 4)	T4 (4 in 4)
First Baseline	M	0.0	0.0	0.2	1.0
	SD	0.0	0.0	0.4	2.9
First Restricted	M	0.0	<u>0.0</u>	0.0	<u>2.2</u>
	SD	0.0	<u>0.0</u>	0.0	<u>2.4</u>
First Extinction	M	0.0	0.0	0.0	2.2
	SD	0.0	0.0	0.0	1.3
Second Restricted	M	<u>0.0</u>	0.0	<u>0.3</u>	0.1
	SD	<u>0.0</u>	0.0	0.5	0.3
Second Extinction	M	0.0	0.0	0.5	0.0
	SD	0.0	0.0	1.2	0.0
Second Baseline	M	0.0	0.0	27.5	43.2
	SD	0.0	0.0	25.6	32.6

Note. Values averaged over the last 12 days of First Baseline, First Restricted, and Second Restricted Stages, and over the 6 days of Second Baseline, First Extinction, and Second Extinction Stages. The response rates over each day that contributed to the averaged response rates of Figure 5.24 and Table 5.7 are shown in Figures 5.25 to 5.30.



Fig. 5.25. Aquarium 4. Lever presses per 15 min over each of the last 12 days on the First Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.26. Aquarium 4. Lever presses per 15 min over each of the last 12 days on the First Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.27. Aquarium 4. Lever presses per 15 min over each of the 6 days on the First Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.28. Aquarium 4. Lever presses per 15 min over each of the last 12 days on the Second Restricted Stage. The vertical bars indicate the feeding times. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.29. Aquarium 4. Lever presses per 15 min over each of the 6 days on the Second Extinction Stage. The broken-lined vertical bars indicate the feeding times on the immediately preceding stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.



Fig. 5.30. Aquarium 4. Lever presses per 15 min over each of the 6 days on the Second Baseline Stage. The lighting regime (main lights on at 8:30 a.m. and off at 5:30 p.m.) is indicated by the horizontal bar at the top.

Figures 5.24 and 5.25 show that, on the First Baseline Stage, responding was almost exclusively confined to the scotophase. There was period of responding that commenced either at, or just before, the offset of the photophase. This was similar to the pattern observed in Aquarium 3. However, on days 6 to 12 there was also a smaller peak in response rate associated with the offset of the scotophase. This latter feature commenced 1 or 2 hr in advance of, and finished soon after, the start of the photophase. In itself, this pre-dawn activity suggests temporal discrimination, as it occurred in advance of a temporally-fixed change in the lighting conditions.

On the First Restricted Stage there was some responding associated with the more frequently reinforced feeding time (T4, always reinforced), but this only reached a low rate in comparison with that observed in Aquarium 3. Figure 5.26 shows moderate rates on days 6 and 12, but very few responses on other days. However, unlike the First Baseline, those responses that were emitted occurred during the photophase. There was little evidence of responding associated with the less frequently reinforced feeding time.

There was very little responding at any time on either the First Extinction Stage (Figure 5.27), Second Restricted Stage (Figure 5.28), or Second Extinction Stage (Figure 5.29). There was no obvious reason for the failure of this group to respond during the consistently reinforced feeding time on the Second Restricted Stage, or for the low rate of responding during the equivalent feeding time on the First Restricted Stage. It could be that the absence of discriminative training would account for the failure to respond during the consistently reinforced feeding time on the Second Restricted Stage, and the partial reinforcement of the lower probability feeding times on both restricted stages will have further reduced the probability of responses being reinforced at the appropriate time. However, these factors can not have affected performance at T4 on the First Restricted Stage. Responses were reinforced at the appropriate time, but they were emitted at a low rate (compared to rates during feeding times in Aquarium 3).

There was responding on the Second Baseline Stage (Figure 5.30), but unlike the First Baseline Stage, this occurred almost exclusively during the photophase. On most days responding commenced at about 10:00 a.m., and continued at a fairly low but stable rate until about 6:00 p.m. As with Aquarium 3, it might be that this change was caused by experience of temporal contingencies modifying the subject's pre-intervention behaviour patterns, but the possibility of a maturational change remains.

5.1.4

Discussion

Although the results from Aquarium 4 provided little evidence of learned temporal discrimination of operant responding, there were some aspects of the data from the other subject groups in Experiment 1 that were consistent with this phenomenon. However, it is not clear which interval was under discrimination. For example, on the First Restricted Stage in Aquarium 1 the discrimination of T2 may have been based on the 23-hr interval between successive T2s, on the interval between T1 and T2, between the start of the scotophase and T2, or simply between the start of the photophase and T2. It is also possible that the regular light cycle provided a direct discriminative cue for the availability of food. In Aquarium 1 the appearance of anticipation could have been due to an acceleration in response rate under the direct control of the daily change in illumination. This seems an unlikely explanation for the response patterns observed in Aquariums 2 and 3, as the accelerations prior to their feeding times commenced several hours after changes in the light cycle. But even here, if, as is common in fixed-interval schedules, responding commenced after a pause, it is possible that these changes functioned as the start of the discriminated interval.

A light cycle was used in Experiment 1 because Davis and Bardach (1965) suggested that it would provide the optimum conditions for the development of temporally coordinated behaviour (see Chapter 3, Section 3.5). However, they also found that a pre-feeding response would develop under continuous light. In

Experiment 2, the consequence of removing the light cycle on operant temporal discrimination was evaluated. If lighting cues were essential to the performance observed in Experiment 1, the pattern of responding should be disrupted by keeping the lights continuously on.

The computer programme was modified for Experiment 2 so that responses during all scheduled feeding times were reinforced. This was done partly to observe the effect of having two consistently reinforced feeding times (as had been planned for Experiment 1), and partly because, if continuous lighting did provide sub-optimal conditions for temporal discrimination, lower probability of reinforcement feeding times may not have been discriminated at all.

The mullet were not used in Experiment 2 because their aquariums were required for use elsewhere. Mullet were not used in any further experiments for the following reasons: Because their response patterns under continuous reinforcement appeared to be biased towards particular times of day, the periods during which restricted feeding times could be set were limited to those where baseline responding was absent. The shaping of discriminations would be more time consuming than with the goldfish because their overall response rates tended to be relatively low. Further, although Experiment 1 demonstrated that using different species in experiments of this type provides valuable comparative data, the number of aquariums available was severely limited, and more replications would be possible if studies were restricted to a single species. Another reason was that there is very little behavioural data on operant behaviour in mullet, and a comparatively large amount on goldfish. The existence of literature on goldfish allows integration of the present data with previous work (e.g., that on the PRE cited above). Finally, mullet can only be obtained by collection from the wild, and they are more difficult to maintain as they require salt water systems. Goldfish are readily obtained from aquarium supplies wholesalers and retailers (and, with a moderate degree of skill, from fairgrounds), and require a smaller investment in maintenance and husbandry.

5.2.1

Method

5.2.1.1 - Subjects. The subjects in this experiment were the groups of goldfish previously used in Experiment 1.

5.2.1.2 - Apparatus. The apparatus and husbandry procedures described for Experiment 1 were used in Experiment 2.

5.2.1.3 - Procedure. The controlling programme was altered so that the dispensers reacted to lever presses during all feeding periods (i.e. the probability of food for all feeding periods was now 4 in 4). The light cycle used in Experiment 1 was maintained, and the fish were put back on the schedule and respective feeding and non-feeding times used in the Second Restricted Stage (see Table 5.1) for a period of 4 weeks. All lights were then set to remain on continuously for a further 10 days.

5.2.2

Results and Discussion

The response rate over 24 hrs, averaged across the 10 days under continuous light, is shown for both groups of subjects in Figure 5.31.



Fig. 5.31. Aquariums 1 and 2. Mean and standard deviation of lever presses per 15 min. Data are averaged over 10 days. The vertical bars (F) indicate feeding times. The laboratory lights were on continuously.

The number of responses in the 30 min prior to the feeding and non-feeding times is presented in Table 5.8.

Table 5.8

Aquariums 1 and 2. Number of responses in the 30 min prior to the feeding (figures underlined) and non-feeding times in Experiment 2.

		Time					
Aquariur	n	T1	T2	T3	T4		
1	М	4.7	22.3	137.8	121.6		
	SD	6.3	14.3	36.4	43.1		
2	М	71.6	11.5	90.6	1.6		
	SD	30.1	23.5	37.1	3.5		

Note. Values averaged over 10 days.

The response rate over each of the 10 days under continuous light is shown for Aquarium 1 in Figure 5.32, and for Aquarium 2 in Figure 5.33.



Fig. 5.32. Aquarium 1. Lever presses per 15 min over each of the 10 days under continuous light in Experiment 2. The feeding times are indicated by the vertical bars.



Fig. 5.33. Aquarium 2. Lever presses per 15 min over each of the 10 days under continuous light in Experiment 2. The feeding times are indicated by the vertical bars.

Figures 5.31, 5.32, and 5.33 show that, in both aquariums, the patterns of response rate associated with the feeding times were similar to those associated with the higher probability feeding times on the restricted stages of Experiment 1. However, the rates of responding associated with each of the feeding times in Experiment 2 were also similar to each other. This suggests that the difference between the higher and the lower probability of reinforcement feeding times in Experiment 1 was indeed due to the direct effects of the schedule, rather than to either their location in the light cycle, or to any effect (e.g., satiation) of having two feeding times per day. The higher rates associated with feeding times are reflected in the relative values for feeding and non-feeding times in Table 5.8.

There was no degradation in discrimination in the absence of a light cycle. Figures 5.32 and 5.33 show that, when compared with the graphs of averaged response rates on the restricted stages of Experiment 1 (Figures 5.5, 5.7, 5.12, and 5.14), accelerations in response rate prior to feeding times were sharper and smoother under continuous light. This increase in definition may have been a result of the modification to the controlling programme. Each feeding time was always reinforced, and so may have supported stronger associations between the passage of time and the reinforcement of responses. In both aquariums, accelerations in response rate commenced between 4 and 5 hr in advance of each of the feeding times. The main exception to this pattern was on days 1 and 2 in Aquarium 2, where there were extended periods with high response rates during the interval between the two feeding times, and also between 4:00 p.m. and 11:00 p.m. This disruption in the pattern of responding may have been an immediate effect of the removal of the light cycle, but response patterns had stabilised by day 3.

The results from both groups maintained under continuous light are consistent with a learned temporal discrimination and suggest that the absence of a light cycle had little effect on the subjects' ability to maintain these discriminations.

5.3 GENERAL DISCUSSION

The results of these experiments provide fairly robust evidence of temporal discrimination in the coordination of operant responding in goldfish. The evidence of this in the behaviour of the mullet may be less compelling (see below), but, at least in some instances, responses did come under the control of temporal contingencies.

In Experiment 1, changes in temporal location between the First Restricted Stage and the Second Restricted Stage did not affect discrimination between the feeding and non-feeding times (except in the case of Aquarium 4). The possibility that environmental disturbances beyond the control of the experimenter (e.g., traffic noise from the road outside) could be perceived by the subjects, and that these may have become discriminative stimuli, can not be ruled out. However, external noise was probably masked by noise made by equipment operating in and around the aquariums (pumps and filters), and was not apparent to the experimenter. Further, it seems unlikely that appropriate stimuli would have occurred before all of the feeding times during the First Restricted Stage. It seems even less likely that four more would have occurred at times appropriate to the new feeding times introduced in the Second Restricted Stage. No differences in response patterns were evident at weekends or during holidays (when the pattern of events outside the laboratory will have been different to that occurring on weekdays).

Although the effect of the varying probability of reinforcement associated with different feeding times may have unbalanced the design and complicated the results of Experiment 1, it did lead to the finding that goldfish are capable of discriminating the time of occurrence of an event, even when that event happens, on average, on only one day in every four.

The averaged data suggested that the rate of responding preceding feeding times may have been partly related to the probability of obtaining reinforcement. In all instances where a higher rate of activity was associated with one of the two feeding times, the lower rate preceded the feeding time with the lower probability of

reinforcement. This would support a conclusion that, while the distribution of responding was under the control of the temporal contingency, the rate was under the control of the probability of reinforcement. The present experiments were not designed to investigate the effects of probability of reinforcement on response rate, and this factor was not adequately balanced, either within or between subjects. However, the obtained relationship between the averaged response rate and the probability of reinforcement was consistent with other data in the temporal discrimination literature. The peak procedure (Catania, 1970; Roberts, 1981) was devised as a method for obtaining a form of temporal generalisation gradient that extends past the accustomed time of reinforcement on fixed-interval schedules. The procedure provides data on the distribution of responding over time on unreinforced trials that are embedded within sessions on a standard fixed-interval schedule. This mixture of reinforced and unreinforced trials is similar to the schedule used in Experiment 1, where the probability that responses would be reinforced during a specific feeding time was either 1 in 4, 2 in 4, or 3 in 4. When the proportion of unreinforced trials is increased in the peak procedure, the time of the peak response rate on these trials remains close to the time at which food would have been delivered on the reinforced trials, but the absolute rate of responding is a negative function of the probability of reinforcement (Catania, 1970; Roberts, 1981).

However, these data are usually presented as the mean distribution of responses from a number of unreinforced trials. For example, Roberts (1981) only collected cumulative data on response distribution over trials, with reinforced trial durations of 20 s and 40 s, and Catania (1970) gave averaged data from schedules where the reinforced interval duration was 10 s and did not report whether data from individual trials were ever examined. In the present Experiment 1, averaging data across 12 days (Figures 5.3 and 5.10) produced plots that were consistent with their findings on the effect of probability of reinforcement on rate, but examination of the daily plots (Figures 5.5, 5.7, 5.12, and 5.14) suggested that this was partly due to the greater variability in rate across days that was associated with the lower probability feeding times. In the absence of data from individual trials, it is possible that the rate

suppressive effect of partial reinforcement reported for short intervals may also have been partly a result of the averaging of variable data. Indeed, although the effect of probability of reinforcement was not examined, a recent study of responding in the probe trials of a short interval peak procedure (Zeiler & Powell, 1994) found that summary measures derived from behaviour on each trial supported different conclusions about temporal control than measures derived from data that are cumulated over trials.

The results of the present experiments are consistent with Davis and Bardach's (1965) findings on pre-feeding activity, and extend them to two additional species. Further, the subjects in the present studies did not merely increase general activity prior to regular feeding times, but performed a specific operant behaviour. The possible commercial implications of these findings and the potential benefits of using endogenous stimuli in controlling fish behaviour have been outlined in Chapter 2.

Davis and Bardach (1965) found that under continuous light their subjects still anticipated fixed feeding times. The results of Experiment 2 were consistent with and extend these findings. The subjects coordinated operant responding in the absence of a light cycle. However, in the present experiments no data were obtained on the acquisition of temporal discriminations under continuous light. This is a matter that will be examined in Chapter 6 (Experiment 4, Section 6.3).

A problem with the present, and with all discrimination experiments, is the possible disparity between a subject's performance and their capability. This is particularly evident in the contrast between the performance of the goldfish and the mullet. Goldfish exhibited a build up in lever pressing activity that spanned several hours prior to the feeding times, whereas mullet tended to start responding only during a short period immediately preceding feeding times. It is not clear whether the higher rate of unreinforced responses emitted by the goldfish is evidence of a lesser ability to discriminate the passage of time, or just a lower threshold for the emission of responses. Indeed, the evidence for operant temporal discrimination in mullet provided by Experiment 1 is less compelling than that obtained in an earlier experiment

(Gee 1990, unpublished). In the earlier experiment, food was delivered at fixed times independently of the behaviour of the subjects, and the operant analysed was movement into the restricted area in which food was delivered. In the present experiments food was more directly contingent on the subjects' behaviour. The fish were not trained to press the lever at particular times, but were left to discover these times for themselves. Given the tendency of mullet to organise their feeding behaviour into bouts of activity followed by long periods of quiescence, it might have been better to have used some form of discrimination training. The mullets' low rate of unreinforced responding may also have been caused by inter-individual inhibition. Mullet are a schooling species (Wheeler, 1978), and so may be more likely to coordinate their behaviour with other members in a group, whereas goldfish and other carp live in less highly coordinated shoals (Lelek, 1987). It may be that greater inhibition of individual deviations from the behaviour of the group in the mullet led to less "speculative" responding. Whatever the cause of the difference in performance between the goldfish and the mullet, it can not be unequivocally ascribed to differences in capacity for temporal discrimination on the basis of the present data. The relationship between performance and capacity in temporal discrimination will be discussed further in Chapter 8.

Subjects in the present experiments were housed and tested in groups of 10. This was because casual observation of individuals from both species suggests that during extended periods of isolation they become easily disturbed, and may exhibit stereotyped behaviour patterns. Some will even refuse food (McMahon, personal communication). As argued in Chapter 4 (Section 4.2), such a subject would not be ideal for this type of experiment. However, although the behaviour of groups is of greater relevance to problems in aquaculture, having 10 subjects with access to one lever leads to problems in the interpretation of results. Although observation of behaviour within the aquariums indicated that the groups predominantly acted in unison, it is not possible to separate out responses made by one individual from another. The acceleration in rate prior to a feeding time might have been a consequence of one fish gradually becoming more active or of a gradual increase in the

number of fish operating the lever as feeding time approaches or a combination of these. Similarly, responses at other times might have been made by a small number of individuals that had not formed temporal discriminations or by all of the subjects responding at a low rate. This problem is avoided in Experiments 3 and 4.

6.0 EXPERIMENTS 3 AND 4

TEMPORAL DISCRIMINATION LEARNING OF OPERANT FEEDING BEHAVIOUR IN INDIVIDUAL GOLDFISH

6.1

Introduction

The experiments in this chapter were, to some extent, designed to overcome the problems in interpretation produced by testing fish in groups. The main difference between the experiments reported in this chapter and those in Chapter 5 was that individual fish were used here. However, there were other differences in the design.

The differing probabilities of reward during specific feeding times in Experiment I resulted in interesting effects, and these warrant further investigation. However, this area is not directly pertinent to the subject matter of this Thesis. When each feeding time was reinforced in Experiment 2, the pattern of responding was less variable, both within and between days. Consequently, in order to minimise variability, reinforcement was provided during every scheduled feeding period in Experiments 3 and 4.

The scheduling of two feeding times per day in Experiments 1 and 2 was also a source of ambiguity. Even under continuous light, it was not possible to determine whether the discriminated interval was the 23 hrs between successive instances of the same feeding time, or whether it was the time elapsed since the immediately preceding feeding time. In order to avoid this ambiguity, only one feeding time per day was used in Experiments 3 and 4.

In Experiment 3, individual goldfish underwent a discrimination training procedure to shape the emission of responses during one fixed feeding time per day. The only temporally configured cues provided were the regular light cycle and feeding schedule. As in Experiments 1 and 2, if time was discriminated, it would be expected that the rate of responding during the period immediately preceding the feeding times would be higher than at other times on the restricted feeding schedule, and higher than at any time on a temporally unrestricted feeding schedule. Further, if feeding times functioned as positive discriminative stimuli, then times not associated with feeding would be expected to function as negative discriminative stimuli.

6.2 EXPERIMENT 3

6.2.1

Method

6.2.1.1 - Subjects. The subjects were 8 goldfish, with a mean standard length of 9.75 cm (standard deviation 1.3 cm), obtained from J & K Aquatics Ltd., Wellington, Somerset. A further 8 goldfish of a similar size were used as "companion" fish (see below) but did not contribute to the data. Prior to the experiments, the subjects were not kept on any fixed feeding schedule or used in any other experiments.

6.2.1.2 - Apparatus. The fish were housed in glass aquariums of the same dimensions used in Experiments 1 and 2. Following an initial training stage, each aquarium was divided in two by a plastic grill placed across the centre of the longest side. The aquariums were screened off from each other with opaque plastic sheeting. The water was maintained at 20 °C and aerated and filtered using standard laboratory equipment. Cleaning of the aquariums took around 10 min and was carried out approximately once every 3 days, between either 9:00 a.m. and 12:30 p.m., or 2:30 p.m. and 7:00 p.m.. The precise time (within these limits) was varied.

A food dispenser controlled by a fish-activated lever was mounted at one end of each aquarium (see Chapter 4, Section 4.3 for details). The dispensers were set to deliver approximately 0.05 g of Hikari[®] staple fish diet in the "baby" pellet size on each activation. A second dispenser was mounted in a similar position at the other end of each aquarium. The second dispenser was activated simultaneously with the first and was not supplied with a separate lever.

As in Experiments 1 and 2, a decoy dispenser was mounted in a narrow space between the rows of aquariums and set to operate in randomly spaced bursts of up to 20 activations.

The control and recording system used in Experiments 1 and 2 was also used in Experiments 3 and 4. This allowed the scheduling of the times during which activation of the lever would result in food being dispensed, and it recorded the time of occurrence of all lever activations.

The lighting system used in Experiment 1 was used in Experiment 3, but the time switch was set to turn the main lights on at 8:00 a.m. and off at 8:00 p.m. each day. This 12-hr on, 12-hr off light cycle allowed a 6-hr interval between transitions in the light cycle and each of the feeding times.

The experiment was housed in the laboratory used for Experiments 1 and 2. The windows were covered with foil to block light from outside.

6.2.1.3 - Design. Experiment 3 was based on the design used in Experiment 1. After lever training there was a baseline stage in which the patterns of responding under continuous reinforcement were recorded. Then there was a restricted feeding stage in which responses were reinforced only during specific periods, which occurred at the same time each day. Next followed an extinction stage in which no responses were reinforced, and finally there was a return to continuous reinforcement. This was done to assess any changes in response patterns in comparison with the First Baseline Stage. The specific procedures used are described below.

6.2.1.4 - Procedure. The apparatus was set so that each lever press produced food at any time. A subject was placed in each of the aquariums together with another fish. This second fish had not experienced any restricted feeding regimes but was already a reliable lever presser. This procedure provided the opportunity for the subject fish to acquire the lever pressing response through observational learning. Intra-specific transfer of learning of a variety of behaviours has been reported for several species of fish (see Chapter 4, Section 4.2), and it was hoped that providing appropriate conditions for observational learning would avoid the need for lever training by successive approximation. No control groups were used to assess efficiency of this technique, but all subject fish were observed to be lever pressing within 7 days.

The experiment was divided into four Stages. The first Stage lasted 14 days and was designed so that the baseline feeding rhythms of the subject fish could be determined. The plastic grill was used to partition the aquariums, with one fish in either end. Only the subject fish had access to the lever, but any presses activated both dispensers. This arrangement removed the need to feed the companion fish by hand and thus reduced disturbances to a minimum. The "companion" fish is so termed because its role was to prevent the subject from exhibiting the stereotyped behaviour patterns that have been observed in goldfish kept for extended periods in total isolation (McMahon, personal communication). Visual, auditory and olfactory contact between the two fish remained possible despite the presence of the barrier.

The second Stage involved restricting the periods when a lever press would be reinforced to a single, 1-hr interval in each 24-hr period. These feeding times commenced 6 hr after the lights were switched on for Subjects 1, 3, 5, and 7 (2:00 p.m. to 3:00 p.m.), and 6 hr after the lights were switched off for Subjects 2, 4, 6, and 8 (2:00 a.m. to 3:00 a.m.). The feeding time for Subjects 1, 3, 5, and 7 was designated a non-feeding time for Subjects 2, 4, 6, and 8 (and *vice versa*). As in Experiments 1 and 2, the non-feeding time was used as a comparison against which

the effect of the feeding time could be gauged. Separate feeding times for different subjects were used to avoid the possibility of a regular external event being used to coordinate responses by all of the subjects. Half of the subjects had the feeding time scheduled during the scotophase, and half during the photophase.

The transition from continuous to restricted feeding was carried out over several days by restricting the period during which the dispenser would respond to a lever press to 12 hr on the first day, and thereafter, reducing the feeding period by 2 hr per day (provided that the subject had responded during the previous day's feeding period). These periods always began at the start time of the target period. This procedure required between 8 and 12 days, and resulted in a progressive lengthening of the interval between periods of food availability, while maintaining the temporal location of the start of those periods. The shaping process was necessary because there was no guarantee that responding would occur during the target period if the transition to restricted food availability were made directly. Experience with the mullet in Experiment 1 had shown that, if all responses occurred outside the feeding times, the operant extinguished fairly rapidly. Once the subjects were responding during the target hour, they were kept on schedule for a further 4 weeks.

The third Stage consisted of an extinction test, in which the dispensers were disabled for 6 consecutive days.

The fourth Stage involved a return to continuous food availability. This was done to in order to see if the restricted feeding regimes had produced any permanent effects on baseline responding. This Stage lasted for 2 weeks.

Data were collected continuously, and recorded as the total number of lever presses in each consecutive 15 min period.
6.2.2

Results

Subject 4 died of a bacterial infection, the remaining seven all reached a stable level of responding during the period of unrestricted feeding (Stage 1). Subjects 2 and 7 responded predominantly within particular periods of the 24-hr cycle during Stage 1. In order to attenuate any effects of preferred feeding times on responding during the Restricted Feeding Stage (Stage 2), these subjects were subsequently allocated to feeding times during which baseline responding had been less frequent.

Figures 6.1 and 6.2 show the development over days of the effect that the contingencies of the various stages of Experiment 3 had on lever pressing during the 30 min immediately preceding the feeding and designated non-feeding times for Subjects 5 and 6, respectively. The response patterns of these subjects were typical of subjects feeding in the photophase (Subjects 1,3,5, and 7) and scotophase (Subjects 2, 6, and 8), respectively. Following the restriction of the feeding periods to 1 hr in Stage 2, the pattern of responding altered markedly. The rate of responding prior to the feeding times increased rapidly and then reached a more or less stable level after about 20 days. The rate prior to the designated non-feeding times remained close to zero throughout.



Fig. 6.1. Subject 5 - Sum of lever presses during the 30 min immediately preceding the designated feeding time (2:00 p.m. to 3:00 p.m.) and non-feeding time (2:00 a.m. to 3:00 a.m.) in Experiment 3, starting with the last 6 days of the First Baseline Stage (Stage 1, CRF), through the shaping and restricted feeding schedules of Stage 2, and the 6 days without food (Stage 3, Extn), to the first 9 days of the Second Baseline Stage (Stage 4, CRF). The ordinate axis is slightly displaced to allow inspection of the lower values, the abscissa denotes the number of days since the start of Stage 1.



Fig. 6.2. Subject 6 - Details as in Figure 6.1, except that the feeding time for this subject was from 2:00 a.m. to 3:00 a.m., and the designated non-feeding time was from 2:00 p.m. to 3:00 p.m.

The rate of lever pressing, averaged over 5 successive 24-hr periods on the initial baseline, restricted feeding, and final baseline schedules (Stages 1, 2, and 4) of Experiment 3 is given for Subjects 1, 2, 3, 5, 6, 7, and 8 in Figures 6.3, 6.4, 6.5, 6.6, 6.7, 6.8, and 6.9, respectively.



Fig. 6.3. Subject 1 - Mean and standard deviation of lever presses per 15 min over the last 5 days of Stages 1 and 2, and the first 5 days of Stage 4. The vertical bar (F) indicates the period during which responses were reinforced in Stage 2. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.4. Subject 2 - Details as in Figure 6.3.



Fig. 6.5. Subject 3 - Details as in Figure 6.3.



Fig. 6.6. Subject 5 - Details as in Figure 6.3.



Fig. 6.7. Subject 6 - Details as in Figure 6.3.



Fig. 6.8. Subject 7 - Details as in Figure 6.3.



Fig. 6.9. Subject 8 - Details as in Figure 6.3.

Typically, a fairly constant rate of 3 to 5 presses per 15 min throughout each 24hr period was observed during Stage 1. When a stable pattern of responding had been reached on Stage 2, a typical daily record would show a level of responding that was close to zero until between 4 and 6 hr before food became available. Once responding had begun, the rate accelerated almost linearly with time until reaching a level of between 20 and 60 responses per 15 min immediately prior to feeding. During the hour of food availability, the rate of responding dropped to around 5 to 15 presses per 15 min, and then back to zero within an hour of the end of the feeding period. Once the subjects were returned to continuous food availability (Stage 4), responding quickly returned to levels and patterns nearly identical with those seen during the First Baseline Stage (Stage 1).

The number of responses emitted during the 30 min prior to feeding and designated non-feeding times, averaged over the final 5 days on Stages 1 and 2 and the first 5 days on Stage 4, is given for all subjects in Table 6.1.

Ta	ble	6.1

Number of responses in the 30 min prior to the feeding (F) and non-feeding (NF) times of Experiment 3.

Sub- ject		Stage 1		Stage 2		Stage 4	
		F	NF	F	NF	F	NF
1	M	0.8	0.0	42.4	0.0	2.6	0.2
	SD	0.4	0.0	9.3	0.0	1.8	0.4
2	M	0.0	6.8	88.0	0.0	5.0	3.6
	SD	0.0	1.8	9.5	0.0	4.3	3.6
3	M	2.0	0.4	81.8	0.4	2.2	1.0
	SD	1.0	0.9	33.3	0.5	1.6	1.7
5	M	3.6	0.0	111.0	0.6	5.6	3.6
	SD	1.1	0.0	15.8	0.8	2.7	2.3
6	M	0.0	3.8	124.0	0.0	2.3	2.4
	SD	0.0	2.7	6.7	0.0	1.6	1.9
7	M SD	0.6 1.3	3.0 3.1	57.0 12.3	$0.0 \\ 0.0$	6.0 3.9	5.4 4.0
8	M	3.8	1.2	37.6	1.2	4.8	3.6
	SD	2.9	2.7	12.4	1.6	3.3	1.9

Note. Values averaged over the last 5 days of Stages 1 and 2 and the first 5 days of Stage 4.

Plots showing the response rate over each of the days that contributed to the averaged response rates on each Stage for Subject 5 (Figure 6.6 and Table 6.1) are given in Figures 6.10, 6.11, and 6.12, and for Subject 6 (Figure 6.7 and Table 6.1) in Figures 6.13, 6.14, and 615. The response patterns of Subject 5 and Subject 6 were typical of subjects that fed during the photophase and scotophase, respectively.



Fig. 6.10. Subject 5. Lever presses per 15 min over each of the last 5 days on the First Baseline Stage (Stage 1). All responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.11. Subject 5. Lever presses per 15 min over each of the last 5 days on the Restricted Feeding Stage (Stage 2). The vertical bar indicates the period during which responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.12. Subject 5. Lever presses per 15 min over each of the first 5 days on the Second Baseline Stage (Stage 4). All responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.13. Subject 6. Lever presses per 15 min over each of the last 5 days on the First Baseline Stage (Stage 1). All responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.14. Subject 6. Lever presses per 15 min over each of the last 5 days on the Restricted Feeding Stage (Stage 2). The vertical bar indicates the period during which responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.15. Subject 6. Lever presses per 15 min over each of the first 5 days on the Second Baseline Stage (Stage 4). All responses were reinforced. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.

Figures 6.10 to 6.15 show that the averaged plots for Subject 5 (Figure 6.6) and Subject 6 (Figure 6.7) accurately reflected the daily pattern of responding on each stage of the experiment. In contrast to the groups of goldfish in Experiment 1, there was little variation in response patterns over days. On the first baseline phase of Experiment 1 there were periods with little or no responding, interspersed with bouts or extended periods with variable response rates. By the second baseline phase responding was spread more evenly over the 24-hr cycle. In the present experiment, responses were fairly evenly distributed over the 24-hr cycle on both baseline Stages. On the Restricted Feeding Stage there was little variation in the pattern of responding over days. There were few responses other than those which started approximately 6 hrs before, and continued through until approximately 1 hr after, the feeding time.

The response patterns of Subjects 1, 2, 3, 5, 6, 7, and 8 over the 6 days of the extinction test (Stage 3) are given in Figures 6.16, 6.17, 6.18, 6.19, 6.20, 6.21, and 6.22, respectively.



Fig. 6.16. Subject 1 - Lever presses per 15 min over the 6 consecutive days of the extinction test (Stage 3). No responses were reinforced, but the vertical bar (broken lines) indicates the period during which responses had been reinforced in Stage 2. The lighting regime (main lights on at 8:00 a.m., and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 6.17. Subject 2 - Details as in Figure 6.16.



Fig. 6.18. Subject 3 - Details as in Figure 6.16.



Fig. 6.19. Subject 5 - Details as in Figure 6.16.



Fig. 6.20. Subject 6 - Details as in Figure 6.16.



Fig. 6.21. Subject 7 - Details as in Figure 6.16.



Fig. 6.22. Subject 8 - Details as in Figure 6.16.

Subject 1 (Figure 6.16) failed to respond at all during the extinction phase. There was no obvious reason for this. The subject had been responding during the preceding day's feeding period, and appeared to be healthy. The pattern of responding of the remaining subjects became less clearly defined over the 6 days of the test. Subject 2 emitted very few responses on the second day, but on day 4 produced a burst of responding close to what had been the feeding time on the preceding stage. On both of the first 2 days, Subjects 3, 5, 6, 7, and 8 responded at the times that had previously been feeding periods, but on the remaining 4 days, response rates dropped close to zero. However, any responses that were made tended to occur near to the previous feeding time.

6.2.3

Discussion

The higher rate of responding preceding the feeding time during restricted food availability (Stage 2) compared with rates prior to the non-feeding time in the same stage and compared with baseline levels (Stages 1 and 4) strongly suggests that individual goldfish are capable of operant temporal discrimination when the interval between opportunities for reinforcement is 23 hrs.

As in Experiments 1 and 2, there was some support for the suggestion that nonfeeding times might take on the properties of a negative discriminative stimulus, as there was a lower rate of responding prior to the designated non-feeding time of Stage 2 than during the equivalent period on the baseline phases. Again, possibly because of a "floor effect", this difference was not large. In future experiments it might be worth exploring methods for raising the baseline rate, perhaps by the use of a variable ratio schedule, so that larger downward deviations would be possible.

The response rates associated with feeding times located in the middle of the photophase and scotophase were very similar. As in Experiments 1 and 2, it is possible that uncontrolled regular external events occurred that allowed the subjects to discriminate these feeding times, but efforts were made to maintain a stable environment, and it seems unlikely that appropriate stimuli would have occurred before both of the feeding times. No differences in responding were evident at weekends or during holidays (when the pattern of events outside the laboratory should have been different to that occurring on weekdays).

Figures 6.3 to 6.9 show that, unlike Experiments 1 and 2, the rate of responding dropped (dramatically in the case of Subjects 2, 3, 5, and 6) at the onset of the feeding periods in Stage 2. This low rate continued throughout the time of food availability, then fell to zero an hour or so after the end of the period. The reason for the low level of reinforced responding when compared with the level of anticipatory responding may be that the subjects were spending time handling food and so had less time in

which to activate the lever. In Experiments 1 and 2, the rate of reinforced responding was usually equal to or greater than the maximum rate of non-reinforced responding. However, in those experiments, any individual that ceased responding might have been replaced at the lever by another from the group. Also, a fish that produced food which was then consumed by others (to borrow a term from social psychology) "free riding" on its labours, would be as little distracted from lever pressing as it had been before the feeding period began. In all three experiments, there were no such distractions from lever pressing during the approach to feeding time.

It is equally true that there were no distractions from lever pressing following the feeding time, and while it is probable that motivational hunger would have been reduced by this time, an increase in response rate over the rate during the feeding period might have been expected. The lack of this effect may be due to the subjects having learned the duration of the feed period as well as the time of day at which it occurred. On the other hand, if this was the case, then it is difficult to see why the subjects continued to respond at all following the end of the feeding times, particularly when they could have learned that as soon as they experienced an unreinforced lever press, reinforcement would not be available for a further 23 hrs.

Dews (1965b) noted a similar phenomenon that occurred with pigeons on fixedinterval schedules of reinforcement when a negative discriminative stimulus was presented in alternation with a positive discriminative stimulus within each interval. The presence of the negative discriminative stimulus exerted a substantial inhibitory effect on responding, but this control was only slowly and progressively attained. If, in the present experiments, the "non-feeding period" that followed the end of the feeding time became a negative discriminative stimulus, it is possible that the continued responding (but at a decelerating rate) that followed the end of the feed period represents a phenomenon of the type observed by Dews (1965b).

As with Experiment 1, the key feature of the pattern of responding during the Extinction Stage (Stage 3) is that, although the magnitude of the response rate extinguished rapidly after the first 2 days, over those 2 days the temporal pattern

remained remarkably constant (Figures 6.16 to 6.22). It could be that the decline in unreinforced responding over successive days on Stage 3 (and, indeed, over the extinction stages of Experiment 1) was simply due to inanition. The fish were given no food at all during extinction, and, as no measures of general activity were taken, no data are available to discount this possibility unambiguously. However, many species of fish undergo long periods of starvation in their natural environment (Larsson & Lewander, 1973), and goldfish have survived several months of starvation in laboratory studies (Love, 1980). Further, Spoor (1946) noted that, while activity declines markedly after a week of starvation, goldfish do not become completely inactive for more than an hour or two even after 2 weeks without food, and that activity levels return to those of unstarved fish within minutes of the reintroduction of food. In the present experiment the rate of reinforced responding also returned to levels similar to those of the First Baseline Stage soon after food was made available.

Even if the low rates of responding observed in the Extinction Stage were a consequence of inanition, the finding that, in most cases, the anticipatory build up persisted in the absence of reinforcement for at least 2 days suggests that, as in Experiment 1, the patterning of responses is unlikely to be entirely dependent on simple homoeostatic or metabolic processes associated with increasing hunger or the emptying rate of the gut. This is concordant with the finding that short-interval operant temporal discrimination in goldfish is independent of simple metabolic rate. Rozin (1965) found no change in relative response rates on a 1 min fixed-interval schedule when ambient temperature was reduced from 30 °C to 20 °C. Goldfish are poikilothermic, and a decrease of this magnitude results in a halving of their metabolic rate.

As with the partial reinforcement of feeding times in Experiment 1, the first day on which reinforcement was omitted is functionally similar to a single unreinforced trial of the type used in the peak procedure. The reasonably symmetrical shape of the distribution and the close proximity of the peak response rate to the expected feeding time are reminiscent of the response distributions obtained from pigeons on intervals

of 10 s (Catania, 1970), 30 s, and 50 s (Gibbon & Church, 1990), and from rats on intervals of 20 s and 40 s (Roberts, 1981).

A regular light cycle was used in Experiments 1 and 3 because Davis and Bardach (1965) found that this provided the optimum condition for the development of prefeeding behaviour. They suggested that the light cycle may act as a zeitgeber, contributing to the regulation of a circadian timing mechanism on which the discriminations are then based (see Chapter 3, Section 3.5). Experiment 2 showed that a light cycle was not essential to the maintenance of operant temporal discriminations, but left open the question of its role in their development. Whether or not these discriminations were related to a circadian process, the presence of a light cycle maintains the possibility that the interval being timed commenced at a transition between light and dark periods. That is, these transitions may have acted as direct discriminative cues signalling the approach of feeding times. The effect of continuous lighting on the goldfish's ability to learn the temporal contingencies of a new feeding time was examined in Experiment 4.

6.3 EXPERIMENT 4

6.3.1

Method

6.3.1.1 - Subjects. These were Subjects 5, 6, 7, and 8 and their respective companion fish used previously in Experiment 3. Only four subjects were used due to lack of laboratory space.

6.3.1.2 - Apparatus. The apparatus was that used in Experiment 3. The aquarium partitions remained in place, and husbandry procedures were carried out as for Experiment 3.

6.3.1.3 - Procedure. The lights were set to remain on continuously and the fish returned to a 1-hr restricted feeding regime directly following the Second Baseline Stage (Stage 4) of Experiment 3. No training or shaping procedure was used. The time of food availability was interchanged between subjects such that fish that had the dispenser active from 2:00 a.m. to 3:00 a.m. during Stage 2 of Experiment 3, now had it active from 2:00 p.m. to 3:00 p.m., and *vice versa*. Data were collected over a 3 week period.

6.3.2

Results

Subject 5 failed to respond during the feeding time, and lever pressing extinguished. The other 3 subjects showed signs of temporal discrimination (accelerations in response rate prior to feeding times) within a week of the imposition of the new schedule. Figure 6.23 shows the development over days of the effect of the schedule on responding during the 30 min immediately preceding the feeding and non-feeding times for these subjects.



Fig. 6.23. Subjects 6, 7, and 8 - Sum of lever presses during the 30 min immediately preceding feeding times and designated non-feeding times, starting with the last 6 days of the Second Baseline Stage of Experiment 3 (Stage 4, CRF), and continuing through the restricted feeding schedule of Experiment 4. In each panel the ordinate axis is slightly displaced to allow inspection of the lower values.

The pattern of the mean response rate over a 5 day period (commencing 2 weeks after the new schedule was imposed) is shown in Figure 6.24. The mean number of responses emitted during the 30 min prior to feeding and designated non-feeding times over this period is given in Table 6.2.



Fig. 6.24. Subjects 6, 7, and 8 - Mean and standard deviation of lever presses per 15 min over the last 5 days of Experiment 4. The vertical bars (F) indicate the periods during which responses were reinforced. The main lights were on continuously.

Subjec	t	Feeding	Non-feeding
6	М	140.0	0.0
	SD	19.9	0.0
7	М	48.4	0.0
	SD	12.7	0.0
8	М	68.4	5.0
	SD	12.1	7.5

Table 6.2.

Number of responses in the 30 min prior to the feeding and non-feeding times of Experiment 4.

Note. Values averaged over the last 5 days of the experiment.

Table 6.2 shows that there was consistently more lever pressing in the 30 min prior to feeding times than prior to the designated non-feeding times. Figure 6.24 shows that the pattern of responding under continuous light was similar to that under a regular light cycle during the Restricted Feeding Stage of Experiment 3 (Figures 6.3 to 6.8).

Plots showing the response rate over each of the days that contributed to the averaged response rates in Figure 6.24 are given in Figures 6.25, 6.26, and 6.27.



Fig. 6.25. Subject 6. Lever presses per 15 min over each of the last 5 days of Experiment 4. The vertical bar indicates the period during which responses were reinforced. The main lights were on continuously.



Fig. 6.26. Subject 7 - Details as in Figure 6.25.



Fig. 6.27. Subject 8 - Details as in Figure 6.25.

For Subjects 6 and 7, the response patterns were fairly similar across days (Figures 6.25 and 6.26). For Subject 8 (Figure 6.27), there was an acceleration in response rate that commenced between 4 hr and 6 hr in advance of the feeding time on each of the 5 days. However, on Day 4 there was also a period of responding between 2:00 a.m. and 3:00 a.m., and on Day 5 between 2:00 a.m. and 8:00 a.m. There was no obvious cause for these periods of responding, but it may be that (as in Aquarium 1 on day 3 of the Second Restricted Stage of Experiment 1) they were initially elicited by the sound of the dispenser operating during the feeding time (2:00 a.m. to 3:00 a.m.) for Subject 7.

6.3.3

Discussion

Figures 6.23 to 6.27 show that response patterns characteristic of temporal discrimination did develop under a continuous lighting regime. Indeed, Figure 6.23 shows that differential rates of responding were associated with the feeding and non-feeding times within a number of days that was similar to that taken for differential rates to develop following the imposition of the temporal contingency in Experiment 3 (Figures 6.1 and 6.2).

In Experiment 2, the temporal discrimination was already established before the lighting regime was modified. In the current experiment, the lack of a light cycle seems to have had little effect on the development of temporal discrimination in three of the subjects. Further, they were able to do this without a shaping procedure. The emergence of temporal discrimination under continuous light is consistent with the findings of Davis and Bardach (1965, Experiment 4) and extends their findings to explicitly operant behaviour. It is not possible to say whether the fish's behaviour could have adapted to the temporal contingencies equally well without the benefit of regular changes in illumination if they had never experienced the temporally contingent schedule of Experiment 3, and this is a matter that requires further investigation.

6.4 GENERAL DISCUSSION

The contingencies operating on the restricted feeding stages of the present experiments might be considered similar to a fixed-interval schedule of reinforcement. On a conventional fixed-interval schedule, the first response following a given interval, measured from the preceding reinforcement, is reinforced (Ferster & Skinner, 1957). As the subjects in the present experiments generally responded throughout the feeding periods, the schedule of reinforcement would be more accurately characterised as a mixed schedule with alternating components of a fixed interval of 23 hrs (FI 23 h) followed by 1 hr of continuous reinforcement (CRF). Nevertheless, previous findings concerning responding on fixed-interval schedules may help to illuminate the effect of the light cycle on the pattern of responding. The use of groups of subjects in Experiments 1 and 2 caused difficulties in integrating data with a literature that is based on the responses of individuals, but the data from Experiments 3 and 4 do not suffer from this problem, and so some comparison can be made.

If the light transitions in Experiment 3 functioned as discriminative stimuli that signalled the beginning of a 6-hr fixed interval which terminated with the feeding time, then an increase in the length of the period of anticipatory activity when the 23-hr fixed interval of Experiment 4 was imposed would be consistent with the observed relationship between interval length and response patterns in other species (Ferster & Skinner, 1957; Lejeune, Richelle, Mantanus, & Defays, 1980; Mackintosh, 1974; Shull, 1971). A comparison of the plots of responding averaged over 5 days in Experiment 3 (Figures 6.7, 6.8, and 6.9) and in Experiment 4 (Figure 6.24) shows that, in Experiment 4, the build up in activity prior to the feeding times did indeed appear to extend over a longer period (typically 8 hr) than it had during Stage 2 of Experiment 3 (typically 6 hr).

The distribution of responses following prolonged exposure to fixed-interval schedules is more often described with reference to the postreinforcement pause (Dews, 1978; Ferster & Skinner, 1957; Harzem, 1969) or to the breakpoint between periods of low and of high rates of responding (Schneider, 1969). In Experiments 3

and 4, responding continued for a short while following the end of the feeding period but was then nearly absent until a few hours before the next feed was due. At this point an acceleration in response rate occurred which continued up to the feeding time. As the response rate progressively increased during this period of activity, it can not be described as a typical break-and-run performance (Schneider, 1969). Equally, the classification of the preceding period of inactivity as a pause would not be strictly equivalent to that used for shorter intervals (some responding did occur within the period of inactivity). If allowance is made for the possibility that the unusual length of the intervals may have supported the emission of a number of "non-timed" responses (Lejeune & Wearden, 1991; Wearden, 1985) occurring within what would otherwise be a pause, then finding that this "pause" extended when the interval was extended would also be consistent with the fixed-interval literature.

However, for conventional fixed-interval schedules, the length of the pause has been described as a negatively accelerating function of increasing interval duration (Lowe, Harzem, & Spencer, 1979; Wearden, 1985). In other words, although the absolute duration of the pause increases with increasing interval length, the proportion of the interval during which responding is absent is smaller for longer interval values. If the difference between the performance observed in Experiment 3 and that observed under the constant lighting of Experiment 4 had indeed been due to an effective lengthening of the fixed interval, then the postreinforcement pause in Experiment 4 would be expected to constitute a smaller proportion of the interreinforcement interval than the pause between the time of the light/dark transition and the onset of responding in Experiment 3. The actual values displayed the opposite relationship. In Experiment 4, the postreinforcement pause spanned approximately two thirds of the interval, whereas in Experiment 3 the onset of responding was almost coincident with the light/dark transition (i.e. there was no pause at all following the change in the light cycle). Further, examination of Figures 6.25, 6.26, and 6.27 (which show responding on each of the days that contributed to the averaged plots for Experiment 4) reveals that, even under continuous light, accelerations that commenced more than 6 hr in advance of the feeding time were the exception rather than the rule. This lack of

any large difference in the pattern of responding between Experiment 3 and Experiment 4 suggests that the light cycle did not simply function as a signal for the start of a 6-hr interval in Experiment 3.

A possible reason for this may lie in a particular feature of schedules that approximate the solar cycle. Such schedules permit the contribution of circadian timing to the task of relating the probability of reinforcement to the passage of time (see Chapter 3, Section 3.4). Even when immediate exteroceptive cues are available, anticipation of a fixed daily feeding period may persist. In an experiment with rats, Terman, Gibbon, Fairhurst, and Waring (1984) found that, on a schedule in which 4 hrs of reinforcer availability were followed by 20 hrs where lever presses were not reinforced, anticipatory lever pressing was reduced but not eliminated by the provision of auditory cues that commenced only minutes before feeding time. This result was attributed to an interaction between circadian and short-interval timing (a more detailed discussion of these experiments is given in Chapter 7, Section 7.4). A similar interaction might have been responsible for the effect of the light cycle in Experiment 3, in that the light transitions may indeed have served as discriminative stimuli, but their control over responding may have been masked by responses under the control of the interreinforcement interval. Alternatively, it could be that the slightly longer average postreinforcement pause seen in Experiment 3 was due to more accurate timing being possible in the presence of a light cycle because, in line with the function suggested by Davis and Bardach (1965), it optimised the synchronization of a circadian pacemaker with the 24-hr cycle, which in turn provided more temporally precise endogenous cues.

If the temporal patterning of responses was dependent on an endogenous circadian rhythm, the time of peak responding would be expected to "free run" in a constant environment (see Chapter 3, Section 3.4). By making the dispensers inoperative for several days following the establishment of anticipation in Experiments 2 and 4, this condition could have been achieved. However, in the extinction stages of Experiments 1 and 3, response rates dropped to near zero levels after only a few

days when reinforcement was withheld (Figures 5.6, 5.8, 5.13, and 5.15, and Figures 6.16 to 6.22), and so it is unlikely that enough data would have been available to provide evidence of any systematic shift in the patterning of responses.

The relationship between chronobiological factors and temporal regulation on operant schedules has received little attention elsewhere (Lejeune, 1990; Lejeune, Richelle, & Mantanus, 1980), and indeed, the present experiments do not adequately address the question of whether the obtained response patterns are best characterised as resulting from control by an unconventional variety of exteroceptively signalled fixed-interval schedule, or from control by circadian timing, or even from a combination of the two.

Despite uncertainty as to the process underlying the performances observed in these experiments, the resultant behaviour patterns are evidence of discrimination. A discriminated operant implies discriminative stimuli. However, the nature of the stimuli controlling temporal discrimination has yet to be identified (see Chapter 3, Section 3.6), and a functional analysis of these stimuli is more problematic than functional analyses of conventional, exteroceptive, discriminative stimuli. This difficulty is due to the way in which stimulus control is achieved. It may seem obvious that a red light presented at one point in time is the same red light when presented at another, and that an operant may come under its control if reinforcement is made contingent on its presence. It is perhaps less obvious that 10:00 a.m. today is the same as 10:00 a.m. yesterday. Although the two points in time are different in historical terms, in a functional sense they may be similar and an association between one instance and the next may be formed. Although the discrimination of exteroceptive cues must ultimately be dependent on endogenous events, this process is initiated independently of the subject. Exteroceptive stimuli are presented, but in temporal discrimination the subject must form an association between reinforcement and an endogenously generated internal state. That is, while the contingencies controlling temporally structured responding of the type studied in the present experiments are external to, and imposed on, the subjects, at some stage the temporal

contingencies become discriminable and salient. Only then may "anticipation" of reinforcement emerge. The discriminative stimuli controlling this anticipation are, presumably, some temporally configured endogenous phenomenon.

As discussed in Chapter 3 (Section 3.6), it is not appropriate to describe a particular time as a stimulus, and arguments have been made against appeals to internal stimuli in an explanation of temporal coordination (Catania, 1970; Harzem, 1969). In an experimental analysis of behaviour, interest is centred on the conditions under which temporal discriminations are acquired and maintained, and this type of analysis does not require reference to internal processes. However, temporally coordinated internal processes are well documented (e.g., Cloudsley-Thompson, 1980), and, even if reference to internal processes is not required in a functional analysis, an assumption that temporally coordinated behaviour of the type examined here is under the control of temporally configured endogenous events may be useful in forming hypotheses to guide the functional analysis.

Even if the stimuli assumed to underlie temporal discrimination had been adequately identified, it is not likely that they could be subjected to direct and immediate manipulation. Indeed, it may be that immunity from immediate external manipulation may engender functional properties in temporal discriminative stimuli that differ from those of exteroceptive discriminative stimuli. In a sense, internal stimuli may be more "reliable". Previous findings on compound stimulus control are derived almost exclusively from experiments on exteroceptive stimuli. If there is a functional difference between exteroceptive stimuli and temporally configured endogenous stimuli, then a functional analysis of their interaction in the control of behaviour might result in findings that would not be predicted on the basis of the previous work.

Consideration of a possible difference in the nature of control by exteroceptive and by temporally configured interoceptive stimuli raises a question as to the extent to which it is appropriate to consider the "anticipation" seen on fixed interval schedules as a form of generalisation. Anticipation might be an adaptive feature of behaviour.

An organism may be more successful if it is able to prepare for events rather than relying on reaction once they have occurred. The peak procedure (Catania, 1970; Roberts, 1981) was devised to obtain a generalisation gradient around the usual time of reinforcement. Generalisation may be defined as the spread of the effects of reinforcement in the presence of one stimulus to other stimuli (Catania, 1991). Through generalisation a number of stimuli may, to a degree that varies according to their similarity with the original stimulus, come to control responding. In contrast, the acquisition of control at times other than that with which reinforcement is associated (anticipation) may be more akin to delayed reinforcement. Essentially, this is the process proposed by Dews (1962), in which specific moments in the interval of a fixed-interval schedule acquire control because responses are reinforced following a specific delay (see Chapter 3, Section 3.2). From this perspective, responses during the interval of a fixed-interval schedule are under the control of the temporal relationship between a particular point in the interreinforcement interval and the time of reinforcement itself, rather than being under the control of generalisation.

However, this account seems less able to explain the control of responses emitted on the declining side of the peak rate on probe trials of the peak procedure. Here the concept of generalisation seems a better description of the process, with less responding supported by times which are less like the reinforced time. Indeed, points during the period after the target time are followed by a long but decreasing delay to reinforcement. Under the delay of reinforcement hypothesis an *increasing* rather than decreasing rate might be expected, although it remains possible that responding during a probe trial is, for example, under a combination of delayed reinforcement and generalisation during the approach to the peak time, and under generalisation alone afterwards.

Regardless of whether responding during the interval of a fixed-interval schedule is under the control of delayed reinforcement, of generalisation, or indeed, of a combination of these, these processes are different from that which would support control by a concurrently presented invariant exteroceptive stimulus. Where a

temporal discrimination exists, control by an exteroceptive stimulus might be acquired by direct conditioned reinforcement if it is contiguous with the reinforcer, or if it occurs with a systematic delay to reinforcement, by secondary reinforcement supported by its relationship to temporally configured endogenous stimuli. If there is a limited degree of control over responding that a reinforcer may support (see Chapter 7, Section 7.1), then competition for that control between concurrent endogenous and exteroceptive stimuli might be expected. However, as there has been no previous work in this area, there is no *a priori* reason to suppose that control acquired by stimuli having different relationships with reinforcement would necessarily be subject to mutual competition.

To summarise these speculations, it is suggested that temporal discrimination may be supported by endogenous discriminative stimuli, and that such stimuli may function differently from discrete exteroceptive stimuli in the control of behaviour. This is because they are relatively immune from manipulation, and may be related to reinforcement by a different conditioning process. The final experimental chapter of this thesis will use the paradigm developed in the preceding experiments to examine the relationship between control by temporal contingencies and by exteroceptive discriminative stimuli.

7.0 EXPERIMENTS 5 AND 6

CONCURRENT TEMPORAL AND VISUAL DISCRIMINATION IN INDIVIDUAL GOLDFISH

7.1

Introduction

Experiments 5 and 6 are concerned with the question of how behaviour is controlled under a schedule where reinforcement is contingent on a fixed interreinforcement interval, and, concurrently, on an exteroceptive discriminative stimulus.

As noted in Chapter 6, there was little evidence to suggest that the regular changes in the light cycle used in Experiment 3 functioned as discriminative stimuli for the start of a 6-hr fixed interval. If the effect of having continuous light in Experiment 4 had simply been to increase the discriminated interval from 6 hr to 23 hr, then it might have been expected that the duration of the period non-reinforced responding would be longer than in Experiment 3. Instead, there was hardly any increase. This was not consistent with findings on the effect of variations in interval duration on fixed-interval schedules in the seconds to minutes range (Lowe, Harzem, & Spencer, 1979; Wearden, 1985).

However, the schedule used in Experiment 3 differed from those used in the study of intervals in the seconds to minutes range in more than the length of the interreinforcement interval. The presence of the light cycle offered the potential for at least two separate temporal discriminations to control responding. For example, the subjects may have simply discriminated the inter-reinforcement interval, or they may have discriminated the interval between a change in the light cycle and the onset of the feeding period. They may even have discriminated both intervals simultaneously.

It is not clear how control is likely to be distributed between concurrent temporal contingencies, or between temporal contingencies and contingencies involving exteroceptive stimuli such as the light used in Experiment 3. Current theories of associative learning (Gibbon & Balsam, 1981; Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) suggest that when two or more stimuli predict the same reinforcer, control by each of the elements of the compound will be a proportion of the control exerted by the compound. Although exceptions have been reported (e.g., Kehoe, 1986), the majority of experiments using compounds of exteroceptive stimuli have produced results that are consistent with these theories (e.g., Kamin, 1969; Tennant & Bitterman, 1975; Wolach, Breuning, Roccaforte, & Solhkahn, 1977). If temporal discriminations are functionally equivalent to other forms of discriminative control, then mutual interference in control (e.g., overshadowing) between the exteroceptive stimulus and the inter-reinforcement interval might be expected. More specifically, control by the inter-reinforcement interval may have overshadowed control which would otherwise have been acquired by the light cycle in Experiment 3.

Experiments 5 and 6 were carried out in order to investigate the specific question of how a discrete exteroceptive discriminative stimulus interacts with an interreinforcement interval in the control of responding. The overshadowing paradigm, and Kamin's (1969) blocking procedure are commonly used in the study of compound stimulus control, and their associated phenomena have been demonstrated with exteroceptive stimuli in both operant (Tennant & Bitterman, 1975) and classical (Wolach et al., 1977) conditioning in goldfish. Operant overshadowing and blocking procedures were used in the experiments reported here. Experiment 5 examined the effect of compounding a temporal contingency with a discrete exteroceptive discriminative stimulus, of imposing a temporal contingency on responding under the control of an exteroceptive stimulus, and of imposing a discrete exteroceptive stimulus on responding under the control of a temporal contingency.
7.2 EXPERIMENT 5

7.2.1

Method

7.2.1.1 - Subjects. The subjects were 10 goldfish, with a mean standard length of 12.6 cm (standard deviation 3.2 cm), obtained from J & K Aquatics Ltd., Wellington, Somerset. An additional 10 goldfish of a similar size were used as "companion" fish (see Chapter 6, Section 6.2.1.4) but did not contribute to the data. Prior to the experiments, the subject fish were not kept on any fixed feeding regime or used in any other experiments. The companion fish had served as subjects in previous experiments.

7.2.1.2 - Apparatus. All apparatus and husbandry procedures were as described for Experiment 3, except that in Experiment 5 each aquarium was fitted with a stimulus light assembly. This consisted of an L.E.S. light bulb (28 v, 40 mA, 3.7 lm), housed inside a white polythene test tube (diameter 15 mm). This was mounted on the inside wall of the aquarium, behind, and 1 cm to one side of, the point at which the tip of the lever entered the water. The tube projected 4 cm below the water surface and gave off a yellow glow when the bulb was switched on.

The experiment was housed in a windowless laboratory, lit by an 20-W fluorescent bulb (Osram Dulux[®] EL) that was on continuously throughout the experiment.

7.2.1.3 - Design. The treatment for each experimental group is described below, and summarised in Table 7.1.

Group	Stage 1	Stage 2	Test	_
L-TL	L		 T	_
T-TL	Т	T&L	L	
TL	T&L		T, L	

Table 7.1Treatments for groups in Experiment 5.

Note. L: Yellow light stimulus; T: Temporal contingency.

Subjects 1, 3, 5 and 7 were assigned to Group L-TL. In Stage 1, this group was pretrained with the yellow stimulus light as a discriminative stimulus for foodreinforced lever pressing. Trials commenced at different times each day. Subsequently, the light was compounded with a temporal contingency by beginning trials at the same time each day (Stage 2). Following Stage 1, discriminative control by the light was assessed, and following Stage 2 control by the temporal contingency was assessed.

Subjects 2, 4, 6 and 8 were assigned to Group T-TL. This group was pretrained on an unsignalled temporal contingency during Stage 1 (responses produced reinforcement only at a fixed time each day). During Stage 2 the yellow stimulus light was compounded with the temporal contingency (light on during periods of food availability). Following Stage 1 control by the temporal contingency was assessed, and discriminative control by the light was assessed following Stage 2.

In order to assess the effect of compounding without prior learning involving either element, Subjects 9 and 10 were assigned to Group TL. These subjects were given the compound stimulus (yellow light signalling food at the same time each day) throughout training. Subsequently, they were tested for control both by the light, and by the temporal contingency. 7.2.1.4 - Procedure. The apparatus was set so that each lever press produced food at any time. A subject and a companion were placed in each of the aquariums. The companion had not experienced any restricted feeding regime, but was already a reliable lever presser. As in Experiment 3, this arrangement was used in order to provide an opportunity for the subject fish to acquire the lever-pressing response through observational learning.

During this lever-training phase the stimulus lights were set to remain on continuously for Groups L-TL and TL. The stimulus lights for Group T-TL were continuously off. After 7 days all subjects were lever pressing, and the plastic grill was used to partition the tanks. This left one fish in each end, but only the subject fish had access to the lever. Any lever presses activated both dispensers, thereby removing the need to feed the companion fish by hand and reducing disturbances to a minimum.

Once visual inspection of plots of response rate indicated that a subject had acquired a stable rate of lever pressing, a "one-in-four days omission procedure" was instituted. Experiment 1 showed that responding in groups of goldfish was controlled by feeding times with a probability of reinforcement of 3 in 4. Indeed, the response patterns controlled by these "3 in 4" feeding times were almost identical to those controlled by feeding times that were always reinforced. This finding suggested a means by which performance during each stage of the present experiments could be monitored with the minimum of disruption to the schedule of reinforcement. Specific implementations are detailed below, but the general strategy was that if the subjects were accustomed to reinforcement being omitted on 1 day in every 4 days, responding on the omitted day should provide an index of discriminative control that was not contaminated by the effect of the direct reinforcement of responses. It would be possible to record the rate of responding controlled by a stimulus light or by a temporal contingency in the absence of immediate reinforcement on 1 day in every 4 days over the course of a stage. The omission procedure during the lever training phase was as follows. The food dispensers were disabled for, on average, one

continuous 24-hr period in each successive 96-hr period. The day on which one of the 24-hr no-food periods commenced was determined according to a computergenerated random number between 1 and 4. Each day a random number was generated for each subject, and if the value returned was "1" then lever presses emitted by that subject would not be reinforced for a 24-hr period. Otherwise food would be available as usual. Even when a no-food period was in progress, the stimulus lights remained on for Groups L-TL and TL. This procedure was continued for 14 days.

The daily period during which lever presses were reinforced was then systematically reduced to a single 1-hr interval in each successive 24-hr period. The one-in-four days omission procedure was suspended during this phase, and food was available every day. The stimulus lights for Groups L-TL and TL were switched on while (and only while) food was available. The stimulus lights for Group T-TL remained off throughout. The period of food availability was initially restricted to 12 hrs in each 24 hrs, and reduced by 2 hrs per day following at least 2 days where the subject had produced a substantial number of responses during its feeding period. After the subject had responded during a 2-hr feeding period, the feeding period was reduced to only 1 hr per day.

The progress of discrimination training was monitored daily by visual inspection of plots showing the rate of responding over the preceding 24-hr period. The schedule for the following 24 hrs was set at 12:00 p.m. each day. For Group L-TL, a computer program that incorporated a random number generator was used to determine the start time of each day's feeding period. These start times could occur at any hour within a 24-hr period, provided that the feeding period did not finish later than 12:00 p.m. (which might have interfered with the following day's schedule). The start time of the feeding period for each subject was generated independently of the start times for other subjects. The feed period for Groups T-TL and TL always began at the same time each day. Subject 2's feeding period began at 7:00 p.m., Subject 4's at 2:00 a.m., Subject 6's at 2:00 p.m., Subject 8's at 10:00 a.m., Subject 9's at 2:00 p.m. and Subject 10's at 4:00 a.m. For Groups T-TL and TL this meant

that although the duration of the feed period was reduced across days, its start time remained constant.

Once responding within the 1-hr period had occurred on 3 consecutive days, the one-in-four days omission procedure was reinstated. Even on days where no lever presses were to be reinforced (omission days) the stimulus lights for Groups L-TL and TL were turned on for a 1-hr period. These periods began at the usual time for Group TL or at a time determined by the program that was used to generate start times for feeding periods on non-omission days for Group L-TL. This Stage (Stage 1) continued for 6 weeks. At this point Group TL was tested for control over responding by the temporal contingency and by the stimulus light (see below). For Groups L-TL and T-TL the last four instances of an non-reinforced trial (i.e. of omission days on which lever presses were not reinforced even in the presence of the light for Group L-TL and on which lever presses had not been reinforced even at the usual time for Group T-TL) on Stage 1 were taken as a measure of responding to an uncompounded visual stimulus and to an uncompounded temporal contingency, respectively.

For Groups L-TL and T-TL, a second stage of the experiment was initiated. In this stage, the visual stimulus and the temporal contingency were compounded. For Group L-TL, the procedure of resetting the feeding time daily was suspended and the feeding time was fixed. For Subject 1 the feeding hour began at 10:00 a.m., for Subject 3 at 10:00 p.m., for Subject 5 at 4:00 a.m., and for Subject 7 at 4:00 p.m.. For Group T-TL, the feeding times were not changed, but the stimulus light was now switched on for the duration of each feeding period. These compound contingencies were in operation for a further 6 weeks. During this time, the one-in-four days omission procedure was continued.

Tests of control over responding by the added element of the compound contingency (the blocking tests) were then carried out. The procedure for Group L-TL was to omit the presentation of the light and the reinforcement of responses at the time that had been used as a feeding time during Stage 2. This procedure was carried out on four separate occasions, spaced over a 3 week period. Each occasion was

determined in the same way as for the one-in-four days omission procedure used over the preceding stages of the experiment. There was normal compounding of contingencies and availability of reinforcement on the intervening days and no "regular" omission days were scheduled.

The procedure for Group T-TL was similar in that, on test days, the presentation of the light and reinforcement at the feeding time was omitted. However, this group also had the light presented (without reinforcement) for a 1-hr period that began either 12 hrs before, or 12 hrs after, the omitted feeding time. On the first test trial, Subjects 2 and 4 had the light presented before the expected feeding time, and Subjects 6 and 8 had the light presented after the expected feeding time. This procedure was carried out on four separate occasions that were determined by the one-in-four days omission procedure. On each successive test the sequential relation between the test light, and the omission of light and food at the established time, was swapped between subjects. For example, on the second test Subjects 2 and 4 had the light after the omitted feed, and Subjects 6 and 8 had the light before the omitted feed.

For Group TL, the tests for control by the light were carried out according to the procedure used for Group T-TL following Stage 2, with the light stimulus being presented either 12 hr before or 12 hr after the omission of a feed period that was itself unaccompanied by the light. Because these tests involved the presentation of a stimulus light 12 hr before or after the omission of a feed period an interval that contained a light test could not be used in assessing temporal control. In these intervals data on control by the temporal contingency would be contaminated with responses made during the tests for control by the light. Instead, data on responding during the interval that immediately preceded the interval during which the light tests were carried out was used to assess temporal control. However, at the end of two of these intervals (those which preceded intervals in which the light test was carried out 12 hr before an omitted feed) lever presses were reinforced. This meant that the rate of responding during these feeding hours could not be used for comparison with the rate during the non-reinforced feeding hours which followed the other two test

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intervals for this group and which followed all of the test intervals for the other groups. Consequently, for the two intervals which were followed by a reinforced feeding time data on the rate of responding under temporal control was taken from the non-reinforced "feeding time" that occurred 24 hrs later (after the light test).

7.2.2

Results

Subject 6 (Group T-TL) and Subject 7 (Group L-TL) died of bacterial infection during Stage 1 of the experiment. For the remaining subjects, response rates during non-reinforced presentations of stimulus lights are presented in Table 7.2, and during the hour in which food was usually available in Table 7.3.

Table 7.2

Discrimination ratios calculated for non-reinforced presentations of light stimuli in Experiment 5. The number of responses made in the presence of the light is given in parentheses.

	Trial	1	2	3	4
Group	Subject				
	1	0.89 (23)	0.93 (14)	0.95 (20)	0.50 (0)
L-TL	3	0.98 (53)	0.98 (131)	0.95 (130)	0.99 (66)
	5	0.74 (90)	0.80 (69)	0.57 (64)	0.86 (35)
T-TL	2	0.97 (37)	0.98 (50)	0.50 (0)	0.94 (15)
	4	0.98 (42)	0.89 (7)	0.96 (26)	0.97 (29)
	8	0.98 (58)	0.94 (14)	0.97 (37)	0.92 (48)
TL	9	0.96 (91)	0.91 (9)	0.97 (114)	0.93 (13)
	10	0.98 (48)	0.99 (72)	0.96 (23)	0.99 (94)

Note. For Group L-TL the values are taken from the final four non-reinforced trials of Stage 1. For Groups TL and T-TL, the values are taken from the four test trials that followed Stage 1 and Stage 2, respectively.

Table 7.3

Percentage of the 11.5 hrs immediately prior to a feeding time that had elapsed when one quarter of the total of responses emitted during that interval had been made. The number of responses made during the feeding hour is given in parentheses.

	Trial	1	2	3	4
Group	Subject				
L-TL	1	87.2 (29)	74.6 (11)	72.6 (6)	84.2 (42)
	3	64.6 (16)	61.6 (12)	56.1 (24)	38.1 (13)
	5	83.3 (83)	53.0 (59)	67.7 (50)	66.8 (59)
T-TL	2 4 8	83.0 (223) 61.9 (50) 82.9 (216)	68.7 (179) 49.7 (20) 91.7 (109)	68.9 (57) 63.7 (90) 82.6 (263)	65.5 (250) 83.2 (38) 79.3 (195)
TL	9 10	71.6 (0) 70.1 (7)	4.0 (0) 65.2 (1)	86.8 (16) 58.0 (0)	91.7 (7) 74.4 (14)

Note. For Group L-TL, the values are taken from the four test trials that followed Stage 2. For Group T-TL the values are taken from the final four non-reinforced trials of Stage 1. For Group TL the quarter-life values are taken from the interval that immediately preceded the four test trials, and the number of responses taken from the feeding time on the test trials that followed.

As absolute rates do not necessarily provide information on discriminative control (see Section 7.4), measures of relative response rates were also calculated. To assess control by the stimulus light, discrimination ratios were computed (Table 7.2). The number of responses during the hour in which the light was present was divided by the sum of the number of responses during that hour and the number of responses during the immediately preceding hour. Because the hour before the stimulus light came on frequently contained no responses at all, a constant of 1 was added to all values before ratios were computed. This meant that the maximum ratio possible was slightly less than 1.0, but it did differentiate between instances where, for example, responding was absent before the presentation of the light, and either high or low during the presentation of the light. Without the addition of the constant, both these instances could result in a very high value. Using this procedure, no discrimination (no responding at all over the 2 hours, or responding at a constant rate before and after the stimulus light was switched on) generates a ratio of 0.5. Increasing values above this figure indicate distributions of responding that are increasingly concentrated in the hour where the stimulus light was present.

A modification of the quarter-life method (Herrnstein & Morse, 1957) was used to assess control by the temporal contingency. The standard quarter life is the time taken for the emission of the first one fourth of the total number of responses made in the inter-reinforcement interval of a fixed-interval schedule. If responding proceeds at a constant rate throughout the interval (no temporal discrimination), then the quarter life is simply one fourth of the duration of the interval. If the distribution of responses is skewed toward the termination of the interval, then the quarter life will be greater than one fourth of the interval. The quarter life is easily computed, highly correlated with other measures of response distribution, and is relatively insensitive to absolute response rate (Dukich & Lee, 1973; Gollub, 1964). In the present case this insensitivity to absolute rate is a desirable property, as responding may come under the control of an effective discriminative stimulus regardless of absolute rate. For the data

in Table 7.3 the Spearman rank correlation coefficient of the quarter-life values with the response rate is 0.3.

The quarter-life measure was modified to avoid the inclusion of responses emitted soon after the end of the feeding hour (these responses can be seen in Figure 7.1). Similar post-feeding responses were observed in Experiments 1, 2, 3, and 4, and comparable patterns of post-feeding activity have also been reported for rats given access to food at a fixed time each day (Honma, von Goetz, & Aschoff, 1983). As the behaviour of primary interest here was temporal control prior to the established time of reinforcement, quarter-life values were calculated using data from the second half of the inter-reinforcement interval only (the 11.5 hr immediately preceding the feeding time). This modification precludes comparison with conventional quarter-life values, but preserves the nature of the measure as an index of response distribution. As data were grouped into 15-min time bins, a linear interpolation was used to estimate quarter-life values that fell between 15-min intervals.



Fig. 7.1. Group Mean and Standard Deviation of lever presses per 15 min over the final four non-reinforced trials of Stage 1 for the 3 subjects in Group T-TL (upper panel), and over the four non-reinforced test trials that followed Stage 2 for the 3 subjects in Group L-TL (lower panel). The abscissa indicates hours before (negative values) or after (positive values) the midpoint of the hour long period (F) during which lever presses would have resulted in food during reinforced trials.

Plots showing the development of temporal control are given in Figure 7.2. Each plot was derived from measures taken on the day before discriminative training commenced, and at weekly intervals thereafter. It can be seen that, for almost all subjects, temporal control was established rapidly when fixed feeding times were introduced, regardless of pretraining. The exception was Subject 10 (Group TL), which tended to respond only in the presence of the light during weeks 4 to 7. However, by the final week of compound training this subject produced response patterns that yielded a quarter-life value of 75%, and maintained similar response patterns throughout the test stage. Group mean quarter-life measures taken from the four test trials (Group L-TL), from the trials immediately preceding the four test trials (Group TL), or from the last four non-reinforced trials on Stage 1 (Group T-TL) are shown in Figure 7.3. These were fairly constant across groups, at around 70% of the interval. In contrast, group means for absolute responding during the non-reinforced "feeding hours" were highly variable across groups (Figure 7.4), with a far greater rate produced by Group T-TL than Groups L-TL or TL. However, the response rate during the feeding hour appeared to be a function of the rate of responding during the preceding inter-reinforcement interval. For Group L-TL on the blocking tests that followed Stage 2, the ratio of the group mean responses in the hour immediately preceding the "expected" feeding time to responses during the "expected" feeding time was 1.07:1. The equivalent ratio for Group T-TL on Stage 1 was similar, at 0.88:1.



Fig. 7.2. Quarter-life values (Q) calculated from the 11.5 hrs immediately preceding reinforcement (see text for details). Each data point was taken from a single trial at weekly intervals, starting from the day before shaping began (A), through the shaping procedure (B), and uncompounded contingency training (C), to the compound contingency training stage (D). The figures in the upper left-hand corner of each panel indicate the subject number. The broken lines indicate the value that would be expected if responding proceeded at a constant rate throughout the interval.



Fig. 7.3. Group mean (±SE) quarter-life values (Q) calculated from the 11.5 hrs immediately preceding the usual time of reinforcement (see text for details). For Group L-TL (N=3) and Group TL (N=2), the values are averaged over each subject's performance in the four test trials, for Group T-TL (N=3) the values are averaged over each subject's performance in the final four non-reinforced trials of Stage 1.



Fig. 7.4. Group mean (\pm SE) rates of responding (responses per hour) during the non-reinforced hour immediately following the intervals used to calculate the quarter-life values shown in Figure 7.3. Details of averaging procedure are as in Figure 7.3.

For subjects in Group L-TL the development of discriminative control by the light is shown in Figure 7.5. It was not possible to compare the development of control by the light across groups. The concurrent temporal contingency of Groups T-TL and TL meant that these subjects were already responding during the hour that immediately preceded the presentation of the light. However, control established by the visual stimulus was assessed during test trials for Group T-TL and Group TL, and during the last four non-reinforced trials on Stage 1 for Group L-TL. The mean discrimination ratios are shown in Figure 7.6, and it can be seen that these were fairly constant across all groups. Group means for absolute responding during these nonreinforced presentations of the light were also similar across groups (Figure 7.7).



Fig. 7.5. Discrimination ratios (DR, see text for details of calculation) for subjects in Group L-TL. Each data point was taken from a single (reinforced) trial at weekly intervals, starting with the first day of the shaping procedure (A), and through uncompounded contingency training (B). The figures in the centre of each panel indicate the subject number.



Fig. 7.6. Group mean (\pm SE) discrimination ratios (see text for details of calculation). For Groups T-TL (N=3) and TL (N=2), the values are averaged over each subject's performance in the four test trials, and for Group L-TL (N=3) the values are averaged over each subject's performance in the final four non-reinforced trials of Stage 1.



Fig. 7.7. Group mean (±SE) rates of non-reinforced responding (responses per hour) in the presence of the stimulus light during the trials used to calculate the discrimination ratios shown in Figure 7.6. Details of averaging procedure are as in Figure 7.6.



Fig. 7.8. Lever presses per 15 min over the interval and non-reinforced feeding time (F) used to calculate the quarter-life value and number of responses given for Subject 10 (Group TL) on trial 3 in Table 7.3. The abscissa indicates hours since the immediately preceding (reinforced) feeding time, and not actual clock time.

7.2.3

Discussion

There was no evidence of blocking or overshadowing of temporal control by visual control or of visual control by temporal control in the quarter-life values and discrimination ratios obtained in Experiment 5. There was, however, a large difference in response rate on the test trials between Group T-TL, and Groups L-TL and TL, during the accustomed feeding hour (Figure 7.4). When both contingencies applied (Group TL, Stage 1; Group L-TL and Group T-TL, Stage 2), the rate of responding during the feeding hour was far below that observed with the temporal contingency alone (Group T-TL, Stage 1). The occasion for this difference is illustrated in Figure 7.1. When a light cue was available, there was a lower rate of responding during the inter-reinforcement interval. On test trials this low rate continued through the non-reinforced feeding hour. This effect was particularly pronounced in Group TL. Indeed, of the eight test trials for this group (Table 7.3), four contained 1 or fewer responses. As the quarter-life values associated with these data show that responses were concentrated in the latter part of the interval (except on the second test trial for Subject 9) it appears that this result was not due to an absence of temporal discrimination. An example of the type of pattern which produced a high quarter-life value even though there were no responses during the feeding hour is given in Figure 7.8. It is not clear why this type of performance should have been

more common in Group TL than it was in Group L-TL. In both groups responses had only ever been reinforced in the presence of the light and so the absence of the light may have functioned as a negative discriminative stimulus. If this were the case then the lower rates where visual and temporal contingencies were compounded in comparison with rates under the temporal contingency alone may have resulted from inhibition in the absence of light. However, this would have been as true for Group L-TL as it was for group TL, and so the cause for the difference in the performance of these groups remains unclear. Although the quarter-life values suggest that responding was under temporal control in Group TL it might be that the overshadowing procedure resulted in greater rate suppression than did the compounding of visual and temporal contingencies following pretraining on the visual or temporal contingency alone. Nevertheless, it would be unwise to generalise from so few data, particularly when there is a measure of variability in the data set. The generalizability of the data reported in this Thesis will be discussed further in Chapter 8.

Despite differences in rate, there was little difference between the three groups in the distribution of responses during the inter-reinforcement interval (as indexed by the quarter-life values, Figure 7.3), suggesting that temporal discrimination developed (Groups L-TL and TL) or persisted (Group T-TL) where an immediate, exogenous discriminative stimulus was concurrently available. The greater weight given to measures of relative rather than absolute rate will be discussed further in the General Discussion (Section 7.4).

Although the results of Experiment 5 suggest an absence of blocking, it is not usual for blocking experiments to be carried out with only one trial per day, and it is possible that blocking simply would not have occurred between *any* stimuli on a schedule of the type used. In order to examine this possibility, a further blocking experiment was carried out. In Experiment 6, the inter-reinforcement interval was maintained, but lights were used as both the pre-trained stimulus and as the to-beblocked stimulus.

7.3.1

Method

7.3.1.1 - Subjects. The subjects were Subjects 2 and 8 (with their respective companions) from Experiment 5. An additional 2 subjects (Subject 11 and Subject 12), obtained from the same source and at the same time as the subjects used in Experiment 5, were also used. Subjects 11 and 12 were kept in a holding facility until required for Experiment 6, and had not been used in any other experiments. Fish that had experience of lever pressing in previous experiments, but that had not been used in Experiment 5, served as companions for Subjects 11 and 12.

7.3.1.2 - Apparatus. The apparatus was that used in Experiment 5, with the following modifications: Subjects 2 and 8 were each provided with an additional stimulus light. These were housed in a tube identical to that used for the yellow light, but with a red silicone rubber filter (Maplin Professional Supplies, YY04E) fitted over the bulb. This transformed the glow to red. The red stimulus light assembly was placed in a position 2 cm to one side of the existing yellow light, so that there was a light 1 cm to each side of the lever. Subjects 11 and 12 had only one stimulus light, fitted with a red filter.

For Subjects 2 and 8, the tank partitions used in Experiment 5 remained in place. For Subjects 11 and 12 the barriers were only introduced following the lever training procedure described for Experiment 5. Husbandry procedures were carried out as in Experiment 5.

7.3.1.3 - Design. The treatment for each experimental group is described below, and summarised in Table 7.4.

Group	Stage 1	Stage 2	Test
L-LL(r)	L	L&L(r)	L(r), L, L&L(r)
L(r)	L(r)		L(r)

 Table 7.4

 Treatments for groups in Experiment 6.

Note. L: Yellow light stimulus; L(r): Red light stimulus.

The performance of Subjects 2 and 8 in Experiment 5 showed that control acquired by the temporal contingency during Stage 1 had not prevented the acquisition of control by the yellow light during Stage 2. In Experiment 6, the effect of this control on the acquisition of control by the newly introduced red light was assessed. Subjects 2 and 8 were re-designated Group L-LL(r); following their tests as Group T-TL, the red light was compounded with the existing yellow light during the hour of food availability. Subsequently they were subjected to tests for control by the red light, then by the yellow light, and finally by the red and the yellow lights in compound. The temporal contingency was maintained throughout.

Subjects 11 and 12 were designated Group L(r). This was a control group run to verify the capacity of the red stimulus light to acquire control over responding. The light was on only during the hour of food availability, and the start time of the feeding hour was changed daily.

7.3.1.4 - Procedure. For Group L-LL(r), the one-in-four omission procedure was continued throughout Experiment 6. For the first 5 days after the final blocking test of Experiment 5, subjects in Group L-LL(r) continued to receive reinforcement for lever presses (in the presence of the yellow light) during their established feeding time. On the 6th day the red light was placed in position. It was illuminated simultaneously with the yellow light during the feeding periods each day for the following 6 weeks. A series of three sets of test trials were then carried out. The first set of tests were for control by the red light, and these consisted of the presentation of the red light alone either 12 hr before, or 12 hr after, the omission of an unsignalled feed period (i.e. a feed period in which no stimulus lights were presented). For both subjects in this group, the first test was carried out before the omitted feed and the second after the omitted feed. Following four tests of responding to the red light, four tests of responding to the yellow light and then four tests of responding to the red light and the yellow light in compound, were carried out. These last two sets of tests were run to check that any decrement in response to the red light (compared with their response to the yellow light following Stage 2 of Experiment 5) was not due to extended exposure to the one-in-four omission procedure or to the cumulative effect of non-reinforced presentation of lights during tests.

The procedure used for lever and discrimination training for Group L(r) was identical to that used for Group L-TL in Stage 1 of Experiment 5. This included the presentation of the light stimulus for 1 hr per day, the procedure for determining the time of each day's trial, and the use of the one-in-four omission procedure. No compounding of stimuli was carried out, and the experiment was not continued beyond a point equivalent to the end of Stage 1 for Group L-TL. The final four non-reinforced presentations of the red light (arising from the one-in-four days omission procedure) were used to assess discriminative control.

Discrimination ratios for light stimuli used in Experiment 6 were calculated in the same way as they were in Experiment 5.

7.3.2

Results

Discrimination ratios and absolute response rates during the test trials with the red light alone, the yellow light alone, and the red and yellow light in compound for Group L-LL(r), and during the final four non-reinforced presentations of the red light for Group L(r), are given in Table 7.5. Group mean discrimination ratios are shown in Figure 7.9, and group mean response rates during the non-reinforced light presentations are shown in Figure 7.10. It can be seen from these data that for Group L(r), the red light produced discrimination ratios and response rates that were similar to those for the yellow light in Experiment 5 (Group L-TL, Stage 1).

parentheses.						
	Trial	1	2	3	4	
Group	Subject					
L-LL(r) Red	2	0.50 (0)	0.83 (4)	0.05 (0)	0.66 (1)	
	8	0.50 (2)	0.50 (0)	0.75 (2)	0.94 (14)	
L-LL(r) Yellow	2	0.87 (6)	0.92 (10)	0.95 (19)	0.92 (22)	
	8	0.97 (28)	0.90 (8)	0.67 (1)	0.50 (0)	
L-LL(r) Red/Yellow	2	0.99 (76)	0.86 (5)	0.98 (41)	0.94 (15)	
	8	0.97 (27)	0.92 (23)	0.50 (0)	0.75 (2)	
L(r)	11	0.97 (35)	0.97 (36)	0.94 (16)	0.89 (16)	
	12	0.99 (65)	0.94 (16)	0.97 (32)	0.95 (41)	

Table 7.5

Discrimination ratios calculated for non-reinforced presentations of light stimuli in Experiment 6. The number of responses made in the presence of the light is given in parentheses.

Note. For Group L(r) the values are taken from the final four non-reinforced trials of Stage 1. For Group L-LL(r), the values are taken from the four non-reinforced test trials with the red, yellow, and compound red/yellow stimuli.



Group

Fig. 7.9. Group mean (±SE) discrimination ratios (see text for details of calculation). For Group L(r) (N=2), the values are averaged over each subject's performance in the final four non-reinforced trials of Stage 1, and for Group L-LL(r) (N=2) the values are averaged over each subject's performance in the four non-reinforced test trials with each of the red, yellow, and compound red/yellow stimuli.



Fig. 7.10. Group mean (±SE) rates of non-reinforced responding (responses per hour) in the presence of stimulus lights during the trials used to calculate the discrimination ratios shown in Figure 7.9. Details of averaging procedure are as in Figure 7.9.

The group mean discrimination ratios for Group L-LL(r) with the yellow light alone, and with the yellow and red lights in compound, were also similar to that for the yellow light in Group L-TL following Stage 1 of Experiment 5. However, for the red light alone, both the group mean discrimination ratio and the response rate, were much lower. The response rates for the yellow stimulus alone, and for the red/yellow compound, were lower than those for the yellow light in Group L-TL, but higher than for the red light alone in Group L-LL(r).

7.3.3

Discussion

The performance of Group L(r) demonstrates that the red light was an effective discriminative stimulus. The performance of Group L-LL(r) when tested with the red light alone suggests that discriminative control by the red light was attenuated by compounding with the pretrained yellow light. Although the performance of these subjects on subsequent tests of responding to the pretrained stimulus (Group L-LL(r) Yellow) and to the compound stimulus (Group L-LL(r) Red/Yellow) shows that this effect was not simply due to increasing experience of the non-reinforced presentation of light stimuli, some effect of serial position is suggested. The mean discrimination ratios and response rates for these last two sets of test trials were marginally smaller than they had been for the same subjects following Stage 2 of Experiment 5. Even so, their response to the uncompounded red light during the uncompounded test trials was substantially lower than in any other condition. This blocking effect occurred even though the blocked stimulus was paired with reinforcement for an entire hour, nearly every day, for 6 weeks.

However, it should be noted that despite the general trends shown in the group means, the data from individual trials given in Table 7.5 are rather variable in places. For example, Subject 8 emitted fewer responses on the third and fourth trials than on

the first and second trials with both the yellow light alone and with the yellow/red compound. The level of variability suggests that further replication is needed to establish the reliability of these data. This issue will be discussed further in Chapter 8.

7.4 GENERAL DISCUSSION

The results of Experiment 5 suggest that temporal control was not overshadowed (Group TL) or blocked (Group L-TL) by the visual discriminative stimulus, and that control by the visual discriminative stimulus was not overshadowed (Group TL) or blocked (Group T-TL) by discriminative control resulting from the temporal contingency. The finding that blocking with an intertrial interval of 23 hr was possible (Experiment 6) shows that the lack of this effect in Experiment 5 was not simply due to the particular schedule parameters used.

The greater emphasis placed here on relative rather than absolute rate requires some further discussion. In the present case, it is assumed that equal degrees of discrimination of the visual stimulus will be reflected in equal discrimination ratios, and that equal degrees of temporal discrimination will be reflected in equal quarter-life values. Relative measures are designed to take account of the effect of baseline rates on subsequent performance and discrimination is, by definition, relative. It need not bear any formal relation to absolute measures as long as there is a consistent difference in performance between two or more instances. An alternative approach might be to compare absolute rates during light presentations or during feeding hours across Stages or across subjects. As noted above, the absolute rates during the temporally-fixed "feeding hours" of Experiment 5 did vary considerably across groups, and if these absolute measures were taken as an index of control then it would be concluded that compounding temporal and visual contingencies (Group L-TL and Group TL) led to a substantially lower degree of temporal discrimination than was the case when the temporal contingency operated alone (Group T-TL). The position taken here is that

compound training did have an effect on behaviour, but, because the quarter-life values were similar across groups, this effect was on absolute rate rather than on temporal discrimination.

The problem of whether to emphasise relative or absolute measures seems less acute when the data on control by the stimulus lights are considered. In Experiment 5, for example, the response rates during light presentations were fairly similar across groups (Figure 7.7) and so provide a picture which is consistent with that provided by discrimination ratios (Figure 7.6). However, the question of whether absolute or relative measures should be emphasised remains even when they happen to agree. Because absolute rates are not adjusted for the baseline from which they arise, comparisons between subjects, let alone between groups, will take less account of individual differences than will relative measures. A finding that the rate of responding of a particular subject is higher than that of another may simply reflect a particular difference in physiology or in behavioural history that is unrelated to the experimental manipulation. For example, a fish that is slightly smaller than average might respond at a lower rate because its energy requirements may be lower, or, indeed, at a higher rate because it has a higher growth rate. In analysing behavioural transitions, it is preferable to use the subject's own behaviour as a baseline against which the effect of an experimental variable is assessed (see Sidman, 1960 for a discussion on this point).

Unfortunately, the nature of a blocking experiment is such that comparisons must be made between subjects. The blocking effect is a result of a particular conditioning history and so can only be assessed in relation to a similar subject that has a different history. Because of the potential for error introduced by individual differences, the use of relative measures in the between-subjects comparison is unavoidable. The possibility that any differences in relative measures of discrimination may have arisen through nonspecific factors (such as maturation) can only be addressed by replication. In the present experiment, this was done within subjects by using a series of four tests rather than relying on data from a single trial, and between subjects by having more

than one subject in each condition. It would have been better to carry out replications with more subjects in each condition (see Chapter 8 for a further discussion on this point), but even so, the data were reasonably consistent across the two or three subjects in each group.

A further problem in the measurement of behavioural transitions is the possibility of an interaction between baseline rate and test rate. More specifically, it could be that the changes in behaviour that are indexed by discrimination ratios could be different where the baseline rate was low compared to where the baseline rate was high. For example, where the number of responses during the hour preceding a light presentation was 0 and the number during the light presentation was 5, the discrimination ratio would (with the addition of a constant of 1) be 0.86. Where the baseline rate was 95 and the test rate was 100, the ratio would only be 0.51. The same absolute change produces a greater relative change for subjects with lower initial rates than for those with higher initial rates, and in practice a ratio is more likely to be high where baseline rates of behaviour are low. However, it might be that a change in rate between 0 and 5 is behaviourally insignificant, whereas an increase from 95 to 100 responses might represent particularly strong stimulus control because the rate was increased close to the maximum that the subject could achieve. Here, perhaps, the calculation of difference scores rather than discrimination ratios would give a less biased picture. In the example under consideration the difference score would be identical. However, this re-opens the question of behavioural significance, but in a slightly different form. The index of change is now equal across subjects, but a difference of 5 responses may be small for a subject which tends to respond at a high rate, it may be large for a subject which responds at a low rate. Indeed, probabilistically there is likely to be greater variation around a higher number than around a lower number but the same absolute change produces a lower change ratio for subjects with a lower baseline rate. For these reasons, comparing scores across subjects that differ substantially in their baseline performance is problematic.

Given that both ratios and difference scores leave the question of behavioural significance open, the ratio is to be preferred. While a ratio has the same shortcomings as a difference score, it has the advantage that a high value is a good indicator of a large change in behaviour in any subject, whereas it is not possible to determine whether a difference score of any particular value represents a change of similar magnitude between subjects. Further, the discrimination ratio has the advantage that it is the more conventional measure of change. In relation to the measurement of discrimination, perhaps the most important question is whether the stimulus reliably affects rate. That is, whether the behaviour of the subject is reliably different in the presence when compared to the absence of the stimulus. This, again, is a question that must be addressed through replication.

The current results are not unique in their failure to show stimulus blocking. The absence of blocking has also been reported in other procedures. For example, Hall, Macintosh, Goodall, and dal Martello (1977) found that prior conditioning to a weak tone only partially attenuated acquisition of responding to a bright light. This result was attributed to the relative salience of the stimuli, but relative salience would not account for the present results because the absence of blocking was symmetrical.

A failure to find blocking has also been reported by LoLordo, Jacobs, and Foree (1982). An earlier study of treadle pressing in pigeons (Foree & LoLordo, 1973) had shown that, in tests of responding to the elements of a previously conditioned tone/light compound, the tone had more control over shock reinforced responding and the light had more control over food reinforced responding. An explanation for these findings was suggested in terms of "biological relevance". The asymmetrical relations between the stimuli and the reinforcers was said to have occurred because the tone was a more relevant stimulus for shock, and the light more relevant for food. LoLordo et al. (1982) examined these interactions further using an experimental design based on the blocking paradigm. Their results indicated that pretraining to asymptote with a tone as a discriminative stimulus for food and then compounding a light with the tone did not block responding to the light during a subsequent test phase. Equally,

pretraining with a light as a discriminative stimulus for shock did not block responding to a tone. As with the present experiment, there was little evidence of attenuation of control by the pretrained stimulus. Again, because the effect reported here was symmetrical, the concept of relative biological relevance would not explain the present results.

Interestingly, it is possible that LoLordo et al.'s (1982) failure to find blocking of a biologically relevant stimulus may have been (at least partly) due to the formation of a temporal discrimination. During pretraining, compound training, and testing, 5-s trials were separated by 15-s intertrial intervals. Responses within the intertrial intervals extended the interval by a further 15 s from the time of the response, and this would disturb the temporal regularity of reinforcement, but by the end of each phase, responses occurred during a mean of 81% of trials, and a high number of trials were received during each 1-hr session (a mean of 147 out of a possible 180). It is conceivable that a temporal discrimination developed as performance on the visual and auditory discrimination tasks improved. For the subjects, the schedule might have effectively become one involving a differential reinforcement of a low rate of responding (Ferster & Skinner, 1957). Any temporal control acquired during training may have persisted during the testing phase, with subjects responding at appropriate intervals regardless of the presentation of exteroceptive stimuli. This would add to, or could possibly be solely responsible for, the effect that was interpreted as the absence of blocking of a biologically relevant stimulus. Further, the formation of a temporal discrimination might explain the lack of attenuation of control by the pre-trained stimulus.

An interaction in control of a type more like that observed here was that reported by Terman et al. (1984). They examined behaviour under conditions where timing based on a circadian process and timing of a cued, non-circadian, fixed interval both predicted reinforcement. Rats were maintained on a schedule where food reinforcement for lever pressing was available for a period of 4 hr at a fixed time each day. Subjects were then provided with one of a range of durations of an auditory cue

that terminated at the onset of the feeding period. When no auditory cue was available, a sustained acceleration in responding began about 9 hr before the feeding period. The provision of auditory cues altered, but did not eliminate this pattern. Precue accelerations in responding were still present, although they started later in the inter-reinforcement interval (at between 7 and 4 hr before the feeding period). Terman and his colleagues suggested an "interaction hypothesis" to explain the perseverance of responding that anticipated the tone. This proposed that, where circadian and noncircadian timing processes predict the same event, response patterns result from an interaction between two classes of internal timer. A circadian timer remains engaged, but the provision of cues for a non-circadian timer allows more conservative probing for reinforcer availability.

As with the schedule used by Terman et al. (1984), the schedule used in the present experiments provided temporally fixed daily feedings, and so the results could have been influenced by circadian timing (see Chapter 3, Section 3.4). However, an alternative explanation of Terman et al.'s (1984) results may be possible. It was evident that temporal control was not substantially attenuated, and that control by the auditory cue was not blocked. Perhaps, rather than resulting from an interaction between two classes of timer, the perseverance of control by the inter-reinforcement interval could be explained, to some extent, by the absence of substantial interference between control by exteroceptive and interoceptive discriminative stimuli. Control acquired by the exteroceptive cue modulated responding under the control of the 20-hr inter-reinforcement interval, but the most striking effect of this modulation appears to been on absolute rather than relative rates of responding. Where the auditory cues were present, overall response rates were far below those observed when the cues were not present.

In Experiment 5 of the present study, the main effect of concurrent visual and temporal contingencies was also an attenuation in absolute rate of responding during the inter-reinforcement interval. This effect occurred even though the exteroceptive cue was presented simultaneously with the period of food availability and so would

not have required any class of timing to function as a discriminative stimulus. It seems unlikely that the reduction in response rate when the light stimulus was made available to subjects in Group T-TL in Stage 2 of Experiment 5 was simply due to a reduction in uncertainty as to the time of reinforcement that allowed more conservative probing. There was no uncertainty associated with the visual stimulus (beyond that caused by the omission procedure, which applied equally to the temporal contingency).

The present results require an explanation that does not depend on concurrent timing processes. While, in common with Terman et al. (1984), it may be reasonable to assume that interoceptive stimuli control temporally coordinated behaviour, and that these stimuli interact with other stimuli in ways that may differ from interactions in compounds of exteroceptive stimuli, it is not necessary to invoke distinct timing processes with peculiar properties. Interoceptive stimuli associated with temporal discrimination may simply control behaviour in parallel, rather than in competition with exteroceptive discriminative stimuli. The primary effect of simultaneous control of this type may operate on absolute rate rather than on discriminative control.

This suggestion is made plausible by data showing simultaneous temporal discriminations. In an experiment with pigeons, Dews (1962) observed temporal discrimination under the control of a negative discriminative stimulus that was presented during the interval of a fixed-interval schedule. Using a similar procedure, Meck and Church (1984) found that rats performed temporal discriminations simultaneously and independently, without mutual interference. If concurrent temporal discriminations can be formed without mutual interference, it may be that they can control behaviour simultaneously with other types of discrimination.

To summarise the results of Experiments 5 and 6, blocking and overshadowing procedures failed to produce attenuation between temporal and visual discriminations, although the blocking procedure did produce attenuation of discrimination between two visual stimuli presented on a similar schedule. These findings are presented in terms of discriminative control of behaviour, and it is argued that they do not require

references to a functionally distinct stimulus class such as that of zeitgeber. The possibility that the lack of substantial interference between temporal and visual discriminations may be a consequence of a more general relationship between interoceptive and exogenous discriminative stimuli warrants further investigation.

8.0 GENERAL DISCUSSION

Temporal control of food-reinforced lever-pressing was demonstrated in groups of mullet and groups of goldfish in Experiment 1, and in individual goldfish in Experiments 3, 4, and 5. Experiments 2 and 4 demonstrated that this temporal control was not dependent on the presence of a laboratory light cycle. In Experiment 5, temporal control developed where responding was already under the control of a discrete, exteroceptive, discriminative stimulus, and control by a discrete, exteroceptive, discriminative stimulus developed where responding was already under temporal control. The results of Experiment 6 suggest that this lack of interference in the acquisition of control was not simply a result of the unusual schedule parameters used in Experiment 5. In the present Chapter, some general issues arising from these results will be discussed. Reversing the order of the concerns of preceding Chapters, the topics will progress from the theoretical to the applied. The first of the theoretical issues to be discused will be the nature of temporal control, particularly under schedules of circadian periodicity. This will be followed by a brief examination of more general problems in the study of temporal discrimination, and finally, the implications of the present work in the fish farming industry will be addressed.

As discussed in Chapter 3, the study of temporal control has been a concern of both experimental psychology and of chronobiology. The two disciplines have, in the main, examined different aspects of this topic and little interdisciplinary work has been undertaken. However, differences in terminology and perspective may, to some extent, have obscured the degree to which the findings of the two areas overlap (see Chapter 3, Section 3.6). Because this thesis addressed the function of exteroceptive stimuli in the regulation of responding on schedules with a circadian periodicity it is perhaps necessary to speculate further on the relationship between what chronobiologists term a "zeitgeber" and what psychologists term a "discriminative stimulus".

It was noted earlier (Chapter 6, Section 6.4) that a chronobiological account of the role of the light cycle used in Experiments 1 and 3 is possible. For example, there was a slightly longer period of responding (on average) under the continuous light of Experiment 4 than there was under a light cycle in Experiment 3. This difference was smaller than would be expected if a transition in the light cycle had functioned exclusively as a discriminative stimulus that marked the start of a 6-hr fixed interval to reinforcement (see Chapter 6, Section 6.4). In chronobiology, the difference between Experiments 3 and 4 might be explained with reference to the coordination of a circadian rhythm (see Chapter 3, Section 3.4) rather than with reference to discriminative stimuli. Under constant environmental conditions, behaviour under the control of a circadian rhythm will "free-run". The period of the rhythm will be slightly longer or shorter than 24 hr and so will run out of phase with "clock" time. A zeitgeber is an environmental variable (such as a regular light cycle) that functions to synchronise a circadian rhythm with clock time. The light cycle used in Experiment 3 (and, indeed, in Experiment 1) may have functioned in this way, providing temporal cues that synchronised a circadian rhythm with the feeding schedule. This more precise rhythm may, in turn, have supported more accurate temporal discrimination, and the removal of the zeitgeber may have caused a reduction in accuracy that was reflected in a longer period of responding prior to feeding time.

However, the results of Experiment 5 raise the possibility that the data from Experiments 3 and 4 may be explained without reference to the coordination of a specific type of endogenous rhythm. Although the difference in the duration of nonreinforced responding between Experiments 3 and 4 was smaller than would be expected if the behaviour of the subjects in Experiment 3 had been controlled exclusively by the interval between light transitions and reinforcement (see Chapter 6, Section 6.4), this might have been due to an independence in control by the light transitions and by the temporal contingency similar to that observed in Experiment 5. As there were major procedural differences, only tentative generalisations between the findings of the two experiments can be made. For example, the lights used in Experiments 5 were only on during feeding times and were localised stimuli presented

close to the lever. Further, the light transitions in Experiment 3 occurred 6 hr before feeding time and, while the change in light intensity was large, might be considered more diffuse stimuli. Nevertheless, a lack of interference in discriminative control might, to some extent, account for the data from Experiment 3. If responding was concurrently under the control of the interreinforcement interval and of the interval between a change in the light cycle and the onset of the feeding period, then, because under continuous light (Experiment 4) responding solely under the control of the interreinforcement interval commenced 6-8 hr before a feeding time, the interreinforcement interval in Experiment 3 would control responding throughout the 6-hr interval between a light transition and reinforcement. That is, in Experiment 3, responding may have continued throughout the interval between a light transition and the feeding time (rather than there being a "fixed-interval pause" following the light transition) because it was simultaneously under the control of the 23-hr interreinforcement interval and of the 6-hr interval between the light transition and reinforcement. Any direct control by the light cycle would be masked because the light transitions coincided with the period during which responding was also under the control of the interreinforcement interval. Indeed, as the duration of responding in Experiment 4 was only marginally longer (on average) than it was in Experiment 3 the evidence for a deterioration in the accuracy of temporal discrimination in the absence of a light cycle in Experiment 4 is weak. If the light cycle had indeed functioned as a zeitgeber then much poorer temporal coordination of responding in Experiment 4 might have been expected.

If masking by control attributable to the interreinforcement interval is suspected, an obvious experiment would be to turn the lights on or off at a time other than the usual one in order to observe any changes in behaviour. Interestingly, this is precisely what is done in chronobiological research to verify the status of an environmental event as a zeitgeber (Aschoff, 1990) and was also the procedure used by Davis (1963) and Davis and Bardach (1965) in their phase-shifting experiments (see Chapter 3, Sections 3.4 and 3.5). The result of this type of experiment is a gradual shifting of the onset of the temporally coordinated behaviour under investigation. Over a few days

the onset of the behavioural rhythm advances or delays until it resumes its temporal relationship with the shifted "zeitgeber". Indeed, it is argued that, because behaviour which anticipates a fixed feeding time can persist when behaviour under the control of one of these "circadian rhythms" is shifted, food anticipation may be under the control of a separate timing system rather than the main, circadian, pacemaker (Aschoff, 1984).

However, the results of Experiment 5 suggest an alternative explanation of the role of a zeitgeber. There seems no pressing reason why the exteroceptive stimuli used in Experiment 5 should be conceived as having any peculiar properties that would justify the use of the term "zeitgeber". The term "discriminative stimulus" would be more appropriate, because it indicates that the lights set the occasion on which responses would be reinforced but does not imply any specific function in the regulation of particular internal processes. Indeed, as discussed in Chapter 3 (Section 3.6), where food-reinforced behaviour is concerned it is possible that the term "discriminative stimulus" is more generally appropriate than the term "zeitgeber". The results of Experiment 5 suggest that the discrimination of an interreinforcement interval and the discrimination of the relationship between an exteroceptive "zeitgeber" and reinforcement might be more or less independent. That is, the interreinforcement interval may control food-related behaviour in parallel with control acquired by the predictive value of the "zeitgeber" (or exteroceptive discriminative stimulus). Both enable the anticipation of reinforcement, but the presence of a "zeitgeber" is not essential to control by the interreinforcement interval. The gradual shifting in behavioural rhythms in response to a shift in the phase of a zeitgeber (described above) might simply be a result of adjustment to new temporal parameters. If a discriminative stimulus (or "zeitgeber") were to be presented later than usual, then behaviour under its control that is emitted at a time that would have been appropriate before the shift would now appear to be early. For example, if a stimulus which occurred at the same time each day were delayed by 6 hr, then responding would commence 6 hr before the shifted stimulus was due. The behaviour may come more precisely under the control of the new temporal parameters only over several days,
thus appearing as the stepwise adjustment considered typical of circadian control. As discussed in Chapter 3 (Section 3.6), this explanation does not require reference to any biological process other than those which must underlie temporal coordination of non-circadian intervals, and the suggestion that interoceptive temporal stimuli may control behaviour in parallel with exteroceptive stimuli would assign no special status to circadian scheduling and does not assign a peculiar role to any stimulus event that might otherwise be classified as a zeitgeber.

The most promising conceptual framework for the suggestion of parallel control may be that developed by Killeen (1992). In his "mechanics of behaviour", behaviour is seen as movement along a path in multidimensional "behaviour space". Behaviour space may be made up of a number of dimensions, including time, level of deprivation, orientation of sensors, and proximity of signs of reinforcement. Reinforcers are said to function as attractors in behaviour space, and conditioning involves the development of a trajectory through behaviour space toward a reinforcer. As conditioning proceeds, the trajectory increasingly approximates a geodesic. Stimulus blocking occurs because, once a trajectory is established through a stimulus to a reinforcer, it is difficult to move the trajectory through a new stimulus that does not offer a more direct route through behaviour space. However, even this conception of behaviour does not explain why an established cue should fail to block the acquisition of control by a novel stimulus. Perhaps the phenomenon reported in Experiment 5 is best conceived of as a consequence of a dimension in behaviour space being made relevant where the relevance of another dimension has already been established. That is, a stimulus space which could have been fully described by a graph with x and y axes, would now require a graph with x, y, and z axes. The shape of the curve described by the x and y coordinates need not be altered by the addition of z coordinates. In terms of blocking, the path of a trajectory through the pretrained dimension would not be affected by the extension of behaviour space when another dimension became relevant. The established trajectory remains the most direct route to reinforcement, and control over responding can not be captured by another stimulus operating in the same dimension. However, if a potential path to reinforcement opens

up in another dimension of behaviour space (e.g. the temporal rather than spatial dimension), then behaviour will be free to follow that path at no cost to the established one.

Nevertheless, blocking between visual and auditory stimuli is well documented (e.g., vom Saal & Jenkins, 1970). Indeed, there is no reason to suggest that this lack of interference would be anything other than specific to interactions between temporal and exteroceptive control. It might be tempting to speculate on similarities between the present results and those in the literature on taste-aversion learning (Revusky & Garcia, 1970) in order to suggest a more general distinction between control by exteroceptive and by endogenous stimuli. Taste-aversion learning is the most widely cited example of a behavioural phenomenon in which stimulus control appears to be subject to interactions which are different to those generally studied. However, the similarities between the present treatment of the results of Experiment 5 and the findings on taste-aversion learning are restricted to the supposition of a role for endogenous stimuli. The key finding in taste-aversion learning is that flavours have a high associative strength relative to an endogenous consequence (toxicosis) and that exteroceptive stimuli have a low associative strength under similar conditions. That is, flavours are preferentially associated with the delayed consequences of ingestion. This phenomenon has, in common with Experiment 5, the relationship between exteroceptive and interoceptive stimuli as the primary deviation from more conventional procedures. However, the arguments used against explanations based on biological significance and relative salience (Chapter 7, Section 7.4) also hold against preferential associability. The taste-aversion literature describes asymmetry in control of avoidance between flavours and exteroceptive stimuli. The lack of interference in control observed in Experiment 5 was symmetrical across the temporal and visual dimensions and so appears to be of a different class of phenomenon to that of taste-aversion learning.

Experimentalists rely on measures of performance (this restriction is not unique to radical behaviourism, but applies equally to psychologists that use behavioural

measures in an attempt to determine internal processes). In the study of performance on fixed-interval schedules, this constraint brings with it an awkward problem. It is not possible to determine the extent to which the responses of a subject reflects its discriminative capacity. In the present experiments, the act of pressing the lever required very little effort, and even if the subjects did have perfect temporal discrimination, there were few other potentially reinforcing activities available. It is conceivable that responses may have been emitted at times other than those during which immediate reinforcement was "expected" on the basis of a temporal discrimination. The comparative aspect of Experiment 1 brings this issue into particularly sharp focus. The mullet emitted far fewer nonreinforced responses than did the goldfish. It was not possible to determine whether this was due to sharper discrimination, or simply a higher threshold for the emission of responses in the mullet. This problem is not restricted to comparative psychology, however. The logic is identical in any comparison of discriminative performance, whether it be between subjects of different species, between subjects of the same species, or even between different instances of the same subject's behaviour.

The possible dissociation between performance and capacity has led to attempts to design what Lejeune (1990) describes as interference-free procedures. That is, procedures which disentangle "pure timing" from confounding variables. One solution to the problem of excluding "surplus" responses in timing experiments with pigeons has been suggested by Jasselette, Wearden and Lejeune (1990). By substituting treadle pressing with a perching response, they made the operant more difficult to perform and, therefore, less likely to be emitted unless there was a high probability that it would be reinforced. It is difficult to conceive of how this technique could easily be applied to lever pressing in fish, but an alternative that could be applicable to many phyla might be to provide two levers on which responses are reinforced. One of these could be set to give reinforcement at a continuous but low rate and the other to be ordinarily inactive but to give a high rate of reinforcement at specific times. On this schedule choice between levers might come under more direct control of temporal discrimination. A similar approach, but with each of two equally

reinforced levers active for only 1 or 2 hrs at different times each day, has been used successfully with rats by Boulos and Logothetis (1990). Subjects in their experiment emitted more responses on the lever that was appropriate for the next scheduled feeding time than on the lever that was inappropriate.

However, it may be that responding before the time at which reinforcement is due would not be eliminated even where alternative operants were available. Precisely fixed intervals are rare in nature, and (away from the equator) even the time of dawn and dusk changes over days. A measure of "inaccuracy" may be needed in order to keep track of any change in interval length. A gradually reducing interval would be tracked by "early" responses, whereas an increasing interval would be tracked by responding that continues past the "expected" time of reinforcement. Rather than reflecting inaccurate timing, it could be that responding during the interval on fixedinterval schedules is a fundamental property of timing behaviour that has evolved in a dynamic environment. This suggestion is consistent with Terman et al.'s (1984) (see Chapter 7, Section 7.4) finding that responding that anticipated a temporally fixed feeding time persisted where auditory cues were available, and with the results of experiments in which an exteroceptive "clock" is present during the interval of a fixedinterval schedule. In these experiments changes in a visual pattern (e.g., Ferster & Skinner, 1957) or in a sequence of visual stimuli (e.g., Palya & Bevins, 1990; Palya & Pevey, 1987) presented above the response key are correlated with successive portions of the interfood interval. Despite the presence of these temporally configured exteroceptive stimuli, responding is maintained to stimuli other than the final stimulus.

The suggestion that responding during the interval of a fixed-interval schedule may reflect an adaptive mechanism is also consistent with a recent proposal that an evolutionary / ecological perspective may be useful in understanding temporal control. Zeiler and Powell (1994) argue that performances observed in the laboratory will reflect processes that may have influenced survival and fitness in the history of a species, and so the development of rigourous techniques for analysing the the effects of temporal control may be required for understanding the mechanisms involved in the

temporal coordination of behaviour. It may be that the quest for "pure timing" procedures would be better postponed until such techniques are available. At present, there may be a temptation to focus on data which are consistent with a particular theoretical account and this may overshadow concern about exceptions. It is just as probable that the effects of phylogenetic contingencies were responsible for the difference in the emission of responses mullet and goldfish in Experiment 1 as it is that there are differences between the two species in discriminative capacity. Given the current inability to resolve the performance / capacity problem it seems that more comparative work is required. Once data on the behaviour of a larger number of species is accumulated, it may be that general principles, including those relating to phylogenetic history and those relating to ontogenetic factors, will become more accessible. Until then, it may be better to concentrate on determining the functional relationship between environmental variables and behaviour than on the development of general theories of timing.

It follows from the above discussion on cross species generality that the generality of findings over a number of other dimensions awaits empirical evaluation. One dimension seems particularly relevant to the speculations about the control of behaviour presented above and in the General Discussion of Experiments 5 and 6 (Chapter 7, Section 7.4). Specifically, the generality of the suggestion that the interaction in discriminative control between temporal contingencies and exteroceptive stimuli may be marked by a lack of mutual interference should be tested. The results of Experiment 5 were consistent with the suggestion, but there have been no attempts at replication with different interreinforcement intervals. If the processes involved in the control of behaviour on schedules which approximate the solar cycle are indeed similar to those of Experiment 5 would be expected where the interreinforcement interval was, for example, 5 hr or 29 hr. Indeed, similar results should be obtained on schedules where the interreinforcement interval is measured in minutes. If this latter possibility proved to be the case then it might have implications for a number of

studies where a temporal regularity is an explicit feature or, as in the case of LoLordo et al.'s (1982) experiments (see Chapter 7, Section 7.4), an incidental variable.

In Chapter 4 (Section 4.4) the general approach used in the analysis of data in this thesis was described. Inferential statistics have been avoided in favour of descriptions of behaviour. This has led to greater analytical resolution, in that the descriptions were more detailed than is likely had group means and critical values been of prime importance, but this resolution is not, in itself, sufficient. Skinner, writing in the late 1930's, addressed the issue of statistics in a way which, in an ideal world, would have been engraved on the cover of statistical textbooks ever since. "The recourse to statistics is not a privilege, it is a necessity arising from the nature of many data. Where a reasonable degree of smoothness and reproducibility can be obtained with a few cases or with single cases, there is little reason, aside from habit or affectation, to consider large numbers." (1938, p. 442). The initial question addressed in this thesis was whether fish are capable of temporally discriminating an operant lever press response, and it may be asserted with a high degree of confidence that, goldfish, at least, are. The relevant data were reproduced with a number of subjects under various procedures and were more or less identical in each case. However, the data on stimulus blocking were less orderly. The discrimination ratios and quarter-life values were generally similar within subjects and within experimental groups, but the amount of variation was sufficient to warrant caution.

Two methods which might help relieve the burden of doubt suggest themselves. One such would be to repeat the experiments with a new set of subjects and to continue repeating the experiments until there were an overwhelming body of evidence pointing one way or the other. The point at which one was overwhelmed would be judged on the basis of personal experience and not on statistical significance. The other method would be to attempt to determine the cause of the variation in the data and to replicate the experiments with these factors eliminated. This method is to be preferred, because larger numbers of subjects would be required only insofar as the data on individuals were variable. Eliminating variation would not only strengthen

confidence in the experimenter's understanding of the behavioural processes under investigation, but also brings with it the possibility of greater understanding of the processes underlying the variation itself. To summarise this argument, the more orderly the data, the fewer data are required. In the case of Experiment 5, more orderly data from a similar number of subjects would be preferred to variable data from a large number of subjects, even if the within group variations were outweighed by between group variations in tests of statistical significance.

The final part of this Chapter will return to the issue of aquacultural applications of behavioural science. During the latter half of the 20th century fisheries disputes have become commonplace. These disputes arise because traditional methods of fishing have been transformed by technology to a point where the problem is no longer the capacity of the industry but the capacity of the oceans themselves to recover from exploitation. There is wide acceptance that conservation measures are needed, but these have amounted to the placing of limits on the size and number of fish that may be taken. This has proved unpopular and difficult to enforce, and has had only limited success in accomplishing its goals. Size restrictions and catch quotas have led to the absurd practice of catching and discarding fish which are undersized or for which the quota has been exceeded in an attempt to harvest other fish which are of an acceptable size and for which the quota has yet to be reached. The discarded fish do not live to grow or to reproduce but are killed in the catching process.

Modern aquaculture has not developed in direct response to such absurdities, but rather because the "management" of marine resources has been such that, through scarcity, the price of fish has risen to a point where profits are to be had even though the intensive methods require a high capital investment and involve substantial running costs. There is, no doubt, potential for improving the efficiency of intensive fish farming by more widespread and sophisticated use of demand feeding technology, but intensive monoculture will continue to require large investments in stock maintenance.

The prospect of less intensive aquaculture using the method of recall ranching is attractive for various reasons. Firstly, because the fish would not be forced into such close proximity with one another the risks of injury and disease would be lower. Secondly, the waste produced by the fish would be spread over a larger area and so the environmental impact of the industry would be lower. Thirdly, the cost of cages and netting would be reduced, particularly for freshwater sites where the ranched area would have natural boundaries, and fourthly, the reduction in natural stocks will not have reduced the carrying capacity of the aquatic environment. The ranching operation may be able to take advantage of resources that once supported a natural population and so reduce the need for external sources of food for the introduced stock. Recall ranching programmes have already been set up (see Chapter 2,Section 2.3), but the problems associated with the sound generating equipment used to produce recall stimuli may limit their viability.

The results of the experiments reported in this thesis suggest that the need for sound generating equipment in such programs might be attenuated if temporally structured feeding regimes were to be employed. This suggestion, while it represents an extrapolation from the data of huge proportions, may be made with a reasonable degree of confidence. This confidence comes from the reliability of the phenomenon of operant temporal discrimination in the two species of fish tested, and from the data reported by other workers both in the laboratory (e.g., Davis & Bardach, 1965) and the field (e.g., Abbott, 1972) which is consistent with the temporal coordination of behaviour which would be necessary. There would be less confidence in suggesting that temporal discrimination could be relied on alone to recall fish to a feeding station, because no similar practice has been attempted under field conditions. Perhaps the strongest proposal that should be advanced at present is that, if acoustic stimuli are to be used in recall it is unlikely that temporal regularity would reduce, and there is a fair chance that it would increase, the number of fish which responded. Indeed, an extrapolation of the results of Experiment 5 might suggest that the temporal contingency and the auditory stimulus could control behaviour more or less independently. Perhaps fish would move into the general area of the feeding station on the basis of a temporal discrimination and engage in specific food-directed behaviour on hearing the sound stimulus.

It would not be difficult to incorporate the suggestion of a temporally predictable feeding schedule in an existing acoustic recall ranching operation. By comparing measures of the behaviour of the fish under the regular feeding regime with measures taken before it was introduced the effectiveness of the technique could be evaluated. The results of Experiment 5 suggest that temporal discrimination would develop even where an auditory discrimination had already been established. If so, the next step might be to discontinue the tone presentation to determine whether the temporal control of behaviour were sufficient alone. If this proved to be the case, it might be possible to substitute an accurate timepiece for the sophisticated sound generating equipment presently required. The benefits of such a technique would include, in addition to the potential for recalling fish from much greater ranges than may be possible using acoustic conditioning, a reduction in equipment costs which might open the technique to more widespread use in areas of the world where the demand for food is high but capital is scarce.

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APPENDIX A

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Temporal Discrimination Learning of Operant Feeding in Goldfish (Carassius auratus).

A report based on Experiments 3 and 4 (Chapter 6.0) of this Thesis, jointly authored with David Stephenson and Donald E. Wright, and published in the Journal of the Experimental Analysis of Behavior (1994, **62**, 1-13).

TEMPORAL DISCRIMINATION LEARNING OF OPERANT FEEDING IN GOLDFISH (CARASSIUS AURATUS)

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Operant temporal discrimination learning was investigated in goldfish. In the first experiment, there was a fixed daily change in illumination. Eight subjects were trained to operate a lever that reinforced each press with food. The period during which responses were reinforced was then progressively reduced until it was 1 hr in every 24. The final 1-hr feeding schedule was maintained over 4 weeks. The feeding period commenced at the same time each day throughout. The food dispensers were then made inactive, and a period of extinction ensued for 6 days. The pattern of responding suggested that the fish were able to exhibit temporal discrimination in anticipation of feeding time. This pattern of responding persisted for a limited number of days during the extinction procedure. The second experiment produced evidence that operant temporal discrimination could develop under continuous illumination.

Key words: temporal discrimination, anticipation, feeding schedules, time of day, fixed-interval schedule, lever press, goldfish

Temporal rhythms are evident in the dayto-day behavior of nearly every living organism. Sometimes these rhythms result from simple reactions to regular environmental events, but often they appear to involve some innate timing mechanism (Cloudsley-Thompson, 1980).

The ability of mammals to apply discrimination of intervals in the order of hours to the regulation of operant responding is well established (Armstrong, 1980; Boulos & Ter-man, 1980; Terman, Gibbon, Fairhurst, & Waring, 1984). Although there have been a number of studies that have demonstrated that fish will learn operant responding under the control of visual or acoustic discriminative stimuli (Abbott, 1972; Tennant & Bitterman, 1975; Wright & Eastcott, 1982) and shortinterval temporal stimuli (Rozin, 1965), there are no reports of operant responding during long-interval temporal stimuli. However, in their natural environment, many species of fish do coordinate their activity with diurnal rhythms such as the onset of dawn and dusk (Müller, 1978).

Classically conditioned, temporally coordinated feeding has been observed in aquariumhoused killifish (Fundulus heteroclitus) and bluegills (Lepomis macrochirus) (Davis & Bardach, 1965). These subjects were exposed to artificially controlled light cycles and were fed by hand at fixed times each day. The fish were given no external cue other than a regular feeding schedule and the amount of time elapsed (typically 6 hr) since the lights were turned on. It was found that regular regimes resulted in distinct bouts of activity that anticipated feeding time. Subsequent shifts in light onset and feeding times resulted in corresponding shifts in prefeeding activity after 1 to 3 days of exposure. Further experiments demonstrated that a prefeeding response developed even when fish were kept in continuous light (as long as food was delivered at regular intervals).

Davis and Bardach (1965) suggested that the prefeeding response was the result of the association between the act of feeding and the phase of an endogenous rhythm. Because the time of the prefeeding activity could be affected by altering the time of the onset of light, they hypothesized that this feature of the environment, although not essential, could be used in conjunction with the regularity of the feeding times to coordinate the endogenous rhythm.

Although Davis and Bardach (1965) did not make food contingent on the behavior of their subjects, several studies of acoustic conditioning (Abbott, 1972; Fujiya, Sakaguchi, & Fukuhara, 1980; Midling, Kristiansen, Ona, & Oeiestad, 1987; Wright & Eastcott, 1982) have shown that fish will learn an operant response

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in regimes that feature some temporal regularity. However, these experiments were not directed at temporal discrimination, and so the temporal contingencies were confounded with immediate, exogenous, acoustic cues.

The present experiments investigated longinterval temporal discrimination in the absence of such cues. In Experiment 1, aquarium-housed goldfish were trained to press a lever in order to activate a food dispenser that was operational only at certain fixed times. The only predictive external cues were the temporal regularity of the light cycle and feeding schedule. If time served as a discriminative stimulus, the number of lever presses immediately preceding these feeding periods would be expected to be higher than at other times during the temporally restricted feeding regime, and indeed, higher than at any time during a temporally unrestricted feeding regime. Further evidence of temporal discrimination would be provided if, when feeding is temporally restricted, there was less lever pressing at times other than those preceding the feeding periods than there was at equivalent times when feeding is unrestricted. In other words, if feeding time becomes a positive discriminative stimulus, then times not associated with feeding should take on the properties of a negative discriminative stimulus.

EXPERIMENT 1

Method

Subjects. The subjects were 8 goldfish (Carassius auratus), with a mean standard length of 9.75 cm (SD = 1.3 cm), obtained from J & K Aquatics Ltd., Wellington, Somerset. An additional 8 goldfish of a similar size were used as "companion" fish (see below) but did not contribute to the data. Prior to the experiments, the fish were not kept on any fixed feeding regime or used in any other experiments. All animals used in these experiments were treated in accordance with the "Ethical Principles of Psychologists" (American Psychological Association, 1981).

Goldfish are an ornamental cultivar of the cyprinid family. Feral populations usually inhabit shallow, densely vegetated pools with muddy bottoms and diversified shorelines (Lelek, 1987), and feed on a broad range of food types, including plants, insect larvae, and plankton (Wheeler, 1978). Because goldfish

have no stomach, their capacity for storing food is limited. When food is continually available, they tend to feed for extended periods rather than taking distinct meals (Rozin & Mayer, 1961). Studies of the relation between the light cycle and the pattern of free feeding (Rozin & Mayer, 1961) and activity (Spoor, 1946) in goldfish have shown a measure of variability among individual subjects. Most are predominantly diurnal, but some display patterns that are predominantly nocturnal, and others show no fixed pattern at all.

Apparatus. The fish were housed in glass aquariums (90 cm by 30 cm by 38 cm). Following an initial training stage, each aquarium was divided in two by a plastic grill placed across the center of the longest side. The aquariums were screened off from each other with opaque plastic sheeting. The water was maintained at 20 °C and was aerated and filtered using standard laboratory equipment. Cleaning of the aquariums took about 10 min and was carried out approximately once every 3 days, between 9:00 a.m. and 12:30 p.m. or 2:30 p.m. and 7:00 p.m. The precise time (within these limits) was varied.

A food dispenser controlled by a fish-activated lever was mounted at one end of each aquarium. The lever consisted of a stainless steel rod (20 cm long, 0.3 cm diameter) with the lower tip sleeved with thick-walled silicone rubber tubing (0.4 cm diameter). This projected approximately 0.5 cm below the water surface, 8 cm to the side of the point where food was dispensed. The rod was held in a near-vertical position and pivoted 7 cm from its lower tip. When the lower end was moved, the upper end passed through an opto-electrical sensor that was connected to the control equipment. The fish activated the lever by pushing the lower tip 0.75 cm forward with its mouth. In order to reactivate the lever it had to be released, at which point gravity returned it to its resting position. A force of at least 0.0004 N was required to activate the lever. This was sufficient to prevent activation by water movement.

Two distinct lever-pressing techniques have been observed with this apparatus. Fish either make a single press by swimming up to the lever, pushing it, releasing it, and then swimming around in an arc to consume any food that has been dispensed or to prepare for the next activation, or they remain stationary in front of the lever and make repeated activations, using their pectoral fins to move forward and backward the required distance.

The dispensers were actuated by a 0.5-s pulse of power to a 22-V solenoid. This moved a sliding plate away from an aperture in the base of a food hopper. The plate was returned to its resting position by means of a steel spring. The size of the aperture was adjustable, and for these experiments it was set to dispense approximately 0.05 g of Hikari staple fish diet (a floating fish food) in the "baby" pellet size on each activation. The need for a 0.5-s pulse of power to activate the dispensers meant that the maximum rate at which reinforcement could be delivered was restricted to 120 per minute. In practice, the rate of responding never approached this figure. The food was delivered to a point 12 cm inward from the center of one end of the aquarium. A second dispenser was mounted in a similar position at the other end of each tank. The second dispenser was activated simultaneously with the first and was not supplied with a separate lever.

One additional dispenser was mounted in a narrow space between the rows of aquariums and was set to operate in randomly spaced bursts of up to 20 activations. This "decoy" feeder was used to reduce the availability of systematic, temporal cues from the sound of dispensers operating in adjacent aquariums. No food was provided by the decoy dispenser.

The control and recording system consisted of a BBC Model B microcomputer and an interface device. This allowed the experimenter to set the times during which activation of the lever would result in food being dispensed; the equipment also recorded the time of occurrence of all lever activations.

Lighting was provided by two 15-W fluorescent bulbs mounted directly above the aquariums. These were operated by a time switch that turned the lights on at 8:00 a.m. and off at 8:00 p.m. each day. In addition, an 11-W incandescent bulb was situated between the fluorescent bulbs and was left on continuously to provide low-level illumination even when the main lighting was switched off. A fixed daily light cycle was used in this experiment because Davis and Bardach (1965) suggest that this provides optimum conditions for the development of temporally coordinated prefeeding behavior. Light intensity at the water surface was 302 lx when the fluorescent bulbs were switched on and 12 lx when they were off.

The experiment was housed in a laboratory that was isolated from main corridors and was rarely used by other workers. The windows were covered with foil to block light from outside. The possibility that environmental disturbances beyond the control of the experimenters (e.g., traffic noise from the road outside) could be perceived by the fish cannot be ruled out. Although these were not apparent to the experimenters and were probably masked by noise made by equipment (pumps and filters), the experimental procedures were designed to reduce the possibility of such environmental stimuli being coordinated with relevant experimental events.

Procedure. The apparatus was set so that each lever press produced food at any time. One subject was placed in each of the tanks together with another fish. This second fish had not experienced any restricted feeding regimes but was already a reliable lever presser. This gave the opportunity for the subject fish to acquire the lever-pressing response through observational learning (Yamagishi & Nakamura, 1981). All subject fish were observed to be lever pressing within 7 days.

The experiment was divided into four stages. The first stage lasted 14 days and was designed so that the baseline feeding rhythms of the subject fish could be determined. The plastic grill was used to partition the tanks, with 1 fish in either end. Only the subject fish had access to the lever, but any presses activated both dispensers. This arrangement removed the need to feed the companion fish by hand and thus kept disturbances to a minimum. The "companion" fish is so termed because its role was to prevent the subject from exhibiting the alternating stereotypy and inactivity often observed in goldfish that are kept for extended periods in total isolation. Visual, auditory, and olfactory contact between the 2 fish remained possible despite the presence of the barrier.

The second stage involved restricting the periods when a lever press would be reinforced to a single 1-hr interval in each 24-hr period. These periods (feeding times) were timed to commence 6 hr after the lights were switched on for Subjects 1, 3, 5, and 7 (2:00 p.m. to 3:00 p.m.), and 6 hr after the lights were switched off for Subjects 2, 4, 6, and 8 (2:00 a.m. to 3:00 a.m.). The feeding time for Sub-



Fig. 1. Subject 5. Sum of lever presses during the 30 min immediately preceding the designated feeding time (2:00 p.m. to 3:00 p.m.) and nonfeeding time (2:00 a.m. to 3:00 a.m.), starting with the last 6 days of the first baseline stage (Stage 1, CRF), through the shaping of the restricted feeding schedule of Stage 2, and the 6 days without food (Stage 3, Extn), to the first 9 days of the second baseline (Stage 4, CRF). The ordinate axis is slightly displaced to allow inspection of the lower values; the abscissae denote the number of days since the start of Stage 1.

jects 1, 3, 5, and 7 was designated a nonfeeding time for Subjects 2, 4, 6, and 8 (and vice versa) for the purpose of analysis. Separate feeding times for different subjects were used to avoid the possibility of a regular external event being used to coordinate responses by all of the subjects.

The transition from continuous to restricted feeding was carried out over several days by restricting the period during which the dispenser would respond to a lever press to 12 hr on the 1st day and thereafter reducing the feeding period by 2 hr per day (provided that the subject had responded during the previous day's feeding period). These periods always began at the beginning of the target period. This procedure resulted in a progressive lengthening of the interval between periods of food availability while maintaining the temporal location of the start of those periods. The shaping process was necessary because there was no guarantee that responding would occur during the target period if the transition to restricted food availability was made directly. If all responses occurred outside the feeding times, the operant would rapidly extinguish. Once the subjects were responding during the target hour, they were kept on schedule for a further 4 weeks.

The third stage consisted of an extinction test, in which the dispensers were disabled for 6 consecutive days. The fourth stage involved a return to continuous food availability. This was done to in order to see if the restricted feeding regimes had produced any permanent effects on baseline responding. This stage lasted for 2 weeks.

Data were collected continuously, and were recorded as the total number of lever presses in each consecutive 15-min period.

Results

Subject 4 died of a bacterial infection, but the remaining 7 subjects all reached a stable level of responding during the period of unrestricted feeding (Stage 1). Subjects 2 and 7 displayed some evidence of a feeding rhythm during Stage 1. In order to attenuate any effects of preferred feeding times on responding during the restricted feeding stage (Stage 2), these subjects were subsequently allocated to feeding times during which baseline responding had been less frequent.

Figures 1 and 2 show the development over days of the effects of the contingencies of the various stages of Experiment 1 on lever pressing during the 30 min immediately preceding the feeding and designated nonfeeding times for Subjects 5 and 6, respectively. The response patterns of these subjects were typical of subjects feeding in the photophase (Subjects 1, 3, 5, and 7) and scotophase (Subjects 2, 6, and 8), respectively. Following the restriction of the feeding periods to 1 hr in Stage 2, the

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Fig. 2. Subject 6. Details as in Figure 1, except that the designated feeding time was from 2:00 a.m., and the designated nonfeeding time was from 2:00 p.m. to 3:00 p.m.

pattern of responding altered markedly. The rate of responding prior to the feeding times increased rapidly and then reached a more or less stable level after a period of about 20 days. The rate prior to the designated nonfeeding times remained close to zero throughout.

The mean level of lever pressing over five successive 24-hr periods on the initial baseline, restricted feeding, and final baseline schedules (Stages 1, 2, and 4) of the experiment are also given for Subjects 5 and 6 in Figures 3 and 4, respectively. Typically, a fairly constant rate of three to five presses per 15 min throughout each 24-hr period was observed during Stage 1. When a stable pattern of responding had been reached in Stage 2, a typical daily record showed a level of responding that was close to zero until between 4 and 6 hr before food became available. Once responding had begun, the rate accelerated almost linearly with time until it reached a level of approximately 40 responses per 15 min immediately prior to



Fig. 3. Subject 5. Mean and standard deviation of lever presses per 15 min over the last 5 days of Stages 1 and 2 and the first 5 days of Stage 4. The vertical bars indicate feeding (F) and nonfeeding (NF) periods. The lighting regime (main lights on at 8:00 a.m. and off at 8:00 p.m.) is indicated by the horizontal bar at the top.



Fig. 4. Subject 6. Details as in Figure 3.

feeding. During the hour of food availability, the rate of responding dropped to around 10 presses per 15 min, and then dropped back to zero within an hour of the end of the feeding period.

The mean level of responding during the 30 min prior to feeding and designated nonfeeding times over the final 5 days in Stages 1 and 2 and the first 5 days in Stage 4 is given for all subjects in Table 1. A repeated measures two-

Table 1 Number of responses in the 30 min prior to the feeding (F) and nonfeeding (NF) periods of Experiment 1.

Sub		Stage 1		Stage 2		Stage 4	
ject		F	NF	F	NF	F	NF
1	M	0.8	0.0	42.4	0.0	2.6	0.2
	SD	0.4	0.0	9.3	0.0	1.8	0.4
2	M	0.0	6.8	88.0	0.0	5.0	3.6
	SD	0.0	1.8	9.5	0.0	4.3	3.6
3	M	2.0	0.4	81.8	0.4	2.2	1.0
	SD	1.0	0.9	33.3	0.5	1.6	1.7
5	M	3.6	0.0	111.0	0.6	5.6	3.6
	SD	1.1	0.0	15.8	0.8	2.7	2.3
6	M	0.0	3.8	124.0	0.0	2.3	2.4
	SD	0.0	2.7	6.7	0.0	1.6	1.9
7	M	0.6	3.0	57.0	0.0	6.0	5.4
	SD	1.3	3.1	12.3	0.0	3.9	4.0
8	M SD	3.8	1.2	37.6	1.2	4.8	3.6

Note. Values averaged over the last 5 days of Stages 1 and 2 and the first 5 days of Stage 4. way analysis of variance (ANOVA) was carried out on these data. All data were squareroot transformed to stabilize variance. All significance levels were adjusted using Hunyh-Feldt epsilon. There was a statistically significant effect of Stage, F(2, 12) = 61.02, p <.0001, and of Time of Day, F(1, 6) = 119.72, p < .0001, on the mean number of lever presses recorded during the 30 min immediately prior to the feeding and nonfeeding times. The interaction between the number of lever presses prior to feeding and nonfeeding times and the three stages was also statistically significant, F(2, 12) = 52.35, p < .0001. Examination of the planned comparisons of means was carried out using the "contrast" facility on Super-ANOVA software (Abacus Concepts, 1989). The level of responding prior to feeding and nonfeeding times during the two baseline stages was not significantly different: Stage 1, F(1)= 0.06, p = .72; Stage 4, F(1) = 0.43, p =.46, but there were significantly higher response levels prior to feeding times during the stage of restricted feeding (Stage 2) than prior to all other times in all stages, F(1) = 216.74, p < .0001.

There was a lower mean rate of responding prior to the nonfeeding time during the restricted feeding stage (Stage 2, a mean of 0.31 presses per 30 min) when compared with the baseline level of responding (feeding and nonfeeding times in Stages 1 and 4, a mean of

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2.67 presses per 30 min), but not to a degree that achieved statistical significance, F(1) = 4.34, p = .08.

The mean level of responding during the 30 min prior to feeding times of the 3 subjects that fed during the dark phase of the light cycle was 83.2 (SD = 43.4) and was 73.05 (SD = 30.07) for the 4 subjects that fed during the light phase. A one-way ANOVA carried out on square-root transformed data suggested that no statistically significant differences in response rate were caused by this factor, F(1, 5) = 0.09, p = .78.

The response patterns of Subjects 5 and 6 over the 6 days of the extinction test (Stage 3) are given in Figures 5 and 6. These patterns were typical of all subjects tested. Over the 6 days of the test, the pattern of responding became less clearly defined. For the first 2 days, a distinct aggregation remained around the times that had previously been feeding periods, but for the remaining 4 days, response rates dropped close to zero. However, any responses that were made tended to occur near the previous feeding time.

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Once the subjects were returned to continuous food availability (Stage 4), responding quickly returned to levels and patterns that were nearly identical to those seen during the first baseline stage (Stage 1).

Discussion

The higher level of lever-pressing activity preceding the feeding time during restricted

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Fig. 6. Subject 6. Details as in Figure 5.

food availability (Stage 2) compared with levels prior to the nonfeeding time in the same stage and compared with baseline levels (Stages 1 and 4) strongly suggests that goldfish are capable of displaying operant temporal discrimination when the interval between opportunities for reinforcement is 23 hr. There was some support for the suggestion that nonfeeding times might take on the properties of a negative discriminative stimulus, because there was a lower mean rate of responding prior to the designated nonfeeding time of Stage 2 than during the equivalent period on the baseline phases. However, this difference did not reach statistical significance. It is possible that the lack of a significant difference was due to a "floor effect." The baseline levels were maintained at a rate from which it would be difficult to drop significantly lower.

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The response rates associated with feeding times located in the middle of the photophase and scotophase were very similar. It is possible that uncontrolled regular external events allowed the subjects to anticipate these feeding times, but efforts were made to maintain a stable environment, and it seems unlikely that appropriate stimuli would have occurred before both feeding times. Further, no differences in responding were evident on weekends or during holidays (when the pattern of events outside the laboratory should have been different to that occurring on weekdays).

Figures 3 and 4 show that the rate of responding dropped dramatically at the onset of the feeding periods in Stage 2. This low rate continued throughout the time of food availability, then fell to zero an hour or so after the end of the period. The reason for the low level of reinforced responding compared to the level of anticipatory responding may be that the subjects were spending time handling food and so had less time in which to activate the lever. During the approach to feeding time, there were no such distractions. It is equally true that there were no distractions following the feeding time, and although it is probable that motivational hunger would have been reduced by this time, an increased level of responding might have been expected. This lack of effect may be due to the subjects' behavior being controlled by the duration of the feeding period as well as the time of day at which it occurred. On the other hand, if this was the case, then it is difficult to see why the subjects continued to respond at all following the end of the feeding times, particularly when an unreinforced lever press indicated that reinforcement would not be available for another 23 hr.

Dews (1965) noted a similar phenomenon with pigeons on fixed-interval schedules of reinforcement when a negative discriminative stimulus was presented in alternation with a positive discriminative stimulus within each interval. The presence of the negative discriminative stimulus exerted a substantial inhibitory effect on responding, but this control was only slowly and progressively attained. If the nonfeeding period that followed the feeding period in the present experiment became a negative discriminative stimulus, it is possible that the continued responding (but at a decelerating rate) that followed the end of the feeding period represents a phenomenon of this type.

The key feature of the pattern of responding during the extinction stage (Stage 3) is that, although the magnitude of the response rate extinguished rapidly after the first 2 days, over those 2 days the temporal pattern remained remarkably constant (Figures 5 and 6). The 1st day on which reinforcement was omitted is functionally similar to a single unreinforced trial of the type used in the peak procedure (Catania; 1970). This procedure was devised as a method for obtaining a form of temporal generalization gradient that extends past the accustomed time of reinforcement. The conventional peak procedure provides data on the distribution of responding over time on unreinforced trials that are embedded within sessions on a fixed-interval schedule. These data are usually presented as the mean distribution of responses from a number of unreinforced trials, so a direct comparison with the single trials presented here is not possible. However, the reasonably symmetrical shape of the distribution and the close proximity of the peak response rate to the expected feeding time are reminiscent of the response distributions obtained from pigeons on intervals of 10 s (Catania, 1970), 30 s, and 50 s (Gibbon & Church, 1990).

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It could be that the decline in unreinforced responding over successive days in Stage 3 was simply due to inanition. The fish were given no food at all during this stage of the experiment and, because no measures of general activity were taken, no data are available to discount this possibility unambiguously. However, many species of fish undergo long periods of starvation in their natural environment (Larsson & Lewander, 1973), and goldfish have survived several months of starvation in laboratory studies (Love, 1980). Further, Spoor (1946) noted that, although activity declines markedly after a week of starvation, goldfish do not become completely inactive for more than an hour or two even after 2 weeks without food, and that activity levels return to those of unstarved fish within minutes of the reintroduction of food. In the present experiment the rate of reinforced responding also returned to levels similar to those of the first baseline stage soon after food was made available.

Even if the low rates of responding observed in the extinction stage had been a consequence of inanition, the finding that the anticipatory buildup persisted in the absence of reinforcement for at least 2 days suggests that the pattern of responses is unlikely to be entirely dependent on simple homeostatic or metabolic processes associated with increasing hunger or the emptying rate of the gut. This is concordant with the finding that short-interval operant temporal discrimination in goldfish is independent of simple metabolic rate. Rozin (1965) found no change in relative response rates on a fixed-interval 1-min schedule when ambient temperature was reduced from 30 °C to 20 °C. Goldfish are poikilothermic, and a decrease of this magnitude results in a halving of their metabolic rate.

A regular light cycle was used in Experiment 1 because Davis and Bardach (1965) found that this provided the optimum condition for the development of circadian temporal



Fig. 7. Mean and standard deviation of lever presses per 15 min over the last 5 days of Experiment 2. Bars indicate feeding (F) and nonfeeding (NF) periods. The main lights were on continuously.

discriminations. They suggested that the light cycle may act as a zeitgeber, contributing to the regulation of a circadian timing mechanism on which the discriminations are then based. Whether or not this is so, the presence of a light cycle in Experiment 1 does leave open the possibility that the interval being timed was 6 rather than 23 hr, with the transition between light and dark periods acting as a direct discriminative cue signaling the approach of feeding time. However, because Davis and Bardach (1965) found that a prefeeding response could develop under continuous light, we sought to evaluate the consequence of removing light cues on the development of operant temporal discrimination. The effect of continuous light on the goldfish's ability to learn the temporal contingencies of a new feeding time was studied in Experiment 2.

EXPERIMENT 2

Method

Subjects. Subjects 5, 6, 7, and 8 and their respective companion fish used previously in Experiment 1 served as subjects.

Apparatus. The apparatus was that used in Experiment 1. The tank partitions remained in place, and husbandry procedures were carried out as for Experiment 1.

Procedure. The lights were set to remain on continuously, and the fish were returned to a 1-hr restricted feeding regime directly following the final baseline stage (Stage 4) of Experiment 1. No training or shaping procedure was used. The time of food availability was varied among subjects such that fish that had the dispenser active from 2:00 a.m. to 3:00 a.m. during Stage 2 of Experiment 1 now had it active from 2:00 p.m. to 3:00 p.m., and vice versa. Data were collected over a 3-week period.

Results

Subject 5 failed to respond during the period of restricted feeding, and lever pressing extinguished. The other 3 subjects showed signs of anticipation within a week of the imposition of the new schedule. The pattern of the mean response rate over a 5-day period (commencing 2 weeks after the new schedule was imposed) is shown for the 3 remaining subjects in Figure 7. The mean level of responding during the 30 min prior to feeding and designated nonfeeding times over this period is given in Table 2.

All data were square-root transformed to stabilize variance, and a repeated measures one-way ANOVA was carried out. There was significantly more lever pressing in the 30 min prior to feeding times than prior to the designated nonfeeding times, F(1, 2) = 21.97, p < .05.

Discussion

Figure 7 shows that temporal discrimination did develop under a continuous lighting regime. This is consistent with the findings of Davis and Bardach (1965, Experiment 4) and extends their findings to explicitly operant behavior. The lack of a light cycle seems to have had little effect on the subjects' ability to develop anticipatory responding. It is not possible to say whether behavior could have adapted to the temporal contingencies equally well without the benefit of regular changes in illumination if the fish had never experienced the temporally contingent schedule of Experiment 1; this is a matter that requires further investigation.

GENERAL DISCUSSION

The contingencies of the present experiments might be considered to be similar to those operating on fixed-interval schedules of reinforcement (Ferster & Skinner, 1957). Consequently, previous findings concerning responding on fixed-interval schedules may help to illuminate the effect of the light cycle used in Experiment 1 on the pattern of anticipatory lever pressing. If the light transitions of Experiment 1 functioned as discriminative stimuli that signaled the beginning of a 6-hr fixed interval, then an increase in the length of the period of anticipatory activity when the 23-hr fixed interval of Experiment 2 was imposed would be consistent with the observed relationship between interval length and response patterns in other species (Ferster & Skinner, 1957; Lejeune, Richelle, Mantanus, & Defays, 1980; Mackintosh, 1974; Shull, 1971). A comparison of Figures 3 and 4 with Figure 7 shows that in Experiment 2, the buildup in activity prior to the feeding times did indeed extend over a longer period (typically 8 hr) than it had during Stage 2 of Experiment 1 (typically 6 hr).

The distribution of responses following prolonged exposure to fixed-interval schedules is more usually described with reference to the postreinforcement pause (Dews, 1978; Ferster & Skinner, 1957; Harzem, 1969) or to the breakpoint between periods of low and high rates of responding (Schneider, 1969). In the present experiments responding continued for a short while following the end of the feeding period, but was then nearly absent until a few hours before the next feeding period was due. At this point an acceleration in response rate occurred that continued up to the feeding time.

Table 2

Number of responses in the 30 min prior to the feeding and nonfeeding periods of Experiment 2.

Subject		Feeding	Nonfeeding	
6	М	140.0	0.0	
	SD	19.9	0.0	
7	M	48.4	0.0	
	SD	12.7	0.0	
8	M	68.4	5.0	
	SD	12.1	7.5	

Note. Values averaged over the last 5 days of the experiment.

Because the response rate progressively increased during this period of activity, it cannot be described as a typical break-and-run performance (Schneider, 1969). Similarly, the classification of the preceding period of inactivity as a pause would not be strictly equivalent to that applied to shorter intervals (some responding did occur during the period of inactivity). However, if allowance is made for the possibility that the unusual length of the intervals involved may have led to a number of isolated lever presses within what would otherwise be a pause, then finding that this "pause" extended when the interval was extended would also be consistent with findings in the fixed-interval literature.

For conventional fixed-interval schedules, the length of the pause has been described as a negatively accelerating function of increasing interval duration (Lowe, Harzem, & Spencer, 1979; Wearden, 1985). In other words, although the absolute duration of the pause increases with increasing interval length, the proportion of the interval during which responding is absent is smaller for longer interval values. If the difference between the performance observed in Experiment 1 and that observed under the constant lighting of Experiment 2 had indeed been due to an effective lengthening of the fixed interval, the postreinforcement pause in Experiment 2 would be expected to constitute a smaller proportion of the interreinforcement interval than the pause between the time of the light/dark transition and the onset of responding in Experiment 1. The actual values displayed the opposite relationship. In Experiment 2, the postreinforcement pause spanned approximately two thirds of the interval, whereas in Experiment 1 the onset of responding was almost coincident with the light/dark transition. This suggests that
the light cycle did not function simply as a signal for the start of a 6-hr interval in Experiment 1.

The reason for this result may lie in a particular feature of schedules that approximate the solar cycle. Such schedules permit the contribution of circadian timing to the relation between the probability of reinforcement and the passage of time (Boulos & Terman, 1980). For example, rats show more distinct anticipatory lever pressing when food is made available according to a 24-hr rather than a 19- or 29-hr cycle (Bolles & Stokes, 1965). Even when immediate exogenous cues are available, anticipation of a fixed daily feeding period may persist. In an experiment with rats, Terman et al. (1984) found that, on a schedule in which 4 hr of reinforcer availability were followed by 20 hr in which lever presses were not reinforced, anticipatory lever pressing was reduced but not eliminated by the provision of auditory cues that commenced only minutes before feeding time. This result was attributed to an interaction between circadian and shortinterval timing. A similar interaction might have been responsible for the effect of the light cycle in Experiment 1, in that the light transitions may indeed have served as discriminative stimuli, but the observed pattern of behavior could have arisen from a combination of conventional fixed-interval and circadian timing processes.

Alternatively, it could be that the longer postreinforcement pause seen in Experiment 1 was due to more accurate timing being possible in the presence of a light cycle because, in line with the function suggested by Davis and Bardach (1965), it optimized the synchronization of a circadian pacemaker with the 24-hr cycle, which in turn provided more temporally precise endogenous cues.

If the temporal patterning of responses was dependent on an endogenous circadian rhythm, the time of peak responding would be expected to "free run" in a constant environment (Boulos & Terman, 1980). This condition could have been achieved in Experiment 2 by making the dispensers inoperative following the establishment of anticipation in continuous light. However, as Figures 5 and 6 show, responding dropped to near-zero levels after only a few days when reinforcement was withheld; thus, it is unlikely that enough data would have been available to show any systematic shift in the patterning of responses. The relationship between chronobiological factors and temporal regulation on operant schedules has received little attention (Lejeune, Richelle, & Mantanus, 1980), and the question of whether the anticipatory behavior shown by the subjects in the present experiments is best characterized as a result of circadian timing, exposure to an unconventional variety of fixed-interval schedule, or indeed, a combination of the two, remains open.

A problem with the present (and all) discrimination experiments is the possibility of a disparity between the subject's performance and its capability. The increase in lever pressing commenced several hours before the feeding times were due. As noted by Ferster and Skinner (1957), a subject with a perfect sense of time should not respond before the feeding time at all. It is not clear whether this long buildup was a consequence of a limit on control by the passage of time or of some other factor, such as a greater tendency to activate the lever when increasing hunger had intensified the motivation to feed. The act of pressing the lever requires very little effort, and for a laboratoryhoused subject there are few other activities to compete for attention.

There is a potential application for operant temporal discrimination in commercial aquaculture. Acoustic discriminative stimuli have already been used to influence the activity of relatively free-swimming fish. This form of aquaculture is known as recall ranching. In Japan, Fujiya et al. (1980) implemented a restocking program that relied on a conditioned tone-food association to keep juvenile farmed fish within the confines of a sheltered bay (away from areas heavily fished by commercial fleets) until they reached a marketable size, and Midling et al. (1987) carried out a similar program in Norway. The results of the present experiments suggest that the need for soundgenerating equipment in such programs might be attenuated if temporally structured feeding regimes were employed. If this proved to be the case, it might be possible to substitute an accurate timepiece for the sophisticated soundgenerating equipment presently required.

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