

Interactions Between Pavlovian Conditioning and  
Behavioural Function in the

Male Blue Gourami

by

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University of Manitoba

This thesis is submitted in partial fulfilment  
of the requirements for the degree of Doctor of Philosophy

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## Abstract

Hollis (1982) postulated the prefiguring hypothesis in an attempt to explain how learning interacts with evolutionary processes. It was postulated that as a result of the stimulus-stimulus (S-S) associations in Pavlovian conditioning an organism was able to prepare for the imminent arrival of biologically significant events. In as much as conditioning was able to permit the organism to interact optimally with a biologically significant event learning was said to increase the probability of successful reproduction or fitness and thus have function.

In support of the prefiguring hypothesis, Hollis (1982, 1984, 1989) demonstrated that blue gouramis, that had been conditioned with prior light-conspecific pairings, were better able to defend their territory than were control conspecifics during a subsequent conflict test. Territorial defense in the blue gourami is critical to fitness because females will only mate with males that can successfully defend a territory. Hollis concluded that the conditioned aggression observed as a conditioned response, resulted in better territorial defense and thus greater reproductive success. Hollis' conclusions were premature for two

reasons. First, associations formed during Pavlovian conditioning may include both response-stimulus (R-S) associations and S-S associations. Second, the relationship between levels of conditioning and actual territorial defense was not directly determined.

The purpose of Experiment 1 was to determine the nature of the associations underlying conditioned aggression in blue gouramis. This was accomplished by employing a US omission procedure. The purpose of the second experiment was to determine the relationship between conditioned aggression and territorial defense in blue gouramis. This was accomplished by correlating indices of conditioning and territorial defense.

Two major observations were made in Experiment 1. First the paired group demonstrated higher indices of conditioning than the omission group which did not differ from the yoked group. And, second the rate of both unconditioned and conditioned responding was low and highly variable. These results might be interpreted to suggest that the associative mechanism underlying conditioning are S-S in nature. However, the substantial variability and low levels of conditioning resulted in a high frequency of paired trials in all groups and may have precluded the

development of R-S associations in the omission group, thus limiting the opportunity for the development of differences between it and the yoked groups. These results mitigate accepting the conclusion that the underlying mechanism of association in conditioned frontal display responding is S-S in nature.

In Experiment 2 it was observed, once again, that while conditioned frontal display responding could be obtained, it was highly variable both within and between subjects. It was also observed that no significant relationships existed between levels of frontal display conditioning and any of a number of indices of territorial defense.

In summary, these results do not support the prefiguring hypothesis. Neither Hollis' assumption that the associative mechanism underlying frontal display conditioning are S-S in nature, nor the conclusion that frontal display increases the probability of successful territorial defense were supported.

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## Introduction

In a series of recent studies, Hollis (1982, 1984, 1989) asserted that male gouramis that had received pairings of a light with the sight of a conspecific male subsequently defended their territory more successfully when the cue light predicted an encounter with a conspecific male. Hollis suggested that her results indicated that (a) the pairings of a cue with the sight of a conspecific produced learning, (b) that the responses acquired to the cue were preparatory to territorial defense, and (c) that the function of learning in this situation was to increase the probability of reproductive success for the trained males by ensuring that it had a territory in which to reproduce. If Hollis's conclusions are valid, then her work will add a significant contribution to the understanding of the role that learning plays in the adaptation of an organism to its environment.

To determine the validity of Hollis's conclusions the following studies examined the first and third of Hollis's conclusions. Specifically, Experiment 1 examined whether or not the learning Hollis observed was the result of Pavlovian

conditioning as she described it. Experiment 2 determined the effectiveness of conditioning in serving Hollis's postulated function, that of increasing the probability of successful territorial defense.

In order to place Hollis's work and the proposed set of studies into an appropriate theoretical context it is first necessary to elaborate on the interaction of conditioning and function in animal behaviour. Following the development of the theoretical position, a critical analysis of Hollis's (1982, 1984, 1989) theory is presented. This analysis leads to the conceptualization that resulted in the research presented.

Animal behaviour has been the subject matter of a number of scientific perspectives. Of these, psychology and ethology have been most prominent. Psychological research has typically been directed at determining the mechanism underlying behavioural changes and deriving performance laws that these behavioural changes follow. On the other hand, ethological research has focused on attempting to explain the performance of behaviour that is predominantly invariant or at best very resistant to change (Thorpe, 1979). In attempting to determine the basis of such behaviour,

ethologists focused not on causal mechanisms underlying performance but rather on causation in terms of the function of behaviour.

The approach to the study of behaviour taken by psychologists tends to emphasize the environmental influences that alter an organism's behaviour. Chief among such influences has been learning.

Learning is generally viewed as limited to the processes involved in the formation of associations. That is, the term references the ability of the animal to develop associations between two or more detectable events (see Dickinson, 1980). In this sense, an association is an organism's representation of a relationship between environmental events, where these events may be either stimuli impinging on, or actions of, the organism. In the strictest sense, the term learning should be modified with the adjective associative to separate the implied relational learning from other possible forms of learning. Nonetheless, I have followed the normal practice of psychologists and used learning to mean associative learning.

Although many different definitions of learning exist, the consensual definition provided by Kimble (1961) stated, "learning is a relatively permanent change in behaviour potentiality which occurs as a result of reinforced practice." (p.6). An important feature of Kimble's definition is the term potentiality which was carefully chosen to indicate that learning was not necessarily manifested immediately or directly in a measurable change in behaviour (Kimble, 1961, 1967). This feature of Kimble's definition is best exemplified by the phenomenon of sensory preconditioning (Brogden, 1939).

In sensory preconditioning, an initial phase occurs in which two stimuli are repeatedly presented in a fixed temporal order. Subsequently, the temporally second stimulus is used as a signal to which a response is trained. Following response training, presentation of the temporally first stimulus shows that it now also controls the response. The transfer of response control to the temporally first stimulus is viewed as confirmation that associations between the two stimuli developed during the initial phase.

Sensory preconditioning phenomena can occur in the absence of measurable behavioral changes in the initial

phase (Cousins, Zamble, Tait, & Suboski, 1971), and as such, it has been argued that sensory preconditioning demonstrates the development of associations between stimulus-stimulus (or S-S) representations (Suboski & Tait, 1971, 1972; Weisman & Dodd, 1979). Since S-S associations need not immediately impact on behaviour, sensory preconditioning confirms the need for the term "potentiality" in a definition of learning.

Because associations are viewed as affecting the potential for behaviour change, associative processes cannot be directly studied and must be inferred from changes in behaviour. As a consequence, psychologists have developed standardized procedures designed to minimize the contribution of nonassociative factors to behaviour change (see Gormezano & Kehoe, 1975; Rescorla, 1967). Using such procedures, the major thrust of research within associative learning has been directed at the identification of conditions that either promote or interfere with the formation of associations, and the identification of the contents of associations when they are formed (see Dickinson, 1980; Mackintosh, 1983; Rescorla & Holland, 1982). Of secondary concern has been the problem of how

associations interface with behaviour. Many theorists assume some form of isomorphic transformation between learning and performance, however phenomena such as sensory preconditioning, indicate that simple translation rules will not suffice for all situations. The lack of a consensus on performance rules creates difficulties in the application of learning procedures to different types of experimental procedures and behaviour. This assertion will be amplified upon when the implications of biological constraints phenomena are presented later in the manuscript.

The study of learning has provided a great body of research and results from which a series of performance laws have been derived. These performance laws are called general laws of learning and are thought to reflect an underlying general process. The underlying process as suggested above, is associative in nature, reflecting the relationship between two stimuli (S-S) or a response and a stimulus (R-S). The former results from classical conditioning procedures in which the experimenter presents the pairings of two stimuli to an animal and monitors the behavioural changes during the first stimulus (see Rescorla, 1978), whereas the latter develops in operant or

instrumental procedures in which the experimenter selects an activity (e.g., pecking at a disk by a pigeon), which if produced by the organism, is followed by a stimulus (e.g., food), called a reinforcer, that has the consequence of increasing the frequency of occurrence of the activity (see Mackintosh, 1983). The general process is presumed to account for all associative behaviour. Thus, all learning-based behaviour is expected to follow the general laws (Revusky, 1977).

The psychological approach to the study of behaviour, while providing a solid understanding of the associative process presumed to interlay behavioural change, has, however, not given us a complete picture of all the variables influencing behaviour (Johnston, 1981). The limitations of this approach were recently brought to the forefront in psychology by the results of a number of studies which did not appear to adhere to the generally observed performance laws.

#### Constraints on Learning

Breland and Breland (1961), in the paper entitled "The Misbehaviour of Organisms", were among the earliest to

observe the peculiarity of the interaction between learning and innate behaviour. They observed that a pig that had repeatedly manipulated an object, such as a token, in order to obtain food often engaged in species characteristic activity. The occurrence of the species-characteristic behaviours often resulted in the delay or omission of the food (reinforcer), which was presented contingent on the pig's carrying and depositing the token. In this situation it was observed that a stimulus, which regularly preceded or signalled the presentation of food, elicited a series of species-characteristic behaviours despite the fact that these behaviours resulted in the delay or omission of a reinforcer. The interference with learning by species-characteristic behaviour was also observed in the conditioning of raccoons and chickens. According to Breland and Breland, this interference represented a breach in the law of reinforcement that could not be explained within the context of general process learning theory. Breland and Breland labelled the phenomena instinctual drift and stated that behaviourism had lost some of its predictive power by denying the existence of instincts.



The phenomenon of instinctual drift did not generate a great deal of attention or interest, perhaps because of the anecdotal forms in which it was presented. However, some work by Garcia and Koelling (1966) did have an enormous impact. Garcia and Koelling (1966) and Garcia, Ervin, and Koelling (1966) found that rats were more readily able to associate gustatory cues than auditory cues with illness; whereas, auditory cues were more readily associated with avoidance reactions to shock than were gustatory cues. It was also observed that conditioned taste aversion could be acquired very rapidly and despite a long interval (in the order of 20 minutes) between the distinctive gustatory conditioned stimulus (CS) and the toxic reaction or unconditioned stimulus (US). Garcia et al. (1966) suggested that such rapid formation of an association between two stimuli across such an extended period was unexplainable on the basis of traditional associative mechanisms.

Research in the area of defensive behaviour has also generated results that were difficult to explain based on the general process learning theory. Bolles (1970, 1975) observed that rats could learn certain avoidance responses much more easily than others. For instance, avoidance

responses such as wheel turning or bar pressing could only be learned with extended training (D'Amato & Schiff, 1964), while running down an alley or jumping out of the box was very quickly learned (Maatsch, 1959). To account for these results, Bolles suggested that the response of frightened rats was restricted to innately determined species-specific defense reactions (SSDR). Bolles also suggested that perceptual factors could play a role in the ordering of appearance of the SSDRs. Blanchard, Fukanaga, and Blanchard (1976) observed that in inescapable situations rats would freeze to a signal preceding shock, while they would flee in a situation that was escapable. Rats will also respond to a stationary CS in an avoidance situation by freezing, and a discrete approaching CS by flight (Blanchard & Blanchard, 1969). Bolles (1979) stated that the acquisition of SSDRs as successful avoidance behaviours could not be understood on the basis of the conventional reinforcement approach.

Shettleworth (1975, 1978) suggested, in much the same vein as Bolles (1979), that certain response-reinforcer (R-S) relationships existed as a function of evolutionary forces and were evidence for constraints on the application of the general process theory laws of learning.

Shettleworth observed that hamsters reinforced with food for various behavioral activities acquired certain of these activities more readily than others. Typically the activities that were acquired most readily were those that were part of the food searching pattern in the hamster. For example, digging, scrabbling (digging against a wall), and open rearing were easily increased in frequency when followed by a food reinforcer (Shettleworth, 1975).

Shettleworth (1973) had previously observed that while bar pressing was also quickly acquired and was certainly not a searching or consumption-related behaviour, its topography did take the form of digging, scrabbling, or gnawing, which are part of the food acquisition pattern in the hamster.

Shettleworth (1975) further observed that punishment was effective in decreasing some activities, like scrabbling and face washing but that other activities, like open rearing, increased in frequency and duration with punishment.

Finally, Brown and Jenkins (1968) observed that pigeons presented with repeated pairings of an illuminated response key followed by response-independent food soon acquired a reliable keypeck response. Brown and Jenkins labelled this phenomena autoshaping. Autoshaping has been observed with

various subjects, responses, and reinforcers, including pigeons and quail keypecking for food (Brown & Jenkins, 1968; Gardner, 1969; Matthews & Lerer, 1987; Terrace, Gibbon, Farrell & Bardock, 1975), chicks pecking for heat (Wasserman, Hunter, Gutowski & Bader, 1975), guinea pigs and monkeys lever pressing for food pellets (Davey, Oakley & Cleland, 1981; Likely, 1974; Poling & Poling, 1978; Sidman & Fletcher, 1968), and target striking in fish for food (Bottjer, Scobie & Wallace, 1977; Squier, 1969; Woodard & Bitterman, 1974). In each of these situations, the behaviour emerged as a result of the pairing of the two stimuli. Major reviews of the autoshaping literature have been presented by Hearst and Jenkins (1974), Schwartz and Gamzu (1977) and Locurto, Terrace and Gibbon (1981).

The significance of autoshaping lies in the type of behaviour that developed to the key light. Historically, key pecking, was observed as a prototype behaviour for the formation of R-S associations. Yet, in autoshaping, pecking at the key emerged even though the researcher had programmed in an S-S (keylight-food availability) relationship. Williams and Williams (1969) employing a variant of the omission procedure confirmed that the S-S relationship had

primary control of the keypeck. After autoshaped responding had been established, the birds received keylight-food availability pairings if they did not peck at the key, and only keylight exposure if a keypeck was delivered. Thus, pecking the key was never followed by food, and, therefore, the maintenance of the R-S association was precluded. Under these conditions, Williams and Williams (1969) observed the maintenance of the keypecking behaviour. Similar observations have been obtained with a number of different species of subjects with various response systems and reinforcers, for example, target striking for food in fish (Woodard, Ballinger, & Bitterman, 1974), rats bar pressing for food (Davey, Oakley, & Cleland, 1981), key pecking for food in pigeons (Peden, Browne, & Hearst, 1977) and chicks pecking for heat reinforcement (Wasserman, Hunter, Gutowski, & Bader, 1975).

The lack of contingency between response and reinforcement in the omission procedure eliminated the possibility of R-S associations persisting and, as such being, the primary basis for responding. Thus, responding that occurred during omission training could only be the result of S-S associations. The importance of the results

of the omission procedures is the recognition that much of conditioned behaviour that was previously ascribed to R-S associations was, at least, in part the result of S-S associations. The autoshaping and omission phenomena presented a number of problems for operant theorists. First, many of the responses, which were traditionally considered arbitrary (key peck, bar press) and under the control of R-S associations, appeared not only to be subject to the influence of S-S associations but also to be predominantly under the control of S-S associations in some situations. Second, many autoshaped responses were gross skeletal-motor responses assumed by some to be responsive only to R-S associations. Third, the responses that came under the control of the discriminative stimulus were species-specific behaviours that appear to be determined by the reinforcer employed (see Moore, 1973).

The phenomena of instinctual drift, taste aversion, avoidance behaviour, and autoshaping appeared to be exceptions to known principles of learning and seemed to represent the interference with learning by adaptive specializations that were species-specific, situation specific, or both. The early explanation of these phenomena

invoked ecological and evolutionary factors which were presumed to permit the development of specialized learning mechanisms to meet the specialized requirement of the species' environment. Thus, the early interpretation followed the precedence of the naturalistic or ethological literature which had long presented examples of specialized learning abilities in a variety of animals. Early examples of such specialization include the navigational skills of the bees (von Frisch, 1971), the memory of the location of nests in digger wasps (Tinbergen, 1972), the salmon's recognition of home streams (Hasler, Scholz, & Horrall, 1978), the parenting behaviour in the herring gull (Hailman, 1967) and the song acquisition in many birds (Thorpe, 1961).

#### Constraints and Psychology

Many learning theorists have suggested that the constraints phenomena are examples of specialized learning or are the result of the interference of specialized learning with other learning. Furthermore, it has been suggested that this specialized learning cannot be accounted for within the traditional framework of the general process theory. For example, Seligman (1970) attempted to elaborate

how these phenomena present difficulty for the general process theory. According to Seligman, the general process theory has as its basic assumption the assumption of equipotentiality (Seligman, 1970). The assumption states that all stimuli, reinforcers, and responses are equally associable and that what an animal learns about is of relative unimportance. A corollary to the equipotentiality assumption is that species differences are relatively unimportant.

Seligman and Hager (1972) addressed the problem of constraints by rejecting the general process theory as they understood it and positing the concept of preparedness. The concept of preparedness proposed that a predisposition for certain associations was innate and determined as a consequence of selective pressure exerted on the species over its phylogenic history. The hypothesis suggested that as a result of evolution the organism had associative apparatus which made certain associations easier to acquire, more difficult to extinguish, and more readily generalizable.

Alternative explanations of the constraints phenomena attempted to incorporate the impact of an evolutionary



factor in the learning process. For example, Breland and Breland (1961) suggested that instinctual drift was the result of evolutionary forces acting on appetitive behaviour. Garcia and Koelling (1966) asserted that the notion of belongingness of gustatory cues with subsequent illness caused the rapid development of taste aversion. This belongingness was, according to Garcia et al. (1966) the result of natural selection. Garcia, Hankins, and Rusiniak (1974) further elaborated on this hypothesis and posited that gustatory cues belonged with internal consequences. Such belongingness presumably resulted from neural specialization due to evolutionary pressures.

Rozin and Kalat (1971) proposed that learning be treated as any other biological characteristic. As such, learning would be subject to natural selection and would evolve to handle specific types of problems. While they accepted that some general form of learning may exist, Rozin and Kalat (1971) rejected the notion of equipotentiality by suggesting that some difference in learning mechanism may exist as a function of both the characteristics of the species and of the situation in which learning occurs. As noted earlier, Bolles (1970) explained avoidance behaviour

based on the animal's phylogenic history. He also suggested that a frightened animal's avoidance responses were restricted to a set of innately determined species-specific defence reactions. By attributing the learning of avoidance associations to the use of species-specific defensive behaviours, Bolles (1970) joined Rozin and Kalat (1971) in rejecting the assumption of equipotentiality.

Constraints and General Process Learning Theory. Many theorists rejected the general process learning, while others attempted to explain the constraint phenomena within the traditional framework (Domjan, 1983; Shettleworth, 1983). The concern for general process theorists was to determine if the constraints phenomena represented qualitative, as opposed to quantitative differences. The general process framework has always recognized that a number of variables have a quantitative effect on acquisition (Hall, 1976). For example, the interval between conditioned and unconditioned stimuli and the intensity and duration of both stimuli affect the rate of acquisition. An orderly decrement in performance as a function of the delay between cue and consequence is reliably observed. Preexposure to either the CS or US interferes with

subsequent learning. The existence of generalization and discrimination gradients identify the degree of control that develops within an association. Each of these variables are said to result in quantitative differences as opposed to qualitative differences and, as such, were not viewed as problematic (Seligman, 1970). It was critical then, to determine if variables known to influence the occurrence and rate of formation of associations affect the constraints phenomena in the same manner or in a qualitatively different fashion.

A number of theorists have challenged the rejection of general process theory because many of the functions obtained in the taste aversion studies paralleled those obtained in the conditioning of other response systems using Pavlovian procedures. Garcia, Ervin, and Koelling (1966), Kalat and Rozin (1971), and Revusky (1978), for example, all observed decreasing taste aversion conditioning as a function of increasing delay between the flavour cue and the toxicosis reaction. Repeated preexposure to the CS and/or the US also reduced subsequent conditioning (Elkins, 1973), while the level of taste aversion conditioning a function of the number of CS-US pairings (Brackbill and Brookshire,

1971). Other functions typically found to result from Pavlovian conditioning procedures have been observed to occur using the taste aversion preparation, these include generalization along the CS dimension (Braum & Snyder, 1973; Domjan, 1975; Nachman, 1963), stimulus discrimination (Domjan, 1977; Rozin, 1969) and overshadowing and blocking (Revusky, 1971). More detailed reviews of the similarity in parametric functions between conditioning of taste aversion and other responses have been presented by Domjan (1980), Logue (1979), and Spiker (1977).

Having determined the parallel between taste aversion and traditional conditioning procedures for many parametric functions, theorists attempted to explain the rapid acquisition across the long CS-US interval. A variety of hypotheses were posited including selective attention or orientation to the CS due to the nature of the US (Gillette, Martin & Bellingham, 1980; Rescorla & Holland, 1976), method of presentation of the CS (Miller & Domjan, 1981), the similarity of spatial and temporal intensity between the CS and the US (Rescorla & Furrow, 1977; Rescorla & Gillan, 1980; Testa & Terne, 1977), and the role of previous experience (Dickinson, 1980; Mackintosh, 1974). The

variables suggested by each of these hypotheses affected associability or rate of acquisition. However, none could explain satisfactorily the strength of the selective association observed in the taste aversion research (Domjan, 1983).

Various attempts have also been made to account for the associative bridging of the long delay between CS and US presentations that typify the taste aversion phenomena. Krane and Wagner (1975) suggested that the taste CS results in an unusually long stimulus trace that decreases the functional interval between the stimuli and permits the association to be formed. Although this hypothesis is tenable, it has received little support. Revusky (1971) suggested that the lack of events similar to the CS occurring during the interval between the CS and US may minimize interference. As a consequence, the association develops despite the long interval. However, research in the area of visual aversion (a preparation analogous to taste aversion with the exception that a visual cue is used as the CS) has obtained learning across similar long temporal intervals (Wilcoxin, Dragoin, & Kral, 1971). Since it is difficult to suggest that events similar to the CS did

not occur and possibly interfere with the putative visual trace, the evidence from visual aversive research mitigates against Revusky's (1971) hypothesis.

Spiker (1977), in an attempt to explain learning across long intervals, has noted that the "gustatory ISI function contradicts a long abandoned prediction from conditioning theory; that the ISI function will be short-ranged and invariant" (p. 761). Gormezano and Moore (1969) and Schneiderman (1972) have suggested that the interstimulus interval (ISI) may in fact be different for each response system studied. As such, the long delay observed in the taste aversion research, although not explained by these authors, is not viewed as necessarily conflicting with the general learning theory.

Attempts have also been made to incorporate the apparent constraint on avoidance learning into the general process theory. It has been observed that the rate of various behaviours previously found difficult to condition as avoidance responses could be improved using various strategies, which include reinforcing successive approximations of the behaviour while punishing competing responses (Ferrari, Todorov, & Galef, 1973; Rachlin &

Hineline, 1967) and pretraining the required behaviour using positive reinforcement (Foree & Lolordo, 1970; Giulian & Schmaltz, 1973).

Jacobs and LoLordo (1980) found that the differential use of auditory and visual cues influence the rate of acquisition of various behaviours that are used as avoidance responses and suggested the possible implication of Pavlovian conditioned aversive motivational states in the stimulation and determination of behavioral potential. Jacobs and Lolordo (1980) also stated that given appropriate stimuli any response could be acquired as an avoidance response. Although not a great deal of research has been carried out in this area of constraints, the results suggest that Bolles's analysis may be incomplete due to its minimal consideration of stimulus aspects (Domjan, 1983).

A variety of explanations have also been posited to account for the differential associability of certain responses and reinforcers. These have included the influence of both unconditioned motivational states [e.g., deprivation (Shettleworth & Juergensen, 1980)] conditioned motivational states (Shettleworth, 1978), and the effect of

contextual CS's interacting with ongoing learning (Pearce, Nicholas, & Dickinson, 1981).

Reviews of how learning theorists have attempted to deal with the constraint phenomena have been presented by Domjan (1983) and Shettleworth (1983). Both concur in their conclusion that it appears unnecessary to discard the general process theory of learning. Constraint phenomena according to these authors, appear to reflect quantitative differences in learning that can be explained within the confines of general process learning theory. The central difficulty in explaining the constraints phenomena within the confine of general process learning theory is viewed to be the assumption of equipotentiality.

The Problem of Equipotentiality. The focus for rejecting the general process theory has been the assumption of equipotentiality. Accordingly, the legitimacy of the assumption of equipotentiality as basic or necessary to general process theory warrants consideration.

Seligman (1970), Seligman and Hager (1972), and Shettleworth (1972) have suggested that the concept of equipotentiality is derived from the works of Thorndike, Pavlov, and Skinner. A brief historical survey of the area



of comparative psychology and of the works of Thorndike, Pavlov and Skinner might be helpful in determining the accuracy of this suggestion.

The comparative analysis of behaviour was focused in North America at the turn of the century by Thorndike. In his work, Thorndike sought general laws of learning, that is, functional relationships between stimuli, responses, and reinforcement. Thorndike was, however, very cautious about extending his findings beyond the animals with which he worked (fish, chicks, cats, dogs, and monkeys). In the first section of his book, Animal Intelligence (1911), he cautioned his reader about overstatement of his findings,

Throughout I shall use the word animal or animals and the reader may fancy that I took it for granted that the associative processes were the same for all animals as in these cats and dogs of mine. I claim for my psychology only that it is the psychology of just these particular animals. What this warrants about animals in general may be left largely to the discretion of the reader. (p. 66)

It seems clear that Thorndike was being very cautious as to the generality across animals not only of the functional

relationships he observed, but also of the processes that he assumed to underlie them.

It has also been suggested that Thorndike assumed that the laws of learning that he observed were generalizable from one set of events to any others. Close reading of Thorndike's work indicates otherwise: "The chick's brain is evidently prepared in a general way to react more or less appropriately to certain stimuli and these reactions are among the most important of its instinct or inherited functions." (p. 167) In a later section Thorndike posited a law of original behaviour or law of instinct, which states, "to any situation an animal will apart from learning respond by virtue of the inherited nature of its reception, connection, and action system" (p. 243). Thus, Thorndike clearly indicated that the evolutionary history of a species constrained the actions of members of that species. Moreover, Thorndike suggested that the behaviour of an organism would in any given situation, be governed by multiple causal determinants.

Thorndike rejected the notion of equipotentiality in 1935 when he proposed the concept of belongingness of events as a determinant of the speed with which the events could be

associated. According to Thorndike's belongingness principal, an association is more easily learned if the response belongs to the situation or if the reinforcer belongs with the response being strengthened. Thus, belongingness is similar to Seligman and Hager's (1972) concept of preparedness. As with preparedness, belongingness reflects the evolutionary history of the species and affects the speed of learning. With this concept, it is clear that Thorndike did not assert the equivalency of different classes of stimuli or classes of responses in the formation of associations. Thus, the assumption of equipotentiality cannot be attributed to Thorndike.

Pavlov has also been said to have adhered to the concept of equipotentiality; however, a comprehensive reading of his work suggests otherwise. For example, he stated,

"...if the extraneous stimuli are strong or unusual, the formation of a conditioned response will be difficult, and in extreme cases impossible. (Pavlov, 1927; p. 29)"

This statement suggests three pertinent things: First, that the relative intensity of the stimulus will be relevant to its capacity to form conditioned responses; second, that the organism's prior experience with a given stimulus will be pertinent to its associability; and third, it notes Pavlov's general awareness that all stimuli are not equally associable.

Pavlov also observed that the physical structure of the effective receptor system for a given conditioned stimulus dictated to some degree its associability,

...a limit is set to the fineness or gradation of such stimuli by the degree of the sensitivity and perfection of the peripheral receptor organs of the organism (Pavlov, 1927; p. 38).

Furthermore, the differential associability of a given conditioned stimulus was noted, not only as it existed between species by virtue of different physiological substrates, but also within species

Of first importance in this connection is the individuality of the animal, the excitability or inhibitable character of its nervous organization... (Pavlov, 1927; p. 74)."

Therefore, although one might suggest that Pavlov's explanation of differential effectiveness of conditioned stimuli is not complete or perhaps even accurate, given current information, one cannot say that he ascribed to the concept of equipotentiality. As Pavlov would suggest:

...any agent in nature which acts on any adequate receptor apparatus of an organism can be made into a conditioned stimulus for that organism. This general statement, however, needs both amplification and restriction (Pavlov, 1927; p. 38).

Skinner has also been said to be one of the original proponents of the premise of equipotentiality (Seligman & Hager, 1972). Skinner addressed the concept of equipotentiality on a number of occasions. In Contingencies of Reinforcement (1969) for example, he states:

"No reputable student of animal behaviour has ever taken the position that the animal comes to the laboratory as a virtual tabula rasa, that species differences are insignificant, and that all responses are equally conditionable to all stimuli" (p. 173).

Skinner (1983) also stated that,

"behaviour arising from natural selection is not always effective in new environments. A means of making slight changes in behaviour during the lifetime of the individual must have had survival value, and the process of operant and respondent conditioning could evolve. Along with the process of operant conditioning there must also have evolved a susceptibility to particular kinds of consequences" (p. 11).

Again it seems clear that Skinner was not a proponent of the premise of equipotentiality.

If Thorndike, Pavlov, and Skinner were not the central proponents of the notion of equipotentiality, what accounts for its pervasive acceptance as fundamental to the general process learning theory? Reading J. B. Watson's work indicates that he had an incomplete knowledge or understanding of the works of Thorndike and Pavlov which may have led him to his apparent adherence to the premise of equipotentiality. Watson (1924) suggested that "So far as we know (actual experimental evidence is lacking) we can take any stimulus calling out a standard reaction and substitute another stimulus for it" (p. 24). He continued: "It is found that we may substitute for food or acid, any

stimulus at will and get the salivary response, provided we apply this stimulus simultaneously with the food or acid stimulus" (p. 30). Regarding Thorndike's work, Watson stated the following:

"They believe that habit formation is implanted by kind fairies. For example Thorndike speaks of pleasure stamping in the successful movements and displeasure stamping out the unsuccessful movement. Most of the psychologists talk, too, quite volubly about the formation of new pathways in the brain, as though there were tiny servants of the Vulcan there who run through the nervous system with a hammer and chisel digging new trenches and deepening old ones" (p. 206).

This quote clearly demonstrates a strong disregard for Thorndike's reinforcement principles and demonstrates Watson's belief that learning strengthens already existing neural structures. Furthermore, despite a professed adherence to Pavlov's work, Watson appears to have misunderstood it, since Pavlov suggested the formation of new pathways in the brain as a result of learning, the very concept Watson appeared to ridicule in Thorndike's work. Although Watson did recognize the influence of evolutionary

variables, his emphasis on stimulus substitution no doubt gave impetus to the premise of equipotentiality.

Two trends in psychology may have helped maintain the notion of equipotentiality. Firstly, Malone (1973) attributed some of the responsibility for the strong foothold of the premise of equipotentiality to

"psychologists over the past several decades (particularly the authors and editors of learning texts) who have distilled Pavlov's contribution to the notion of stimulus substitution and Skinner's to the Law of Effect. This gross oversimplification was made for the purpose of setting up and clarifying paradigms for the general process learning theory" (p. 305).

Secondly, Beach (1950) noted that psychologists had by and large ignored animal behaviour in the natural environment and concentrated on laboratory experiments. Furthermore, psychologists went on to study only a few species, of which the rat was the most common. As a result of this narrow approach to comparative psychology, Beach suggested that "psychologists are led to neglect many complex patterns of responses that stand in urgent need of systematic analysis" (p. 121). Of these complex patterns he cited instinct or



unlearned behaviour. The possibility of recognizing species-specific behaviour with such a narrow approach is obviously decreased.

Whalen (1961) stated that, 10 years after Beach's (1950) paper, the problem still existed. In a review of the articles published in the Journal of Comparative and Physiological Psychology from 1956 to 1959, 55 % of the animals used in research were rats. The restricted use of rats began to wane in the 1960s (Hodos & Campbell, 1969), and a greater variety of species are currently being studied.

According to Beach (1950) and Whalen (1961), the results of the trend toward studying a restricted number of species and responses has been to minimize the possible observation of effects other than associations on behaviour. Furthermore, the probability of observing or studying species-characteristic behaviour or specialized learning phenomena was minimal. The effect of this trend was to give the appearance of equal associability of stimuli and responses across organisms and, thus, contribute to the assumption of equipotentiality.

It may be difficult to trace the basis of the adherence to the assumption of equipotentiality as a required assumption of the general process theory of learning, however, it is clear that there is no legitimate reason for it to be accepted as such. Although the phenomena said to evidence constraints on learning do represent deviations from both the general body of results obtained from the research in learning and from the principles derived, there is, as yet, no reason either to presume the existence of distinct processes or to reject the general process theory of associative learning. However, psychologists must, as a result of the constraint phenomena, recognize the implication of evolutionary forces on behaviour and learning. In an effort to explain behaviour in the natural setting and in the search for general laws of behaviour, learning theorists originally chose to study "arbitrary" behaviours in controlled laboratory settings. Behaviours defined as arbitrary were those viewed as uninfluenced by evolutionary forces. It would appear that contemporary psychology has forgotten this original concern and has attempted to explain behaviour clearly known not to be arbitrary as though it were. It is curious to note the

surprise of learning theorists in observing that the precise variable (evolutionary forces) for which they sought the control, has an effect, which prevents them from generalizing the observed laws of learning outside the laboratory situations.

Learning theorists have developed a number of procedures or paradigms that generate learning. These procedures have resulted in a number of laws of learning and in the assumption of a general underlying process of association. In using these general laws of learning to explain behaviour in the natural setting, theorists have overlooked a few important considerations. First, the paradigms from which the general laws were derived may not be the only ones operating to determine behaviour in the environment. Second, the separate paradigms that are known to generate learning in the laboratory may be interacting to generate behaviour in the environment that could not be explained as a result of an individual paradigm. Third, the realization that the general laws were derived in laboratory situations that have attempted to control for evolutionary forces makes questionable the logic of attempting to generalize these laws to behaviour which may be, in part,

the result of adaptation to a given environment. Finally, it must also be noted that deviation from laws describing performance need not imply different underlying processes of association. These are the very considerations that have focused the theorizing and research in ethology.

### Constraints and Ethology

Ethologists have long recognized that while behavioral research conducted on arbitrary behaviour (if, indeed, this can be done) might serve to understand the presumed underlying process of association, it would not explain all the causal variables in behaviour in the natural environment (Hinde, 1982). In attempting to explain behaviour, ethologists have developed an approach to the problem which has a radically different perspective. Ethologists study behaviour that is presumed to be the least influenced by associative learning. In effect, they study much of the behaviour that psychologists would suggest is the result of specialized learning or reflects constraints on learning. This development is a natural consequence for ethology as it emerged as a science.

As it is currently defined, ethology is the comparative study of the natural behaviour of animal species (Thorpe, 1979). The accurate and systematic description of animal behaviour began in the 16th and 17th centuries with John Ray in England and Baron von Perneau in Germany. However, the origin of the use of the term ethology can be traced first to 18th century France where it signified one who acts or mimics. By the turn of the 19th century it denoted the science of ethics. It was not until the mid-nineteenth century that the current usage of the term was first introduced, in France, by Isidore St. Hilaire. In England, however the term was used until the mid-19th century to signify the science that determines the type of character produced by the elementary laws of the mind as discovered by psychology. Shortly thereafter it took on the more conventional definition.

The study of ethology spread to the European community as a result of the publications of the Academie de Science during the mid-19th century, and by the 20th century a stronghold of ethology had developed in Europe under the influence of O. Heinroth, K. Lorenz, K. von Frisch, and N. Tinbergen. However, as an approach to the study of animal

behaviour, ethology was not very influential until the mid-20th century. The delay in the impact of ethology is often ascribed to the use of the naturalistic observation method of studying the subject. This method was perceived as less than scientific, and received less than enthusiastically (Thorpe, 1979). North America witnessed an extended delay in the rise of ethology that has been ascribed to the strong foothold in North America of behaviourism with its attending insistence on the experimental method and the importance of environmental influences.

The general subject matter of ethology is not distinguished from that of other sciences such as psychology, psychiatry, or sociology. What makes ethology distinctive, is the type of questions that ethology asks about behaviour (see Hinde, 1982; Thorpe, 1979). Ethologists attempt to account for a behaviour in terms of the proximate and ultimate causes of that behaviour (Baker, 1938 as cited by Hailman, 1982). Proximate causes are mechanisms that control the immediate occurrence of an episode of a behaviour and mechanisms that affect the development of the ability to perform the behaviour (Tinbergen, 1963). Such mechanisms are activated by stimuli

that are either internal (in psychology the internally generated causes would correspond to motivational processes) or external to the individual. Thus, proximate factors affect the behaviour of individual organisms and must be studied at the individual level. On the other hand, ultimate causes operate at the level of the species and must be studied in populations of organisms rather than in the individual (Hailman, 1982). Ultimate causes are ecological and genetic mechanisms and ultimate causes reference the effects of the evolutionary processes of natural selection (ecological mechanisms) and phylogeny (genetic mechanisms) on behaviour. While the four types of causes are readily separated logically, the occurrence of a behavioral episode can involve the interplay of the different causes, and this poses a formidable challenge to the researcher.

The central concern of early ethologists was to study and explain the rigid patterns of movement found in animals to be as strikingly similar within species as they were different between species. These movement patterns, called fixed-action patterns, were thought to be stereotypic in form, to be as consistent within a species as any morphological feature, to originate phylogenetically, and to

be imbedded in the genome (Lorenz, 1981). The features that distinguished the fixed-action patterns from other movement patterns were their taxonomic distribution and their presumed resistance to modification. The observation of the species-specificity of the fixed-action pattern and the absence of learning in its development was used to invoke the ultimate cause of phylogenetic history or genetic control of the behaviour.

Subsequent study of fixed-action patterns found them to occur in specific situations and to be triggered by specific stimuli called releasers or sign stimuli. A releaser was postulated to act on an innate releasing mechanism which served as a stimulus filtering mechanism and ultimately triggered the performance of a fixed-action pattern.

The fixed-action pattern, as described by Lorenz (1966) was presumed to be driven by an action-specific energy that accrued across time and was stored within the organism. The intensity of performance of the fixed-action pattern was perceived to be a conjoint function of the amount of action-specific energy that had accrued since the last occurrence of the fixed-action pattern, and the adequacy of the sign stimulus. As the progressive accrual of action-specific



energy occurred, the fixed-action pattern could be released by progressively less complete sign stimuli.

Thus, for an individual organism, the elicitation of a behavioral episode was the conjoint influence of proximate and ultimate causes. The proximate causes were processes that lead to the encounter with the sign stimulus, and the action of the sign stimulus. The ultimate cause would be the reproductive success in previous generations. Similarly, the behaviours displayed would be under conjoint control. The intensity of the behaviour was controlled by proximate factors (i.e., the amount of action-specific energy accrued); whereas the form of the behaviour, because it was innate, was controlled by ultimate factors.

Ethology has advanced well beyond Lorenz's original analysis of innate behaviour. The original concepts have been modified and supplemented by additional processes, and the details of some of the mechanisms have been identified. Developments in three areas are particularly pertinent to the present studies. The first was the challenge to the concept of the fixed-action patterns as stereotypic, rigid behaviour in response to a given stimulus. The second development was the introduction of the concept of

directional stimuli, finally, the third pertinent development was the emergence of the importance of the ecological impact, or function of behaviour, as an ultimate cause of behaviour. These developments which are outlined in the paragraphs to follow yielded a conceptual framework which allowed for the interfacing of associative learning to ethology.

In searching for the causal mechanisms of behaviour (Hinde, 1982; Thorpe, 1979), investigators attempted to clarify the relationship between fixed-action patterns and releasers. For this system to function efficiently two innate knowledges were required to be on the part of the organism, first, the capacity to engage in the fixed-action pattern, and second the capacity to recognize the releaser (Hinde, 1982). Given the apparent rigidity of fixed-action patterns it was presumed that a hierarchically organized physiological substrate might interlay them. Such a physiological substrate was discovered in Tritonia (a sea slug). Tritonia respond to the touch of the star fish, one of its many predators, by a sequence of rhythmic movements which propel it away from its enemy. A single executive neuron has been isolated which when excited artificially

will set in motion the rhythmic movement which constitutes the fixed-action pattern. When inhibited, this same executive neuron will inhibit the escape reaction (Dorsett, Willows, & Hoyle, 1973). Thus, a complex, repetitive motor pattern was confirmed to be triggered by the physiological status of a single neuron. Although this observation supported the notion of a genetic basis for fixed-action patterns, it also might erroneously be viewed as supporting the presumed rigidity of the form of the behaviour. It should be noted however that the fixed-action pattern has been found to be much more flexible to proximate causes than originally thought (Thorpe, 1979). Lorenz (1981) asserted that only a small core of the fixed-action pattern is indeed fixed, while the greater portion is flexible and responsive to various environmental influences. Tierney (1986) indicated that such variables as injury, diseases, malnutrition, hormonal change, use, and disuse modify the form, strength, and probability of fixed-action patterns.

Work by ethologists subsequently focused on the releaser of the fixed-action pattern. Although animals appear to respond innately to many releasers, it seemed unreasonable to assume that the genes could encode schema or

detailed pictures of the numerous situations that an organism might encounter (Lorenz, 1981). It did, however, seem possible that the specific neural circuitry required to receive and filter out various simpler stimuli could be under genetic control (Gould, 1986; Lorenz, 1981).

Hailman's (1969) classic experiment with gull chicks clearly demonstrated that these animals did not respond to a situation or schemata as originally thought but rather to very discrete stimuli.

Hailman (1969) studied the gaping behaviour of gull chicks for food in the presence of an adult. He observed that a disembodied bill was just as efficient at releasing gaping behaviour as was the gull parent. Hailman further observed that colour was relatively unimportant. Instead the orientation and specific movement of the bill was critical to releasing the response. In effect, a vertical orientation of the bill accompanied by horizontal movement at a given rate readily elicited gaping. It was soon found that the moving bar receptors in the chick's eyes respond exclusively to such stimuli. Thus, Hailman's (1969) conclusions support the notion of a relatively simple physiological substrate for releasing stimuli.

In summary, research on the relationship between fixed-action patterns and innate releasers point to two conclusions. First, many fixed-action patterns appear sensitive to proximate causes. Second, genetic encoding for detecting simple but precise stimuli seem to form the basis of releasing mechanisms (Hailman, 1969; Lorenz, 1981; Tierney, 1986).

The second development of interest was Lorenz's (1981) observation that part of the behavioral sequence that could be elicited by the sign stimulus was more appropriately viewed as behaviour which increased the probability and efficiency of interacting with the specific goal event. This type of behaviour was labelled appetitive behaviour, whereas the behaviour that dealt directly with the goal object was labelled consummatory behaviour. Lorenz suggested that appetitive behaviour could occur in the presence of either the sign stimuli or directional stimuli. The latter were defined as stimuli that were a part of the situation in which the sign stimuli typically occurred. The appetitive behaviours, while broadly considered a part of the fixed-action pattern, were very flexible in their form. Furthermore, appetitive behaviours were viewed as

preparatory in nature. By this, Lorenz (1981) meant that the appetitive behaviours prepared the organism for interaction with the goal object. The concept of the directional stimuli and the distinction between appetitive and consummatory behaviour further increased the flexibility to the previously assumed rigid relationship between releaser and fixed-action pattern. It is in the context of the directional stimuli and the appetitive behaviour that Lorenz (1981) saw the potential interaction of learning with innate behaviour, although he did not elaborate extensively on the presumed nature of this interaction.

A third concern in contemporary ethology was to understand the function of innate behaviour. Specifically ethologists sought evidence to support their contention that these behavioral propensities that were of benefit to the organism vis-a-vis its survival could be transmitted across generations. It is important to recognize that it is not the behaviour itself that is presumed to be inherited but rather the physiological substrates responsible for it. It is equally important to understand that the genetic control of behaviour does not imply that behaviour is controlled by one gene and is thus fixed but rather that variations in the

physiological substrates relevant to behaviour have a genetic basis upon which selection may operate (Dawkins, 1986).

Given the assumption that a genetic basis existed for the physiological substrates that control both the fixed-action patterns and the innate releasing mechanisms, the transmission of these patterns or substrates must be the result, at least in part, of natural selection. However, natural selection could not be operating at the level of either the genes or the physiological substrates controlling behaviour but rather at the level of the reproductive fecundity of the individual. Thus, innate behaviour is a necessary intermediate step between the occurrence of a gene in one generation and its occurrence in the next.

The function of behaviour in this context addresses the issue of why an organism engages in a given behaviour, that is, what the purpose of a given behaviour might be. Asking why an organism engages in a given behaviour does not imply that one presumes the organism engages in conscious goal-directed behaviour with an implicit guiding strategy. The term function, as it is used here, references solutions to the biological problems associated with being able to

survive and reproduce (Hinde, 1982). The capacity to survive and reproduce is critical to a species' ability to successfully occupy or adapt to a particular environment. This capacity is called fitness and is reflected in the number of offspring an organism generates. Inasmuch as a given behaviour contributes to fitness, that behaviour is said to have a function. Accordingly, to determine that a behaviour has a biological function, it is ultimately necessary to show how that behaviour affects the reproductive success of an organism (Dawkins, 1986). The concept of fitness does not require that fit behaviour be under tight genetic control. How a behaviour enters an organism's behavioral repertoire is not the immediate concern, only whether the behaviour contributes to reproductive success. However, if a given behaviour has greater function than some other of its variants, then the organism displaying such behaviour will have a greater fitness. Furthermore, if the behaviour in question has a genetic basis, it may by virtue of natural selection become more common in the population given a consistent environment. Again, the concept of function and natural selection is not intended to explain what originally caused



a given behaviour to occur on the basis of its genetic control, but rather to account, in part, for its maintenance in the species.

In summary, ethologists focus on the function of behaviour. The contribution of behaviour to reproductive success is viewed as a central determinant of the ultimate causation of the behaviour.

#### Learning and Function

Many recent attempts to account for the adaptive function of learning have defined learning as a process for changing behaviour. Johnston (1985) defined learning "as the modification or maintenance of the behavioral relationship between an animal and its environment as a result of experience." (p.6) Similarly, Hailman (1985) claimed that learning is "a process mediated by factors external to the animal by which its preexisting behaviour is permanently altered" (p. 27). Finally, Wilson (1975) asserted that learning is "a diverse array of peculiar biological adaptations" (p. 126).

Defining learning as a change in behaviour facilitates examining the adaptive function of learning. If learning is

a change in behaviour, then it should be sensitive, as other behaviours are sensitive, to the action of natural selection. Thus, learning should in some fashion, increase the fitness of the species. Moreover, since behaviours within a species can differ in their degree of canalization, changes of different behaviours should also be canalized. This leads to the expectation of specialized learning mechanisms for different classes of behaviour (e.g., Rozin, 1976).

However, as indicated at the beginning of this manuscript, defining learning as a change in behaviour is not an adequate definition of the phenomenon. Associative learning is defined as a change in behavioral potential. Accordingly, the mechanisms of associative learning do not necessarily directly affect behaviour. How learning occurs (i.e., the mechanisms of learning) and how learning affects the performance of an organism (i.e., the function of learning) are separable, orthogonal questions (Shettleworth, 1983). While behaviour that is canalized by natural selection might constrain learning by precluding or retarding either its development or its performance, the mechanisms that produce learning need not be directly

affected (Shettleworth, 1983). From this perspective, an understanding of the function of learning will be determined by understanding the mechanisms that transcribe associations into performance.

The Prefiguring Hypothesis. Hollis (1982) reinitiated theorizing about how associative learning might interact with innate behaviour to maximize function and presumably fitness. Hollis suggested that the S-S associations formed during Pavlovian conditioning allowed an organism to predict or anticipate the imminent occurrence of a biologically significant event (the US), such as the availability of food or the arrival of a predator. The anticipation of the impending important biological stimulus provided the organism with the opportunity to prepare to deal with the upcoming event. The manner in which the organism prepared for the US was identified by the anticipatory conditioned responses (CRs) that developed to the predictive stimulus (CS).

The conditioned behaviours could be any combination of skeletal and autonomic responses. The CRs could be similar in form or topography to the URs or differ considerably from the URs. For Hollis (1982), the critical feature of the CRs

was that the type of behaviours that occurred would maximize the organism's encounter with the biologically significant event (i.e., obtain food or more of the food; avoid the predator). The ability to behave optimally to biologically significant events was asserted to result in a selective advantage for the organism relative to organisms that did not have the ability to acquire predictive relationships. Thus, Hollis (1982) was postulating that the function of learning was to maximize other biological functions through the acquisition of conditioned behaviours that facilitate the performance of the biological functions. This postulation about the function of Pavlovian conditioning Hollis (1982) labelled the prefiguring hypothesis.

Hollis credited Pavlov with originating the prefiguring hypothesis for the conditioning of autonomic responses. However, she erroneously stated that Pavlov did not extend this assumed adaptive purpose for conditioning to the conditioning of skeletal responses. It is true that Pavlov chose to work predominantly with autonomic responses, however, it is also true that he conceptualized the adaptive function of conditioning to be broader than his experimental

context. The following passage from Conditioned Reflexes (1927) demonstrates this broader scope:

"The strong carnivorous animal preys on weaker animals, and these if they waited to defend themselves until the teeth of the foe were in their flesh would speedily be exterminated. The case takes on a different aspect when the defense reflex is called into play by the sights and sounds of the enemy's approach. Then, the prey has a chance to save itself by hiding or by flight." (p. 14)

Parenthetically, Pavlov used the term reflex quite differently from contemporary North American usage. Currently, a reflex is viewed as a simple physiological response that has a clearly defined afferent and efferent structure. Pavlov's usage is one of the alternative meanings that was prevalent earlier in this century (see Fearing, 1930) and essentially referenced a Cartesian mechanistic model of the nervous system. Thus, when Pavlov references the defensive reflex or freedom reflex (which was invoked to account for a dog's attempt to free itself from experimental apparatus) he was not asserting that the behaviour was a Sherringtonian reflex but rather that the

behaviour would ultimately be accounted for by the mechanistic action of the laws of neurophysiology.

A second quote will further clarify Pavlov's position on the adaptive significance of conditioning.

"It is essential to realize that each of these two reflexes -the alimentary reflex and the mild defense reflex to rejectable substances - consists of two distinct components, a motor and a secretory. Firstly the animal exhibits a reflex activity directed toward getting hold of the food and eating it or, in the case of rejectable substances, towards getting rid of them out of the mouth; and secondly, in both cases an immediate secretion of saliva occurs, in the case of food, to start the physical and chemical processes of digestion and in the case of rejectable substance to wash them out of the mouth. We confined our experiments almost entirely to the secretory component of the reflex." (p. 17)

As the quotation clearly shows, Pavlov by no means addressed only autonomic responses. Therefore, the earliest conceptualization of the prefiguring hypothesis must be attributed to Pavlov.

Pavlov's view of the adaptive function of conditioning was not lost on early ethologists. Lorenz (1981) indicated that he had previously postulated that the pairing of a neutral stimulus with a sign stimulus would produce the conditioning of innate response mechanisms and the resultant fixed-action patterns. Furthermore, Lorenz (1981) credited Pavlov with advocating an extension of his concept of conditioning to include innate behaviour (Pavlov, 1928)

"To those reflexes which have long been subject to physiological investigation, and which concern chiefly the activities of separate organs and tissues, there should be added another group of inborn reflexes. These also take place in the nervous system, and they are the inevitable reaction to perfectly definite stimuli. They have to do with the organism as a whole, and comprise that general behaviour which has been termed instinct." (Pavlov, 1928 p.9)

Thus, Pavlov's concept of conditioned reflexes included the conditioning of what are now called fixed-action patterns. Furthermore, Pavlov recognized the functional value of such conditioning.

The similarity between the conditioning of reflexes as presented by Pavlov and the conditioning of innate behaviour as presented by Lorenz is striking. Conceptually, the directing stimulus and the conditioned stimulus are identical. Both must be paired with a stimulus that reliably elicits a response (i.e., a sign stimulus and an unconditioned stimulus, respectively). Furthermore, the difference between Lorenz' appetitive response and Pavlov's conditioned response is purely semantic. In both cases, the responses result from pairings between a neutral stimulus and one that reliably elicits a response. In both cases, the response that develops is preparatory in nature and is suggested to contribute to the fitness of the organism.

In summary, Hollis's (1982) prefiguring hypothesis has historical roots in both learning theory (Pavlov) and ethological theory (Lorenz). By maintaining the associative-performance distinction and viewing associative learning as a supplement that facilitates biological functioning, Hollis has reintroduced a potentially powerful explanatory tool to the study of animal behaviour.

#### Experimental Test of the Prefiguring Hypothesis



Hollis (1984) investigated the prefiguring hypothesis by attempting to condition to a red light (the CS) the species-specific aggressive responses of blue gouramis (Trichogaster trichopterus) which can be elicited by the sight of a conspecific. Hollis postulated that if aggressive responses become conditioned, then a gourami that reacted to the CS would be more successful in defense of its territory against the intrusion of a conspecific who did not have the advantage of such conditioning. Greater success in territorial defense was presumed to result in greater fitness because, for male gouramis, maintaining a territory is necessary for reproductive success. If such a result were obtained, then associative learning would be shown to contribute to the biological function of territorial defense.

Hollis (1984) found that relative to control groups, gouramis that received pairings of the red light and presentation of the conspecific developed a frontal display (defined as the unfolding and spreading of the dorsal, ventral, and caudal fins (fin erection) in the characteristic face-to-face posture) to the CS. Because only the subjects receiving the pairings demonstrated a

frontal display, Hollis concluded that Pavlovian or classical (she used the terms interchangeably) conditioning had been successful and had yielded S-S associations. Moreover, because frontal display is one of the earliest behaviours in the aggressive sequence of gouramis, Hollis concluded that aggressive behaviours had been conditioned to the CS. Therefore, the results were viewed as support for the prefiguring hypothesis. Finally, in a test that occurred following conditioning, Hollis observed that gouramis that received the CS were more aggressive than control subjects when a confrontation with a male conspecific occurred. This observation was interpreted as demonstrating that the conditioned fish were superior at territorial defense and therefore the fitter organisms. Thus the adaptiveness of the prefiguring hypothesis (Hollis, 1982) was confirmed.

The validity of Hollis's (1984) supporting demonstration of the prefiguring hypothesis rests on accepting three assertions. First, that the procedure used for conditioning is controlled predominantly by S-S associations. Second, that the measures of aggression reflect effective territorial defense and third that

territorial defense can serve as a currency to determine fitness. In the paragraphs to follow, it will be argued that none of these assertions are supported by the procedures that Hollis used. More appropriate procedures will be outlined and these will form the basis for the proposed experiments.

Pavlovian Conditioning. The prefiguring hypothesis asserts that the formation of CRs is the exclusive result of S-S associative mechanisms. However, the paradigm that Hollis employed is directly analogous to autoshaping, and therefore, both S-S and R-S associations could be operating to control the conditioned frontal displays (Eldridge & Pear, 1987). Hollis's (1984) experimental procedures are not amenable to identifying the type of associative processes operating in the situation. The source of this discrepancy between methodology and interpretation may perhaps be found in Hollis's interchangeable use of the terms classical conditioning and Pavlovian conditioning.

Procedurally, the two conditioning paradigms differ subtly (Gormezano & Kehoe, 1975) and the importance of the distinction is not always recognized (e.g., Hearst, 1979). Yet the differences have profound implications for the

possible mechanisms that control the conditioned behaviour that is observed.

In order to be called a classical conditioning paradigm an experimental procedure must meet the following criteria (Gormezano & Kehoe, 1975): a) a stimulus (the conditioned stimulus or CS) that does not initially elicit a response from the system to be conditioned must be selected, b) a stimulus (the unconditioned stimulus or US) which reliably elicits the response systems to be conditioned (the unconditioned responses or UR) must be found, and c) the two stimuli must be repeatedly paired. As well as meeting these criteria, the experimenter must ensure that the following two requirements are met. First, the delivery of the CS and US must be independent of the behaviour of the organism being conditioned. That is, no response by the organism must be required to receive the stimuli, nor can any response or lack of response modulate their delivery. Second, to index the occurrence of classical conditioning, the response that serves as an index of conditioning must be selected from within the effector modality of responses elicited by the unconditioned stimulus. These last two requirements ensure that in classical conditioning, the

conditioned response (CR) is not the result of R-S associations (Coleman, 1975; Coleman & Gormezano, 1979).

On the other hand, the procedures for Pavlovian conditioning do not include the two corollary criteria from classical conditioning. As a result, in Pavlovian conditioning, the experimenter programs both the parametric features and the nominal temporal occurrence of the stimuli. However, the actual receipt of one (usually the US) or both of the stimuli is controlled by the experimental subject. An example may serve to clarify this point. In autoshaping, the experimenter programs pairings of key-light and feeder activation to occur. However, to obtain the food, the organism must advance to the feeder and consume it. Thus, the response of advancing to the feeder is followed by food (a reinforcer), and the conditions for creating an R-S association have been met.

In Hollis's (1982, 1984) procedures, the gouramis serving as experimental subjects controlled their exposure to the conspecific US. Therefore, Hollis's procedures were Pavlovian conditioning procedures, but not as the term is used interchangeably with Classical conditioning. The Pavlovian conditioning procedure employed by Hollis has

the potential for conditioning responses based on the formation of both S-S and R-S associations.

Given that the paradigm Hollis (1984) employed was Pavlovian, there is a concern about the contribution of the R-S associations to the control of the conditioned frontal display responses. This concern is particularly valid in light of substantial evidence indicating that operant contingencies readily control species-specific behaviours. That the presence of a conspecific is a positive reinforcer and will increase the probability of engaging in species-specific aggressive or agonistic behaviour has been observed in a variety of species, including cocks (Thompson, 1964), mice (Tellegen et al., 1969), rats (Polsky, 1975), and fish (Bronstein, 1986; Hogan, 1967; Hollis & Overmeier, 1982; Sevenster, 1973; Thompson, 1963, 1966; Thompson & Sturm, 1965).

Because aggressive behaviours are sensitive to their consequences, it is possible that the behaviour Hollis (1984) recorded was primarily under the control of R-S associations. While this concern does not affect the adaptive consequence of the acquired behaviour, it does challenge Hollis's (1982) assertion that the learning

mechanism of prefiguring was primarily S-S, and it also challenges the notion that aggression will result from the pairings of a signal and a conspecific.

Given the possibility of R-S associations, it can not be determined that Hollis's (1984) procedures produced behaviour that was under the control of S-S associations. The only way to determine that the situation was primarily controlled by S-S associations is to conduct an omission study (Coleman & Gormezano, 1979; Sheffield, 1965). In the omission procedure, if the target response (e.g., frontal display) occurs during the CS, then the occurrence of the US is omitted. Therefore, it is not possible for the behaviour to be followed by a positive or a negative reinforcer, accordingly, if the behaviour increases in frequency during the CS, the increase must be due primarily to S-S associations. Experiment 1 of this proposal employed an omission procedure within Hollis's (1984) paradigm in order to identify the primary associative mechanism.

Aggression and Territorial Defense. Hollis's (1984) test of fitness consisted of a single encounter between a signalled conditioned fish and a control subject. Greater aggression was displayed by the conditioned gouramis and

interpreted as enhancing territorial defense and hence the fitness of the conditioned fish. However, there are problems with the assumptions that increased aggression during the conflicts was related to conditioning, that increased aggression particularly as assessed in one conflict is an accurate measure of territorial defense, and lastly, that territorial defense is an effective currency for reproductive success.

In terms of aggression, fish with different experimental histories were placed in conflict therefor, the greater aggression in the conditioned fish relative to the control groups could have been caused by, a) conditioning, that is, the pairings of the CS and the US, b) by a decrease in aggression of the rivals due to the control procedures inhibiting performance as noted by Hollis (1984) or c) by a differential effect of the pre-exposure regime on the experimental and control subjects.

Hollis's experimental test for fitness is presumed to be an analogy to the processes that occur during territorial defense. In nature, territorial defense involves repeated encounters or episodes with rivals (Hinde, 1982; Lorenz, 1981). Reproduction will occur, only if the male is



consistently successful in defending his territory. While momentary factors could influence the course of any given episodic encounter, it is the repeated success that will lead to breeding. Thus, the experimental analogy and the inferential arguments would be enhanced if a closer mimic to the natural situation were employed. Instead of basing statements about fitness on a single episodic encounter, repeated encounters should be employed. It is also questionable as to whether or not the measures of aggression employed by Hollis (1984) were measures of territorial defense. None of the experimental subjects in Hollis's study actually defended their territories during the conflict sessions. The conditioned subjects left their territories and intruded, in full display, into the rivals territory. In effect, no measure of the capacity to defend a territory was determined, rather an unusual aggressiveness on part of the conditioned fish was observed. Charging in full display into the territory of a nonaggressing conspecific is not a behaviour commonly found in dominant males, Miller (1964) notes that dominant fish rarely react to a conspecific, even one intruding into its territory, by engaging immediately in any agonistic behaviour. This

aggressiveness is also unusual because in the natural setting, during critical reproductive activities, successful territorial defense is defined by the male keeping intruders away but not by leaving the nesting site unattended lest it be destroyed or the fry eaten by predators. The aggressive behaviour displayed by the conditioned subjects may not represent effective defense but unusual aggressive behaviour.

Finally, the notion that aggressive behaviour represents a currency that can measure reproductive success is also questionable. While the capacity to defend a nesting site may be the basis for reproductive success, it does not follow that failing to defend a particular site due to a challenge by a dominant conspecific decreases reproductive capacity. It is equally possible that, at the species level, leaving a site and living to reproduce in a less desired site and perhaps with a less desired mate contributes to reproductive success. This is particularly likely in situations where there is an abundance of adequate nesting sites and adequate mates. If this argument stands, it follows that not all gouramis will attempt to engage in conflict, rather they would respond to a cue signalling an

intruder by preparing to undertake in the most viable response as determined by their own history. Recall that a test of fitness is intended to identify the ultimate cause of the behaviours being observed. Because of the difficulties in directly measuring fitness (i.e., differential reproductive success), a gain in fitness is usually an inference based on a plausible logical argument (Dawkins, 1986). In Hollis's test of fitness, what is measured is the relative degree of intraspecific aggression. Aggressiveness is translated into a fitness statement through the following assumptions: First, intraspecific aggression is assumed to be a necessary component of successful territorial defense; and second, maintaining a given territory is assumed to be a necessary component of reproductive behaviour for the male gourami. If the validity of the logical network is accepted, then it follows that intraspecific aggression in the male gourami is a necessary component of reproductive success. Accordingly, processes that differentially increase aggression in the male will differentially increase that male's reproductive success (that is increase its fitness relative to its competitors). Thus, the control of aggression by the

purported S-S associations would increase the fitness of the individuals who developed the associations relative to those that do not.

The problem with the above argument is that it is incomplete. To complete the argument it is necessary to add the effects that are expected over subsequent generations (i.e., look at the expected effects of natural selection). If fitness is increased by increases in intraspecific aggression, then the more aggressive males will produce more offspring than the less aggressive males. Accordingly, other things being equal, the mean level of aggression in the succeeding generations should be increased over the mean level for the current generation. Repeating this process over many generations, should produce a very aggressive species! That is, the prefiguring hypothesis predicts an unbounded, feedforward loop for the increase in intraspecific aggression.

Several theorists (e.g., Dawkins, 1986; Maynard-Smith & Price, 1973) have asserted that predictions like those generated by the prefiguring hypothesis produce nonviable evolutionary outcomes. At some point in time, the increase in physical damage and deaths that result from the

aggressive interactions will exceed the reproductive gains and the species will go into decline. A more viable evolutionary strategy is to maintain a balanced level of aggression within the species. Two evolutionary developments that could fulfil this strategy are as follows. First, a species could maintain a composition of individuals who vary in their level of aggressiveness (see Dawkins, 1986). Second, the aggressiveness of an individual could vary as a function of the context in which the individual needed to be aggressive (Dawkins, 1986; Lorenz, 1981; Mayr, 1942). Lastly, a mixture of the two strategies would also be possible.

A reanalysis of Hollis's prefiguring hypothesis suggests that neither of the viable evolutionary strategies can be generated from it. If a species is maintaining a distribution of various levels of aggression across individuals, then for that species, reproductive success can not be solely determined by the level of the aggressiveness of the individual. Accordingly, the fact that aggressiveness can be conditioned would not necessarily affect the fitness of the species. Hollis's prefiguring hypothesis is somewhat more successful with the second

viable strategy. Because conditioning is stimulus specific, differences in conditioning histories in different contexts would yield different levels of conditioned aggression in those different contexts. To the extent that the conditioned aggression would contribute to the overall aggressiveness of the individual, and conditioning would assist in maintaining different levels of aggression in different contexts for the individual.

However, a clear expectation from the second viable evolutionary strategy is that the level of aggression for an individual can vary on repeated exposures to various situations and various conspecifics. Under these conditions, the prefiguring hypothesis can only predict an increase in conditioned aggression over the repeated exposures. This increase would occur because the S-S association can only increase with increased number of CS (context) - US (the conspecific) pairings (The S-S association can be weakened through extinction and other inhibitory procedures. However, such procedures require that the US not be present. This requirement is not met in the scenario proposed by the evolutionary theorists). Because the prefiguring hypothesis cannot yield a decrease

in subsequent aggression as a result of an encounter with a conspecific, the hypothesis can not provide a complete account of the second viable evolutionary strategy.

The failure of the prefiguring hypothesis is a result of the inadequacy of the S-S associative mechanism that Hollis proposed. However, it is possible to generate an alternative associative mechanism that would yield the expectations of the second evolutionary strategy. Hollis has asserted that the associative mechanisms involved in prefiguring result from Pavlovian conditioning. Having defined the Pavlovian conditioning procedure as resulting in the formation of only S-S associations Hollis has restricted her theorizing to only one of the two associative processes that occur during Pavlovian conditioning.

As previously indicated, Pavlovian conditioning yields both S-S and R-S associations. While the conditioned behaviour may be predominantly under S-S control, consideration of both associative processes and their interactions is necessary to provide a full account of the conditioned behaviour. For example, in Hollis's (1984) conditioning phase, the presentation of the male conspecific has the potential to act both as a an eliciting stimulus or

US and a reinforcer. Therefore, the conditioned aggressive behaviour can be both primed by the CS and reinforced by its consequence. In an actual confrontation, the S-S association would be strengthened (if it was preasymptotic) by the pairing. The R-S association for aggressive behaviour would be strengthened if the fish was successful in the confrontation. However, the punishing effect of an unsuccessful confrontation would suppress the R-S association for aggressive responding. Thus, the net aggression controlled by conditioning could increase or decrease as a result of the outcome of a confrontation with a given conspecific. It is also possible that an avoidance response consisting of withdrawal from the site could be conditioned.

This alternative proposal, which I will call the Pavlovian prefiguring hypothesis in order to distinguish it from Hollis's hypothesis, would result in a population that would not respond aggressively in all situations. All subjects would benefit from the predictive capacity afforded by the S-S associations but responding either aggressively or not would depend on the subjects reinforcement history. The Pavlovian prefiguring hypothesis would therefore result



in subjects that aggress if they have a high probability of success and therefor generate offspring perhaps in preferred nest sites with preferred females while those subjects with a history of less successful conflicts would withdraw to less preferred nesting sites and take less preferred females, however, they would survive to contribute to the species and maintain the natural variation we observe.

In summary, an analysis of Hollis's (1984) evidence for the prefiguring hypothesis suggests that there is inadequate support for both the proximate (associative mechanism) and ultimate (test for fitness) causes for the behaviour that develops in the situation. The research being proposed will address both of the inadequacies. Experiment 1 will attempt to identify the proximate cause through the use of the omission paradigm. Experiment 2 will address the ultimate cause by providing a superior test for fitness that will have repeated confrontations. In addition, Experiment 2 will provide an opportunity to determine the level of aggressive responding in a larger sample of gouramis and the relationship between conditioning and territorial defense.

## Experiment 1

The purpose of Experiment 1 was to determine if S-S associations contribute to the conditioning of the frontal display in male blue gouramis. In an effort to accomplish this task, subjects were randomly divided into three groups. Subjects in the first group were presented with light-rival pairings. Subjects in the second group were given omission training, in which the light was followed by rival presentation only on trials where the subjects did not produce or display the targeted agonistic behaviours. Finally, subjects in the third group, called a yoked group were matched to subjects of the second group for the sequence of paired and CS alone trials. The purpose of the yoking procedure was to parcel out the partial reinforcement effect produced by the omission schedule in the second group.

Conditioning parameters were selected on the basis of previous reports of successful conditioning of a variety of fish. Previous effective CSs have included red and green lights, either diffuse (Hollis, Martin, Cadieux & Colbert, 1984) or discrete (Zerbolio & Wickstra, 1980). White and

blue lights have also been used as CSs (Squier, 1969; Zerbolio, 1981), as have a variety of tones (Zuckerman & Blough, 1974). The durations of CSs that support conditioning range from 200-msecs (Zerbolio & Wickstra, 1980) through 15 to 20-secs (Hollis et al., 1984 and Bottjer, Scobie & Wallace, 1977 respectively). Mild shock has also been used as a CS, however, this procedure created some problems because the response to shock interfered with the performance of the CRs (Adler & Hogan, 1963). Based on these considerations the present study used a 15-sec red light as the CS. The US, was a presentation of a male conspecific which has been found to elicit a number of agonistic behaviours, including frontal display and approach (Hollis, 1984; Hollis et al, 1984; Hollis et al, 1985). As in the Hollis studies, the US duration was 15 seconds.

## Method

### Subjects

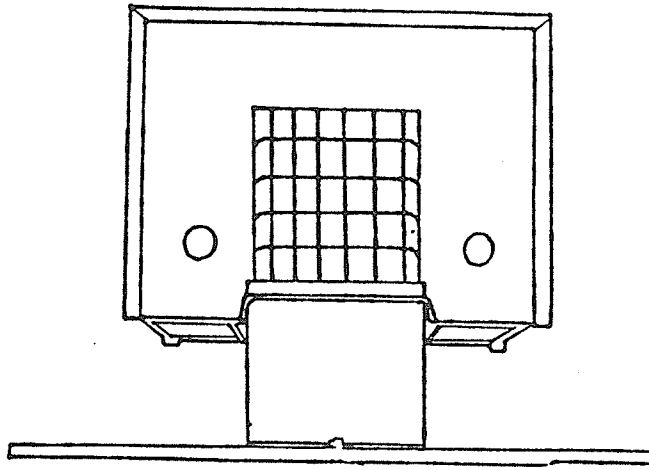
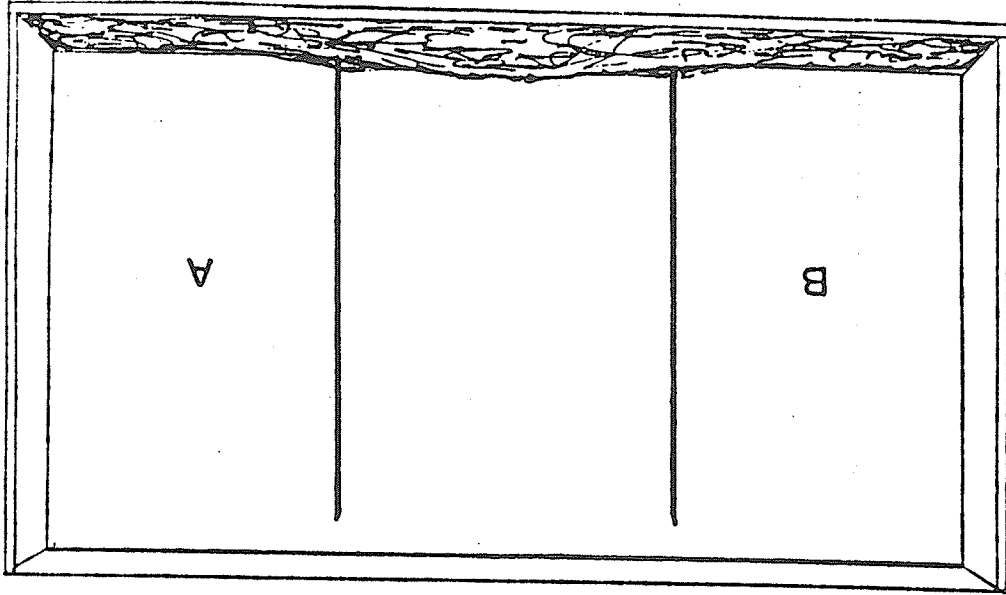
The subjects were 36 adult male blue gouramis (Trichogaster trichopterus) selected from the stock of a

local supplier. The fish selected were consistent in body size and fin depth.

### Apparatus

The apparatus consisted of three experimental tanks measuring 64 cm in length x 29 cm in width x 30 cm in height. The tanks were maintained at 27 degrees Celsius with a 12 hr light-12 hr dark illumination schedule. The tanks were filtered by means of an undergravel filtering system requiring a 3-cm gravel base. Figure 1 presents a diagram of the stimulus panel (upper panel) and the tank (lower panel). Each tank was divided into three separate areas by removable partitions painted black with Cabot's Flexible Protective Paint (#3230). The removable partitions prevented visual contact between the fish. The outer right and left areas of the tank were experimental chambers of equal dimensions (21 cm in length x 29 cm in width x 30 cm in height) and were labelled chambers A and B respectively. Chambers A and B each housed a subject while the centre area which measured 11 cm in length x 29 cm in width x 30 cm in height was reserved for the removable stimulus panel. The stimulus panel (Figure 1, upper panel) consisted of a

Figure 1. The upper panel shows the stimulus panel, which was moved between tanks during conditioning. As can be seen two light which protrude from the face of the panel can serve as CSs. The lower panel of this figure shows the division of a tank into three separate areas. Areas A and B served as experimental chambers and housed subjects while the centre area contained the stimulus panel during conditioning sessions.



submersible glass box measuring 11 cm in length x 29 cm in width x 27 cm in height. The 29 cm x 27 cm sides of the panel had a 12 cm x 12 cm aperture in the centre which resulted in the creation of a tunnel between chambers A and B. The apertures were covered by doors which could be raised or lowered independently by a pulley system connected to motors located in an adjoining room. The opening or closing of the doors took 1 sec. The interior of the stimulus panel was constructed such that a conspecific could be housed within the tunnel behind the doors in a wire mesh cage measuring 12 cm x 12 cm x 11 cm. Opening the doors on either side of the panel permitted visual contact between the conspecific and the subject but did not permit intrusion into subject's chamber. When the wire mesh was removed the conspecific US could access the subject's territory when the appropriate door was raised.

Each side of the stimulus panel had a red and green light bulb (24V) protruding 3 cm into the tank. The red bulb was on the left side and the green on the right side of the panel. Both lights were located 6 cm from the top and 4.5 cm from the edge.

The timing of the lights and the doors was controlled by a Coulbourne solid state logic system located in an adjoining room.

Sessions were recorded by an RCA video camera (Model CKC021) and recorder (Model VLP 950HF), and simultaneously viewed on a Panasonic colour television monitor (Model PC-20L13). The camera was mounted on a movable stand that was positioned such that the lens was perpendicular to, and 25 cm from the centre of the front side of the experimental chamber. Markers on the floor ensured appropriate and consistent placement of the camera across experimental tanks and days. An 11-88 mm video zoom lens was used to record all sessions. The video recorder and the monitor were located in an adjoining room, so as to minimize any possible disruption of the sessions by the presence of the experimenter in the experimental room.

A 15-sec presentation of the red light served as a conditioned stimulus (CS) and a 15-sec presentation of a male conspecific served as the unconditioned stimulus (US). The male gouramis that served as USs were not used for any other purpose during the study. The same conspecific was used as a US across days for one experimental subject only.



All gouramis that served as USs were kept in individual tanks between sessions.

Ten minutes prior to the onset of each session the tankmate of the subject being conditioned was removed and placed in a small receptacle filled with water from the home tank. The stimulus panel was then lowered into the centre area of the tank. Approximately 5 minutes prior to the first trial, the conspecific was placed in the stimulus panel. The appropriate partition was taken out to present the stimulus panel to the subject at session onset.

#### Procedure

Eighteen subjects were randomly assigned to one of three groups. The group consisted of a paired group (P), an omission group (O), and an yoked group (Y). The subjects were placed in their appropriate chambers 5 days before the experiment began, this time period was more than sufficient to permit the establishment of individual territories (Frey and Miller, 1968). The remaining 18 fish served as USs and were individually housed between sessions.

On the sixth day after their arrival, the acquisition phase consisting of 15 daily sessions was implemented. On each day subjects in the paired group (Group P) were presented with 10 trials separated by a mean interval of 10 minutes ranging from 8 to 12 minutes. Each trial consisted of a forward pairing of the red light CS, followed by the rival presentation US. The interstimulus interval was 10 seconds resulting in a 5 second overlap of the CS and US. The subjects in the omission group (Group O) were given presentations of the CS on the same schedule as in Group P. The US was presented when none of the behaviours targeted for conditioning occurred during the interstimulus interval. On trials where one of the agonistic behaviour occurred during the interstimulus interval, the CS was not followed by a US. Subjects in the yoked group (Group Y) were matched to subjects in Group O and presented with precisely the same sequence of stimuli as their matched subjects of Group O.

Given the restricted number of experimental chambers the study was run in three successive replications of 6 subjects. Each replication contained two members from each of the three experimental groups. A restriction on the randomization of subjects to chamber was the requirement

that in each replication one subject from each group was placed in an 'A' chamber, and one in a 'B' chamber. Across replications, the order in which the subjects were given conditioning was counterbalanced to equate for time of days across groups. Since there were experimental subjects in each of the adjacent chambers of each tank, all subjects in chambers A were presented with the daily session followed by all subjects in chambers B. This precluded any subjects being run within one hour after the subject in the adjacent chamber. This precaution was taken in order to minimize the possible disruption of conditioning by earlier activities in the adjacent chamber.

#### Response Specifications

During acquisition the following responses monitored:  
1) frontal display, 2) approach, 3) biting and 4) tailbeating. Frontal display was defined as a spreading of the dorsal, ventral, and caudal fins. A space within 10 cm of the stimulus panel was defined as the approach area. Approach was defined as having occurred when the subject entered the approach area such that the its head was in this area to or past its gill covers (opercula). Biting was

defined as contacting the CS light fixture, the door or the conspecific with an open mouth, following an abrupt forward lunge. Finally tailbeating was defined as a side to side undulation of the body.

Agonistic behaviour was monitored during the following three intervals: a) a 10-sec Pre-CS interval, b) the 10-sec CS-US interval and c) during the 15-sec US interval. The end of the US presentation defined the end of the trial. This monitoring procedure yielded measures of baseline responding (Pre-CS interval), conditioned responding (CS-US interval), and unconditioned responding (US interval) for each response monitored.

For the frontal display and the approach responses, the mean per cent daily responding across trials and subjects was calculated. The mean duration of responding on each trial was also calculated for each session. Finally the mean latency of the first response on each trial, and the frequency of responding on each trial was also calculated for all three time intervals. For biting and tailbeating the same measures of responding were taken save for the duration of responding.

Measures of interobserver reliability were computed on a trial by trial basis for each subject on three of the 15 daily sessions. Interobserver reliability was determined for the occurrence of frontal display and approach responding in each group. The frequencies of biting and tailbeating responses were too low to compute valid measures of interobserver reliability. An index of interobserver reliability was determined by taking the total number of joint agreement of occurrence of the response and dividing it by the total number of joint agreements plus disagreements (Barlow, Hayes, and Nelson, 1984). The mean reliability coefficients for Groups P, O, and Y were 81.8, 95.3, and 90.8 respectively. Table 1 presents the interobserver reliability coefficients for frontal display and approach responding across each group and for each of the three time intervals during which responding was monitored. The interobserver reliability coefficients were high and indicated that the data collected were reliable and accurate.

Table 1. Interobserver reliability co-efficients for frontal display and approach responding during the Pre-CS, CS-US, and US intervals for the Paired, Omission and Yoked groups.

<u>Paired Group</u>	Pre-CS	CS-US	US
Frontal display	50	96	88
Approach	94	76	87

<u>Omission Group</u>	Pre-CS	CS-US	US
Frontal display	100	100	88
Approach	88	100	96

<u>Yoked Group</u>	Pre-CS	CS-US	US
Frontal display	100	81	89
Approach	82	93	100

## Results

The responses monitored during Experiment 1 were, frontal display, approach, biting and tailbeating. For frontal display and approach the measures taken were: per cent responding during each session, the mean duration of responding during each session, the latency to the first response on each trial, and finally, the frequency of responding on each trial. For biting and tailbeating the measures of responding were identical to those monitored for frontal display and approach save for measures of duration.

Prior to discussing the results it is important to note that the level of conditioning in Group O determined the degree to which both Group O and Y came into contact with the omission contingency. Conditioning in Group O was such that the omission contingency was effective on 10 per cent of the trials across subjects and days.

The data from Experiment 1 were analyzed as follows. Responding during the Pre-CS, the CS-US and the US interval was analyzed between group by means of repeated measures mixed effect analysis of variance (ANOVA) and orthogonal components for trend analysis, followed by a priori tests of

significance using t-tests. Subsequence to these analysis, correlations and analysis of covariance (ANCOVA) were undertaken for a number of responses. ANOVAs and ANCOVAs were conducted using the BMDP Statistical Software package (Dixon, 1985). Within group results were then analyzed between intervals by means of dependent t-tests.

Statistical analysis were not applied to the latency or frequency of responding on trial because all subjects did not respond on all trials. These measures were reported for their descriptive value. The results will be presented for the frontal display, approach, biting and tailbeating responses in turn. For each response, the results for responding during the Pre-CS interval will be presented, followed by the results for responding during the CS-US interval and finally, the results for responding during the US interval. Between group analysis will be presented followed by within group analysis of responding.

### Frontal Display

Per Cent Responding. The mean per cents for frontal display responding during the Pre-CS, the CS-US and the US intervals are contained in the upper left hand matrix of



Table 2. No differences appeared to exist between groups during any of the three time intervals. As can be observed, the mean per cent frontal display responding for all groups was least during the Pre-CS interval and greatest during the US interval.

The mean per cents for frontal display responding as a function of days during the Pre-CS, the CS-US and the US intervals for Groups P, O, Y, are depicted in the upper, middle and lower panels respectively of Figure 2. An ANOVA applied to the daily mean frontal display responding during the Pre-CS interval for Groups P, O, and Y confirmed that no significant ( $p > 0.05$ ) group ( $F(2,15)=1.94$ ), days ( $F(14,210)=0.46$ ) or days by group interaction ( $F(28,210)=1.32$ ) existed. Thus the baseline levels of frontal display responding were equal between groups and were stable over the course of the experiment.

Figure 2, (middle panel) depicts the mean frontal display responding for Groups P, O, and Y, during the CS-US interval. As can be observed responding increased over days with Group P responding at a slightly higher level than the other groups. A mixed effect ANOVA however, indicated that there was no significant group effect ( $F(2,15)=1.23$ ) or

Table 2. Frontal display responding in the Paired (P), Omission (O), and Yoked (Y) groups (G) during the Pre-CS, the CS-US, and US intervals (I).

Frontal Display

Per Cent Responding

G	I	Pre-CS	CS-US	US
P		4.2	19.0	32.4
O		3.3	10.2	48.4
Y		5.6	13.0	32.0

Response Duration (seconds)

G	I	Pre-CS	CS-US	US
P		1.5	2.7	4.2
O		1.0	2.4	5.1
Y		1.7	2.6	4.7

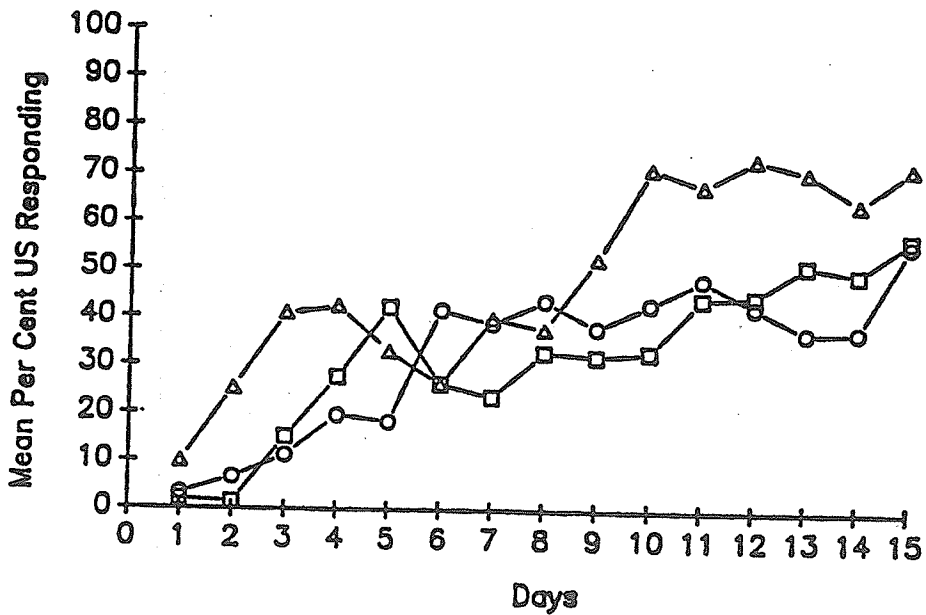
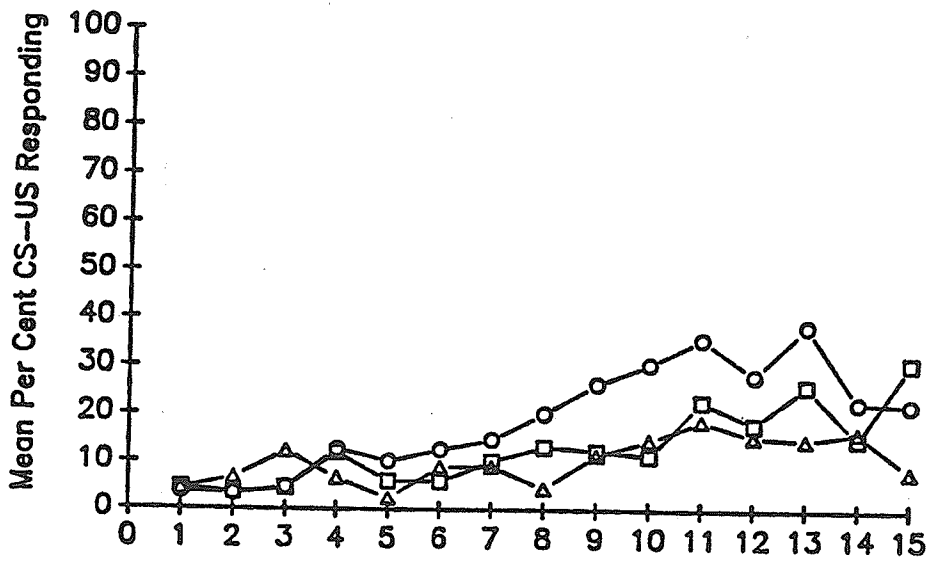
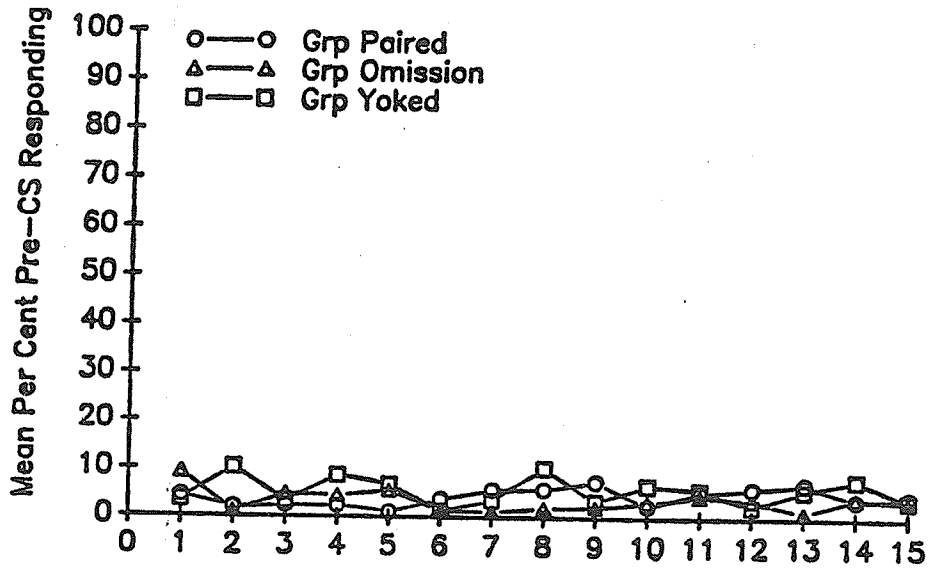
Onset Latency (seconds)

G	I	Pre-CS	CS-US	US
P		5.5	4.8	5.4
O		6.4	5.4	7.8
Y		5.6	4.7	6.1

Frequency per Trial

G	I	Pre-CS	CS-US	US
P		1.0	1.1	1.1
O		1.0	1.0	1.0
Y		1.0	1.1	1.0

Figure 2. Mean per cent frontal display responding as a function of days for Groups P, O, and Y, during the Pre-CS, the CS-US and the US intervals (upper, middle, and lower panels respectively).



group x days interaction ( $F(28,210)=0.99$ ). A significant days effect ( $F(14,210)=5.45$ ,  $p<0.01$ ), which was comprised of a significant linear component for trend ( $F(1,15)=10.51$ ,  $p<0.00$ ), confirmed the increase in responding over days.

To determine whether frontal display responding during the CS-US interval exceeded that of the Pre-CS interval, a mean score for each subject during each of the time intervals in question was calculated by averaging across days. Dependent t-tests were then applied to the means. The results indicated that a significant difference in performance between the Pre-CS and the CS-US interval existed in Group P, ( $t=5.90$ ,  $df=10$ ,  $p<0.01$ ), Group O, ( $t=4.87$ ,  $df=10$ ,  $p<0.01$ ), and Group Y ( $t=3.38$ ,  $df=10$ ,  $p<0.01$ ). For each group responding during the CS-US interval was significantly higher than during the Pre-CS interval.

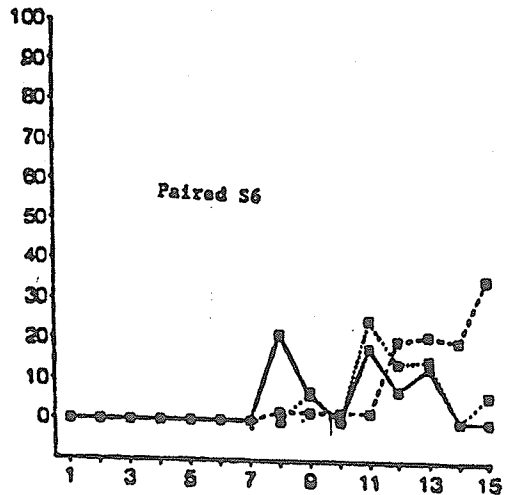
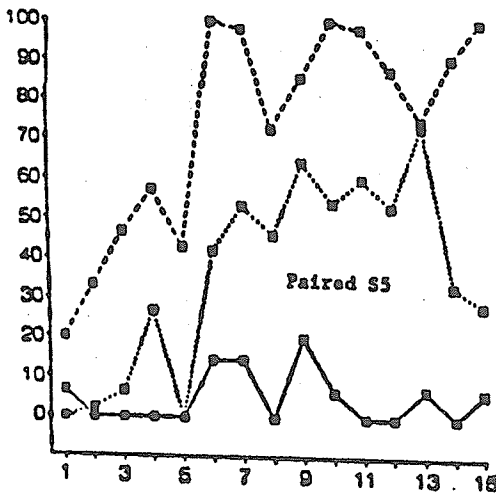
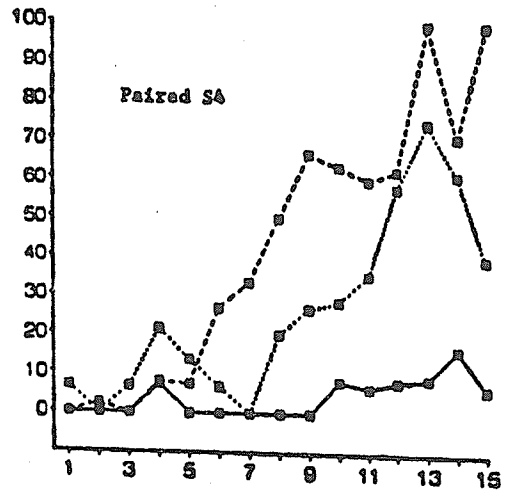
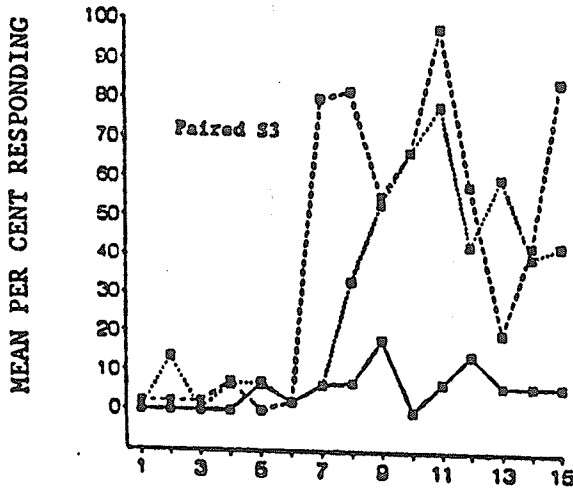
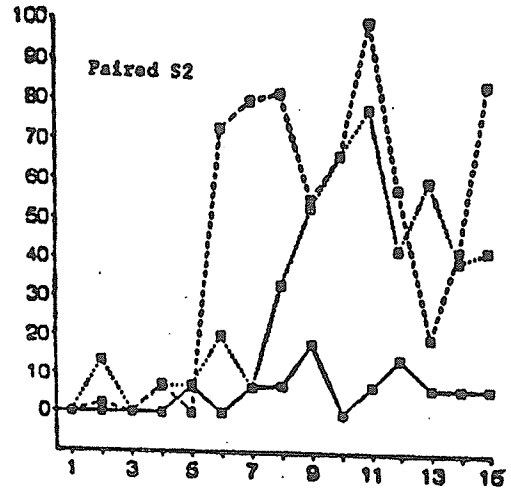
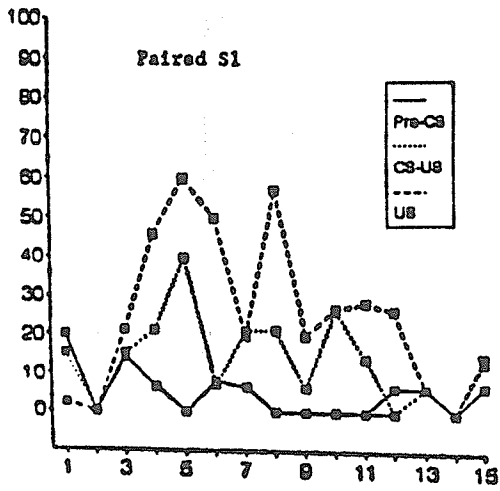
The mean per cent frontal display responding during the US interval can be seen in the upper left hand matrix of Table 2, and does not appear to differ between groups. The lower panel of Figure 2 shows the mean per cent frontal display responding during the US interval as a function of days. No differences appear to exist between groups

although responding increased over days. An ANOVA applied to the daily mean per cent frontal display responding during the US interval for Groups P, O, and Y revealed neither significant ( $p > 0.05$ ) group ( $F(2,15) = 1.19$ ) nor a days by group interaction ( $F(28,210) = 0.59$ ). However, the ANOVA did confirm the presence of a days effect ( $F(14,210) = 6.17$ ,  $p < 0.1$ ) which was comprised of a significant linear component for trend ( $F(1,15) = 13.30$ ,  $p < 0.1$ ) indicating an increase in unconditioned responding across days.

Frontal display responding during the US interval for each of the three groups appeared to be substantially greater than the per cent responding during the CS-US interval. Dependent t-tests applied to the performance during the US and the CS-US interval within each group confirmed the presence of a significant differences in performance for Group P, ( $t = 5.17$ ,  $df = 10$ ,  $p < 0.01$ ), Group O, ( $t = 9.00$ ,  $df = 10$ ,  $p < 0.01$ ) and Group Y, ( $t = 6.78$ ,  $df = 10$ ,  $p < 0.01$ ).

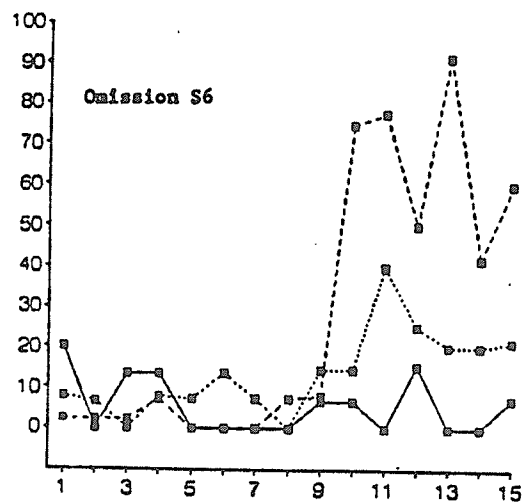
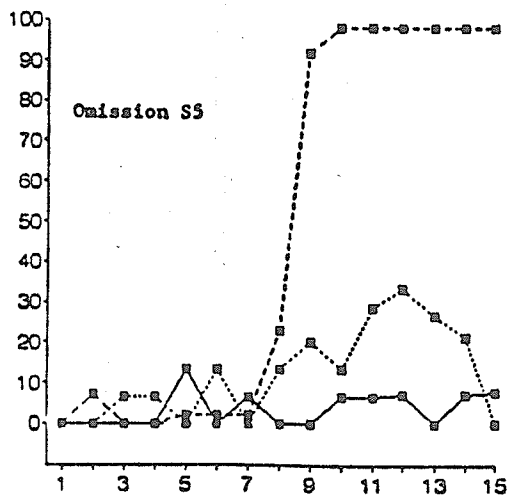
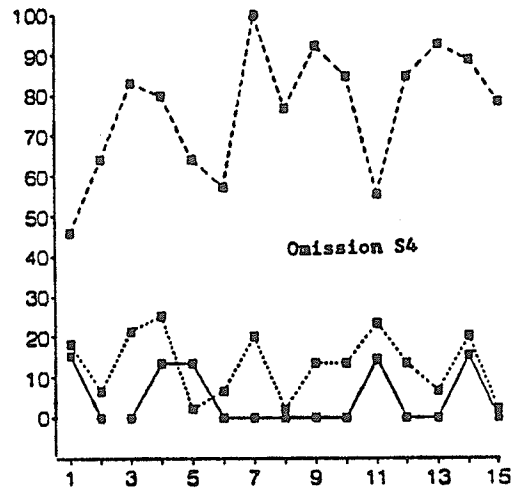
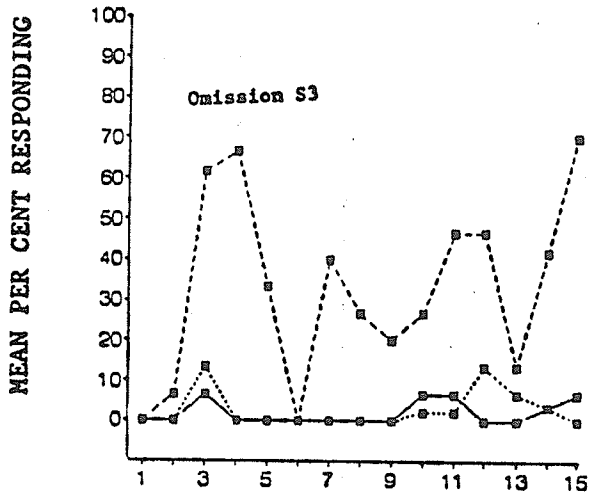
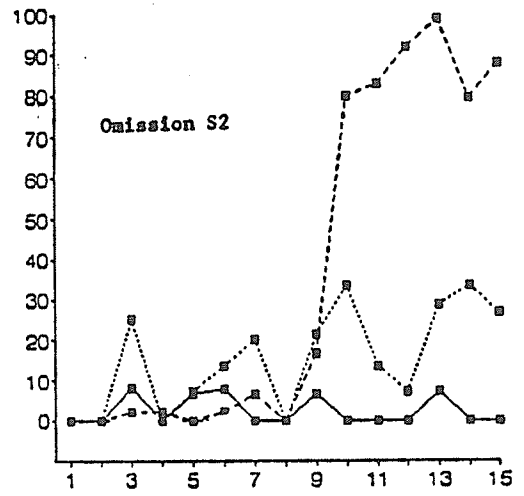
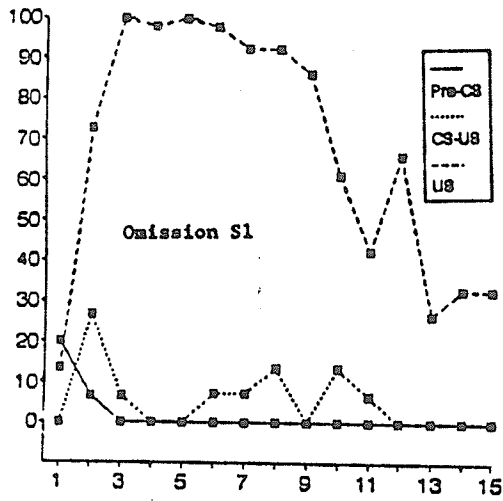
Figure 3 presents the mean per cent frontal display responding for individual subjects in all groups during the Pre-CS, the CS-US and the US intervals. The Figure suggested that the lack of group difference in frontal

Figure 3. Mean per cent frontal display responding as a function of days during the Pre-CS, the CS-US and US intervals for individual subjects in Groups P, O, and Y.

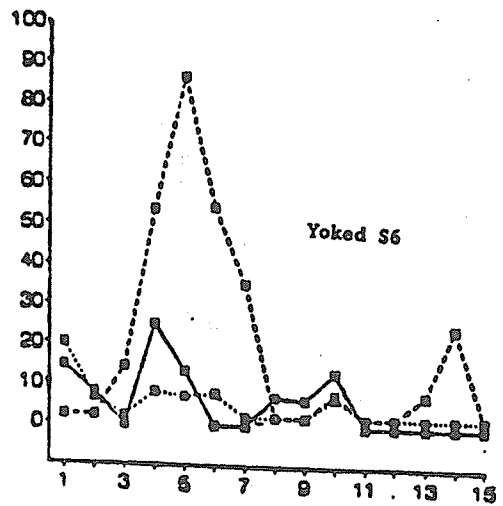
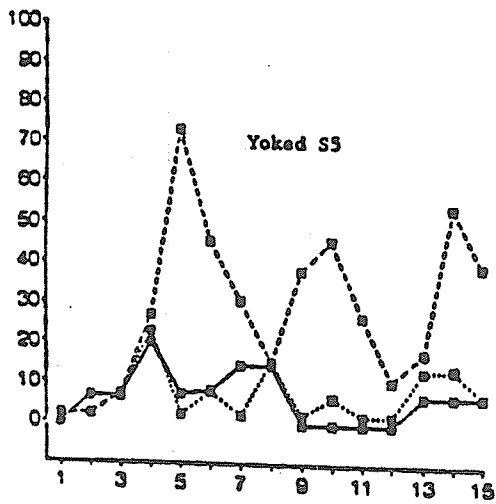
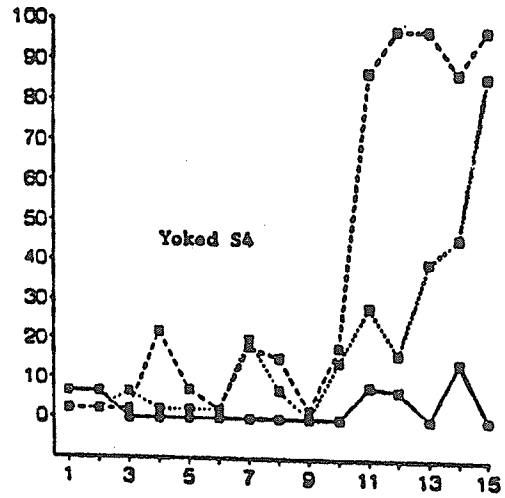
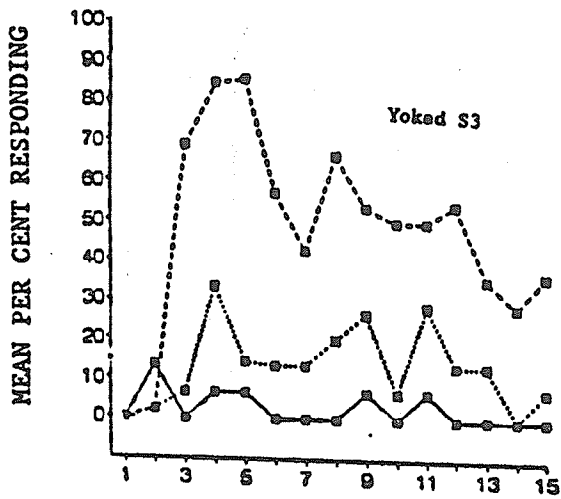
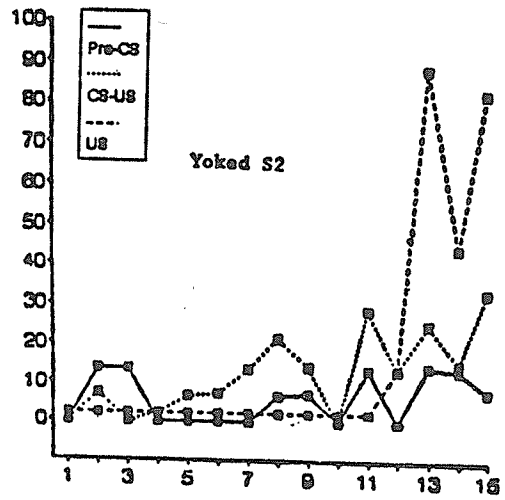
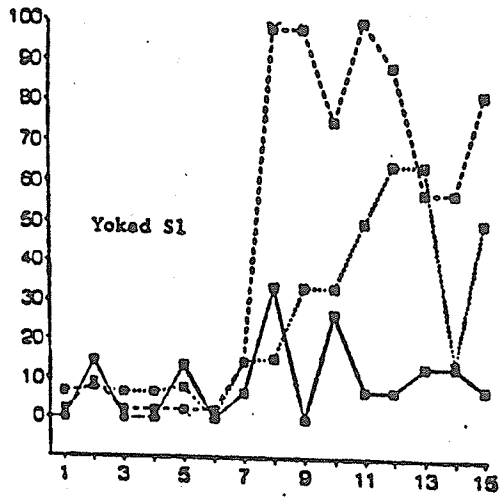


DAYS





DAYS



DAYS

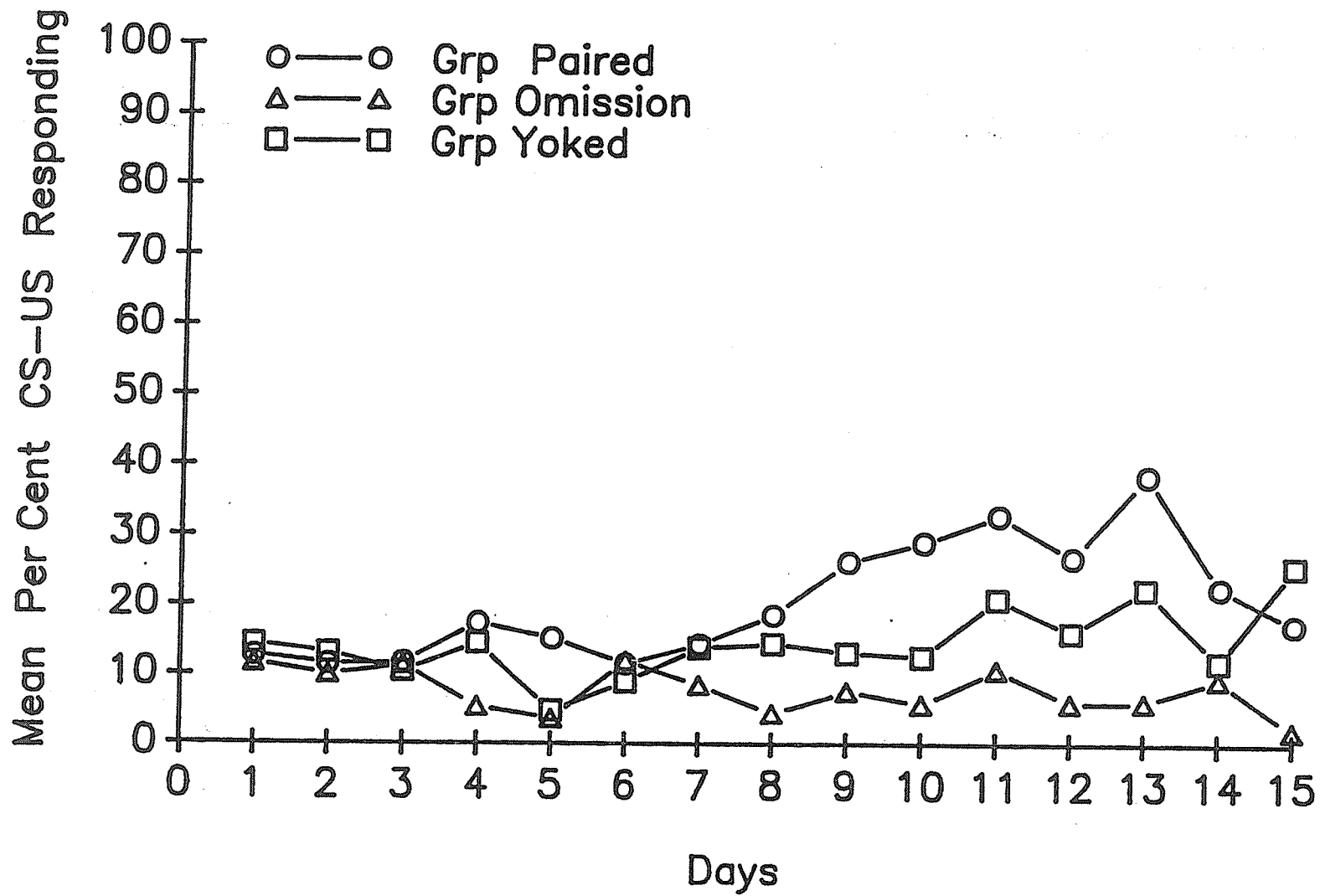
display responding during the CS-US interval may have been a function of the substantial variability in individual levels of responding. The differences include widespread variability in responding during the US period. The latter observation suggests that the US's were not equally effective. Because conditioning depends on the reliability of the UR given the presentation of the US (see Gormezano and Kehoe, 1975), the variability in responding during the CS-US interval might be due to the differential effectiveness of the US. To explore this possibility a correlation ( $N=270$ ) was conducted between frontal display responding during the CS-US interval and the US interval, across each of the three groups. A significant relationship of 0.57 ( $p<0.01$ ) was found between these variables. Because differential effectiveness of the US appeared to be effecting responding in the CS-US interval, the responding during this period was reanalysed using an ANCOVA with the US interval responding serving as the covariate. The ANCOVA revealed the presence of a significant group ( $F(2,14)=5.08$ ,  $p<0.05$ ), and days effect ( $F(14,209)=1.94$ ,  $p<0.05$ ), as well as a significant group x days interaction ( $F(28,209)=1.59$ ,  $p<0.05$ ). A Newman-Keuls Multiple Range Test was applied to

the adjusted means of all three groups for frontal display responding during the CS-US interval. At  $p=0.05$  the Newman-Keuls analysis revealed that a significant difference existed between the responding in the Paired and Omission groups. No other significant differences were found.

Figure 4 presents the mean per cent frontal display responding during the CS-US interval as a function of days and adjusted for the level of frontal display responding during the US interval. As can be observed Group P showed more responding across days than either Groups O, or Y, which do not appear to differ. These results suggest that the levels of unconditioned frontal display responding differ significantly between subjects and must be taken into account when studying conditioned frontal display responding.

Duration. The mean duration of frontal display across days for each group during the Pre-CS, the CS-US and the US intervals can be seen in the upper right matrix of Table 2. Group differences in the mean duration of frontal display responding appear to be absent in all three time intervals. It may also be observed that the duration of frontal

Figure 4. Mean per cent frontal display responding in Groups, P, O, and Y, during the CS-US interval, across days and adjusted for levels of responding during the US interval.



responding for all three group appears to increase between the Pre-CS, the CS-US and the US intervals.

A repeated measures ANOVA applied to the daily mean duration of frontal display during the Pre-CS interval for Groups P, O, and Y confirmed that there was no significant group ( $F(2,15)=1.72$ ), days ( $F(14,210)=0.54$ ) or days x group interaction ( $F(28,210)=1.14$ ). Thus the duration of frontal display during the Pre-CS interval did not differ between groups and appeared to be stable over the course of the experiment.

Similarly, a repeated measures ANOVA applied to the mean duration of frontal display responding during the CS-US interval confirmed that no significant group effect ( $F(2,15)=0.11$ ) or group x days interaction was present ( $F(28,210)=0.66$ ). However, the ANOVA did reveal the existence of a days effect ( $F(14,210)=1.73$ ,  $p=0.052$ ), composed of a linear trend ( $F(1,15)=5.01$ ,  $p<0.05$ ). These results indicate that the duration of frontal display responding during the CS-US interval did not differ between groups but increased over days.

The data in the upper right hand matrix of Table 2 suggests that the duration of frontal display during the CS-

US interval increased relative to responding during the Pre-CS interval for all groups. Dependent t-tests comparing the duration of frontal display responding in the CS-US interval to that during the Pre-CS interval determined that significant differences existed for Group P, ( $t=4.42$ ,  $df=10$ ,  $p<0.01$ ), Group O, ( $t=5.99$ ,  $df=10$ ,  $p<0.01$ ) and Group Y ( $t=2.61$ ,  $df=10$ ,  $p<0.05$ ). The results indicate that the duration of frontal display responding during the CS-US interval was greater than during the Pre-CS interval for all groups.

The duration of frontal display responding during the US interval does not appear to differ between groups. The application of an ANOVA to the mean duration of frontal display for Group P, O, and Y during the US interval revealed that no significant group effect ( $F(2,15)=0.39$ ,  $p>0.05$ ) or group x days interaction existed ( $F(28,210)=0.56$ ,  $p>0.05$ ). The ANOVA did however confirm the presence of a significant days effect ( $F(14,210)=4.18$ ,  $p<0.01$ ), which was comprised of a significant linear component for trend ( $F(1,15)=10.58$ ,  $p<0.01$ ). Thus, the duration of responding during the US interval did not differ between groups but increased over the course of the experiment for all three groups.



It may be observed from the data in the upper right hand matrix of Table 2 that the duration of frontal display for each group during the US interval appears to be greater than during the CS-US interval, however, a direct comparison between the US interval and the CS-US interval cannot be made because the duration of the US interval was 15-secs while that of the CS-US interval was only 10-secs. In order to compare the two intervals, the duration of responding during the US interval must be multiplied by .66. The resulting means for the duration of frontal display during the US interval are 2.77 secs. for Group P, 3.39 secs for Group O and 2.83 secs for Group Y. Given the transformation, the mean duration of responding during the US interval does not appear to differ from the duration of responding during the CS-US interval for any of the groups. Dependent t-tests comparing the duration of frontal display responding during the CS-US interval and the US interval for all three groups confirmed that there was no significant difference for either Group P ( $t=0.45$ ,  $df=10$ ,  $p>0.01$ ), or Group Y, ( $t=1.07$ ,  $df=10$ ,  $p>0.01$ ). However, a significantly greater duration of responding was observed during the US

interval relative to the CS-US interval for Group O ( $t=3.41$ ,  $df=10$ ,  $p<0.01$ ).

Latency and Frequency During Each Trial. The mean latency to first response on each trial and the frequency of responding on each trial during the Pre-CS, the CS-US and the US intervals for Group P, O, and Y can be seen in the lower left and right matrices, respectively, of Table 2. As can be seen neither the latency nor the frequency of responding appears to differ between groups nor to change within groups across the Pre-CS, CS-US or US intervals. The data include only trials during which subjects responded as opposed to a group mean. Given that many subjects responded on very few trials, it was not possible to conduct a meaningful statistical analysis on these data. These descriptive data are presented because they have not been reported to date.

The principle observations for the frontal display response were that both the per cent and the duration of responding were greater during the CS-US than during the Pre-CS interval and that both increased over training during the CS-US period. In addition, when responding during the CS-US period was adjusted for differential effectiveness of

the USs, Group P showed a significantly greater per cent frontal display relative to Group O, with Group Y falling between the two.

#### Approach Responding

As noted earlier approach was defined as the intrusion of the subject into the area 10 cm forward of the stimulus panel. Approach was said to have occurred when the subjects had entered the area up to its gill covers or opercula.

Per Cent Responding. The mean per cent approach responding during the Pre-CS, the CS-US and the US intervals for Groups P, O, and Y can be seen in the upper left matrix of Table 3. As can be observed no differences appear to exist between groups during the Pre-CS, CS-US or the US intervals. The per cent approach responding for each groups was lowest during the Pre-CS interval and greatest during the US interval. Figure 5 depicts the mean per cent approach responding as a function of days for group P, O, and Y, during the Pre-CS, the CS-US and the US intervals (upper, middle and lower panels respectively).

A repeated measures ANOVA applied to the daily mean per cent approach responding during the Pre-CS interval

Table 3. Approach responding in the Paired (P), Omission (O), and Yoked (Y) groups (G) during the Pre-CS, the CS-US, and US intervals (I).

Approach

Per Cent Responding

G	I	Pre-CS	CS-US	US
P		23.2	30.5	45.5
O		20.1	24.1	60.7
Y		29.0	33.6	40.5

Response Duration (seconds)

G	I	Pre-CS	CS-US	US
P		2.1	3.7	5.6
O		3.7	3.7	7.5
Y		4.5	41.6	6.0

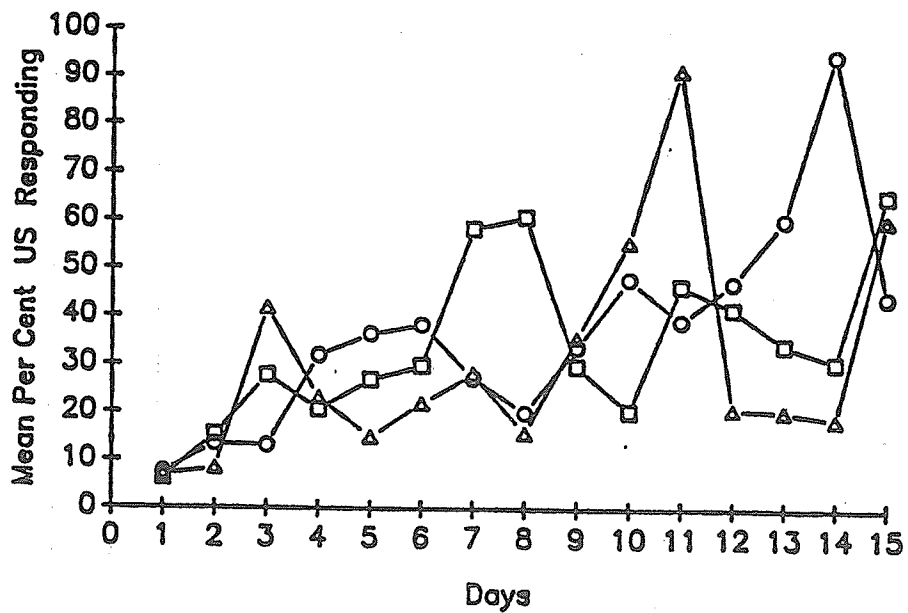
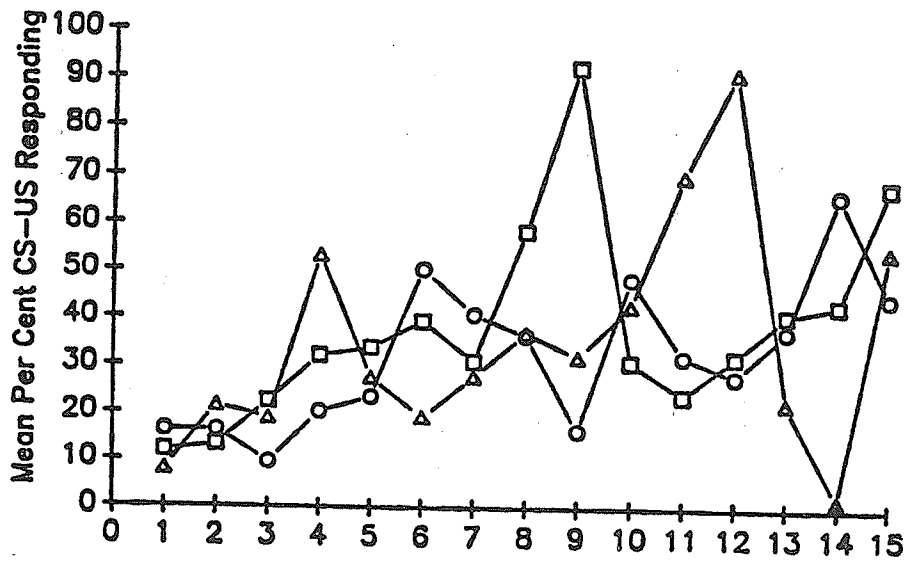
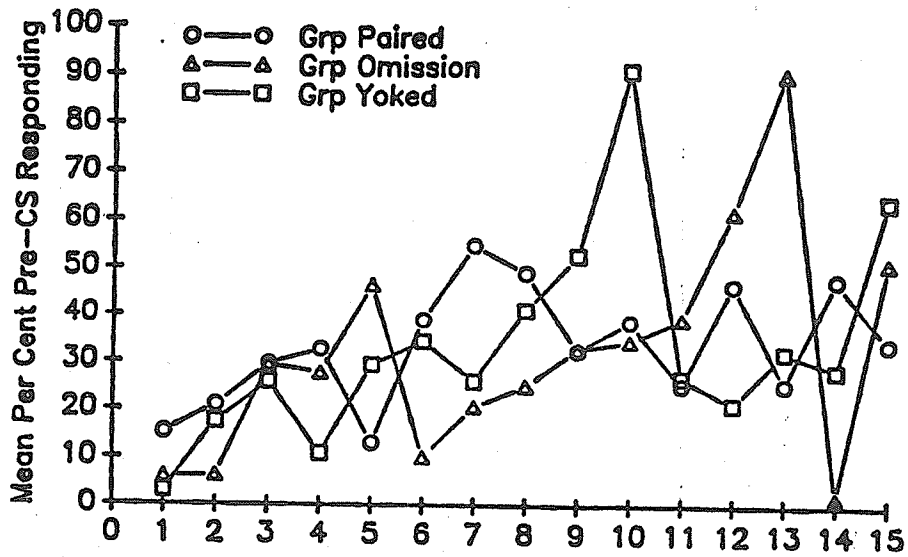
Onset Latency (seconds)

G	I	Pre-CS	CS-US	US
P		4.8	4.8	5.2
O		4.9	5.0	5.9
Y		4.8	4.8	5.0

Frequency per Trial

G	I	Pre-CS	CS-US	US
P		1.0	1.0	1.0
O		1.0	1.0	1.0
Y		1.1	1.1	1.1

Figure 5. Mean per cent approach responding as a function of days for Groups P, O, and Y during the Pre-CS, CS-US, and US intervals (upper, middle and lower panels respectively).



confirmed that no significant group ( $F(2,15)=1.13$ ) or days  $\times$  group interaction existed ( $F(28,210)=0.87$ ). The ANOVA identified the existence of a days effect ( $F(14,210)=2.65$ ,  $p < 0.01$ ) which was comprised of a significant linear component for trends ( $F(1,15)=9.58$ ,  $p < 0.01$ ). These results indicate that although there was no group differences in approach responding, baseline responding increased in all groups over days.

For the mean per cent approach during the CS-US interval for Groups P, O, and Y, Figure 5 suggests that no significant differences between groups exists although there does appear to be an increase in responding across days. A repeated measures ANOVA confirmed that no significant group effect ( $F(2,15)=0.64$ ), or group  $\times$  days interaction existed ( $F(28,210)=0.59$ ). The ANOVA did however confirm the presences of a significant days effect ( $F(14,210)=6.15$ ,  $p < 0.0$ ) comprised of a linear component for trends ( $F(1,15)=35.93$ ,  $p < 0.0$ ). Once again, although no group differences were found it was observed that the mean per cent approach responding increased over days.

Dependent t-tests between approach responding during the CS-US interval and the Pre-CS interval for each group

were conducted in order to determine if significant differences existed. No significant difference existed for Group P, ( $t=2.80$ ,  $df=10$ ,  $p>0.01$ ), Group O, ( $t=1.55$ ,  $df=10$ ,  $p>0.01$ ), or for Group Y, ( $t=2.54$ ,  $df=10$ ,  $p>0.01$ ).

As noted above, and as depicted in Figure 5, the mean per cent approach during the US interval does not appear to differ between groups. A repeated measures ANOVA applied to the per cent approach responding between groups during the US interval confirmed that no significant group effect ( $F(2,15)=0.97$ ,  $p>0.05$ ), or days x group interaction existed ( $F(28,210)=0.69$ ,  $p>0.05$ ). The ANOVA did however confirm the existence of a days ( $F(14,210)=12.75$ ,  $p<0.01$ ) effect comprised of a significant linear component for trends ( $F(1,15)=35.13$ ,  $p<0.01$ ).

As can be observed in the upper left hand matrix of Table 3, the mean per cent approach responding appears to be greater during the US interval than during the CS-US interval for each group. Dependent t-tests between approach responding during the US interval and the CS-US interval confirmed that there existed a significant difference with more responding in the US interval for Group P, ( $t=4.81$ ,  $df=10$ ,  $p<0.01$ ), and O ( $t=6.46$ ,  $df=10$ ,  $p<0.01$ ).



For Group Y, no significant difference was found in responding during the US and the CS-US intervals ( $t=1.90$ ,  $df=10$ ,  $p<0.01$ )).

Duration. The mean duration in the approach area for Groups P, O, and Y, during the Pre-CS, the CS-US and the US intervals can be seen in the upper right matrix of Table 3. No significant differences for duration in the approach area appear to exist between groups during the Pre-CS, the CS-US or the US intervals. As can also be seen in the table no differences appear to exist within groups between the Pre-CS and CS-US interval for any of the three groups.

The repeated measures ANOVA's for the mean duration of approach across days for the Pre-CS, the CS-US, and the US interval failed to identify either groups or groups x days effects. In addition, the dependent t-tests comparing Pre-CS and CS-US interval responding for each group failed to identify significant differences. The only significant changes observed were increases in duration across days in the CS-US interval ( $F(14,210)=3.26$ ,  $p<0.01$ ) and US interval ( $F(14,210)=12.09$ ,  $p<0.01$ ).

To compare the duration of responding within groups between the CS-US and the US intervals, the response

durations during the US intervals were multiplied by .66 to adjust for the different duration of the interval. The means resulting from this transformation for responding during the US interval are 3.70 secs for Group P, 4.95 secs for Group O, and 4.00 secs for Group Y. These means were used for the purpose of within group comparisons.

Dependent t-tests comparing the duration in the approach area during the US and the CS-US intervals confirmed that no significant difference existed for Group P ( $t=0.05$ ,  $df=10$ ,  $p>0.01$ ), or Group Y ( $t=0.34$ ,  $df=10$ ,  $p>0.01$ ), while the duration of approach during the US interval was significantly greater than during the CS-US interval for Group O ( $t= 3.32$ ,  $df= 10$ ,  $p< 0.01$ ).

Latency and Frequency During Each Trial. The mean latency and frequency of approach responding during the Pre-CS, the CS-US and the US interval can be seen in the lower matrices of Table 3. As can be observed there appears to be little difference in latency or frequency of approach responding between groups or within groups. As noted earlier no statistical analysis were conducted on this data, the latency and frequency measures were taken to determine the nature of individual responding.

In summary, for both the mean per cent approach responding and the duration of approach responding no difference were observed between groups in the Pre CS, CS-US or US interval. For the mean per cent approach responding an increase across days was observed during the Pre-CS, the CS-US, and the US interval. For the duration of approach responding, an increase in response duration was observed during the CS-US and the US intervals, while the duration of responding was stable across days during the Pre-CS interval.

#### Biting and Tailbeating

The mean percent of trials on which biting and tailbeating occurred, as well as the mean latency to first bite, and frequency of biting and tailbeating on each trial during the Pre-CS, the CS-US and the US intervals can be seen in Tables 4 and 5 respectively. It should be noted that the means presented are the result of limited responding by 1 or 2 subjects and should not be construed as reflecting group performance. By virtue of the limited amount of data no statistical analysis were undertaken.

Table 4. Biting in the Paired (P), Omission (O), and Yoked (Y) groups (G) during the Pre-CS, the CS-US, and US intervals (I).

Biting

Per Cent Responding

G	I	Pre-CS	CS-US	US
P		0.0	0.2	13.4
O		0.0	0.0	32.7
Y		0.0	0.0	32.7

Onset Latency (seconds)

G	I	Pre-CS	CS-US	US
P		---	12.8	10.7
O		---	---	8.7
Y		---	---	9.1

Frequency per Trial

G	I	Pre-CS	CS-US	US
P		---	1.5	1.9
O		---	---	1.6
Y		---	---	1.3

Table 5. Tailbeating in the Paired (P), Omission (O), and Yoked (Y) groups (G) during the Pre-CS, the CS-US, and US intervals (I).

Tailbeating

Percent Responding

G	I	Pre-CS	CS-US	US
P		0.0	0.0	0.8
O		0.0	0.0	1.9
Y		0.0	0.0	1.2

Onset Latency (seconds)

G	I	Pre-CS	CS-US	US
P		---	---	9.2
O		---	---	10.2
Y		---	---	8.3

Frequency per Trial

G	I	Pre-CS	CS-US	US
P		0.0	0.0	3.7
O		0.0	0.0	2.5
Y		0.0	0.0	2.7

## Discussion

Two major observations were made in Experiment 1. First, the paired group demonstrated higher indices of conditioning relative to the omission group, which did not differ from the yoked group. And second, the rate of both unconditioned and conditioned responding was low, and highly variable between subjects. These two observations will be discussed in turn in the paragraphs that follow.

The interpretation of an omission study depends very much on the qualitative characteristics of the US ( see Macintosh, 1974). If the US is a positive reinforcer, then the response levels in the omission group should be lower than in the paired group because the response (frontal display) is never reinforced. On the other hand, if the US is a negative reinforcer, then the omission group should perform at a higher level than the paired group because the omission schedule maximizes the reinforcement of the avoidance response (frontal display). In both cases, there should also be differences between the omission group and the yoked group if the response-consequence relationship is controlling performance in the omission group. Otherwise,

all differences could be attributed to the differences in the percentages of pairings that occur between the omission/yoked subjects and the paired group.

Intuitively, the presentation of a male conspecific and the subsequent territorial aggression is an aversive situation. This intuition suggests that the US is a negative reinforcer. However, the results are inconsistent with intuition. The omission group was not superior to the paired group. In fact, it had significantly poorer performance. This observation is consistent with the presentation of the US conspecific acting like a positive reinforcer. Although performance indices for the omission were lower than in the yoked group, the differences were not significant. Thus, most of the poorer performance of the omission group relative to the paired group can be attributed to the partial reinforcement schedule that the omission generates. This leads to the conclusion that the major mechanism controlling the development of frontal display is the relationship between the CS and the US (i.e., S-S learning).

However, a caveat is in order. The substantial variability in unconditioned frontal display responding may

account for the overall low levels of conditioned responding in all groups. As noted the omission contingency was only effective for 10 per cent of the trials thereby minimizing the opportunity for any R-S relationships to develop in the omission group. Given the minimal conditioning in the Omission group and the subsequent high percentage of paired trial, the opportunity for the development of differences between the omission and yoked groups is minimized.

Therefore the conclusion that all responding in this study can be accounted for by S-S associations does not mitigate the implication of R-S associations. That R-S associations can occur in an omission paradigm was demonstrated by Murray (1973) who, with a selected population of aggressive Betta splendens (i.e., with a high incidence of unconditioned responding), showed R-S control of frontal display and a number of other agonistic responses.

The second observation, that of high between subject variability, was not anticipated given previous findings with Trichogaster trichopterus (Hollis, 1984; Hollis, Martin, Cadieux & Colbert, 1984; Hollis, Cadieux & Colbert, 1989). Hollis's studies found that the between subject



variability in both conditioned and unconditioned responding was very low.

In the present study some subjects showed evidence of strong unconditioned responding (see Figure 3, subjects P4, P5, O4, O5, and Y1), while others showed evidence of very modest unconditioned responding (see Figure 3 subjects P1, P6, O3, Y2 and Y6). For conditioned responding the same variability in responding was noted, with some subjects demonstrating conditioning (see Figure 3, subjects P4, P5, Y1 and Y4) while others showed no sign of conditioning at all (P6, O1, O3, Y2 and Y6). As in the Hollis studies, a strong relationship was found between levels of unconditioned and conditioned frontal display. However, frontal display was neither elicited nor conditioned with the reliability and stability reported by Hollis.

Although sample size in the present study was relatively modest, the results nonetheless suggests that the level of agonistic activity in the general population of Trichogaster trichopterus is more variable than previously reported in the conditioning literature (Hollis, 1984; Hollis et al 1984; & Hollis et al 1989). The observed variability in agonistic responding is consistent with the

ethological observations made by Miller (1964). Miller (1964) found that for the most part Trichogaster trichopterus are nonaggressive. However, aggressive interactions were observed during the reproductive or nesting phases, during feeding, when new fish are introduced and when two well balanced fish test each other. However, aggressive interactions were described as being brief and ephemeral and were followed by very little aggressive behaviour. It is clear that ongoing aggression is not the norm when male Trichogaster trichopterus come into contact. Miller (1964) observed that nonreproductive fish in groups of 2 to 11 rarely show any aggressive behaviour.

Miller (1964) also points out that many encounters occurring at the boundaries of two territories may have no lateral display at all and that boundary encounters were so varied that none is typical. Conditioning occurs at the boundaries of the two territories, and our observations of Trichogaster trichopterus' behaviour during conditioning supports the observations made by Miller (1964) in as much as we found low levels and substantial variability in the frontal display responding both within and between all subjects. The observation in the present study of

substantial variability in agonistic responding in Trichogaster trichopterus, has also been noted in other species that are reputed to be very aggressive, such as the Betta splendens, commonly called the Siamese fighting fish. Betta splendens (subfamily Maccropodinae) and Trichogaster trichopterus (subfamily Trichogasterinae) are of the family Belontiidae and sufficiently closely related phylogenetically to bear comparison. Betta splendens, have long been recognised for their aggressive nature, and have for many years been the subjects of choice for numerous studies in aggression (Noble, and Borne 1941; Smith, 1937; Haller and Wittenberger, 1988).

However, the notion that Betta splendens are fighting fish is not entirely accurate. Some conspecifics of the species were found to be decidedly nonaggressive (Bronstein 1981,1985a; Hogan 1961). In examining the pattern of behaviour during intraspecific encounters of Betta, Lissman (1932) identified three levels of intensity of interactions. The first level, consisted of approach, colour change, fin erection and gill-cover extension; the second level included lateral orientation and undulating movements; and the third level involved the exchange of bites. Hogan (1961) using

Lissman's (1932) levels, categorized aggressive Bettas into three classes based on their reactions. The first class, which included the largest number of fish demonstrated all three intensity levels. The second class of reaction included all the behaviours in level 1 except approach and finally the last class exhibited none of the fighting behaviour described by Lissman (1932) but rather a blanching and dropping to the bottom. Hogan's description of the reactions of male Bettas to a male conspecific parallels that described for Trichogaster trichopterus by Miller (1964).

And finally, Bronstein (1985a), observed a number of attack behaviours including frontal display, biting, and tail beating in a study of 279 bettas. He noted that the distribution for aggressive behaviours such as frontal display and biting were bimodal. These observations appear to contradict the research which find bettas to be aggressive and ideally suited to serve as subjects in studies of aggression.

A close observation of the selection procedure for the subjects in many of the studies on aggression with Betta splendens suggest, on examination of how subjects were

selected for inclusion in the experiment, that the subjects used were carefully pre-selected for aggressive behaviour and not randomly selected to reflect levels of aggression in the general population (Baenninger, 1984; Bronstein, 1985b; Bronstein, 1986; Clayton & Hinde, 1968; Hogan, 1967; Hogan Kleist & Hutchings, 1970; Murray, 1973; Woodard Cain, Jessen & Flanagan, 1980). Subjects in a number of studies were even excluded post hoc for failing to engage in aggressive behaviour notwithstanding the fact that they were pre-selected on the basis of their having done so (e.g. Hogan, Kleist and Hutchings, 1970; Murray, 1973). In attempting to study aggression in bettas it is required that aggressive Betta be selected, however the conclusions from these studies must be restricted to the population sampled, that is aggressive bettas, and not the entire population of bettas. In the present study, it is possible that the random selection procedure used may account, in part, for the variability in both unconditioned and conditioned responding. The random sampling procedure in the present study resulted in a sample representative of aggression in the population and not of aggression in aggressive Trichogaster trichopterus.

## Experiment 2

The results of Experiment 1 indicated that a substantial variability existed between subjects in terms of both the elicitation and acquisition of frontal display. Similar variability in the agonistic responding of Betta splendens was noted by Bronstein (1985). Bronstein (1985) stated that a continuum of degree of aggressiveness existed in the population of Betta splendens. If we accept that the similarity in phylogenetic relationship between Betta splendens and Trichogaster trichopterus is sufficient to allow for the application of Bronstein's observations to Trichogaster trichopterus then the observed variability in Experiment 1 may result from the variability in aggressiveness in the population of Trichogaster trichopterus. If the reliability of frontal display to the presentation of a conspecific is a population variable, then it is possible that frontal display, as an index of aggression is neither a typical reaction nor related to successful territorial defense.

In light of these possibilities, the second experiment had two purposes. The first was to determine the range of

conditionability of Trichogaster trichopterus with a larger group of subjects than used in Experiment 1. The second purpose was to determine, using a split half analysis, whether conditionability was related to confrontation behaviour and successful territorial defense (Hollis, 1984). In order to determine the ability of the pairings of a CS with a US conspecific to yield conditioned frontal display and approach responding, 16 blue gouramis were presented with CS-US pairings following the procedure delineated for Group P in Experiment 1. In an attempt to determine what, if any, relationship might exist between levels of conditioning and measures of territorial defense, test conflict sessions were alternated with reconditioning sessions in a second phase of the experiment. During the test conflicts the experimental subjects were presented with the CS followed by the door opening and the US rival having full access to the experimental subject's territory. The reconditioning sessions following the conflict sessions were used to see if the conflict outcome affected performance to the CS and US.

According to Hollis's (1982, 1984) prefiguring hypothesis, successful territorial defence will be related

to successful conditioning of aggressive behaviour as indexed by the conditioning of frontal display. In order to test this hypothesis, the performance of the eight most effectively conditioned subjects was compared to the performance of the least conditioned fish in terms of territorial defense measures.

#### Method

##### Subjects

The subjects were 32 adult male gouramis (Trichogaster trichopterus). The fish were consistent in body size and fin depth, and were purchased from a local supplier.

##### Apparatus

The apparatus was identical to that described in Experiment 1, except that eight experimental tanks were employed in this experiment.



## Procedure

Sixteen gouramis were randomly picked as experimental subjects and placed, one each, in chambers A and B of the eight experimental tanks. The remaining gouramis served as USs and were housed individually until required. The subjects were placed in their appropriate chambers five days before the experiment began in order to permit the establishment of individual territories.

On the sixth day after their arrival the first phase of the two-phase experiment began. Phase 1 consisted of thirteen daily sessions during which all subjects were presented with light-rival pairings as in Group P in Experiment 1. As in Experiment 1, the tank-mate of the subject being conditioned was removed during the conditioning session.

Phase 2 consisted of three test conflict sessions alternating with four reconditioning sessions which were presented over seven days. The sequence of test conflict (TC) and reconditioning (RC) sessions was as follows: TC, RC, TC, RC, TC, RC, RC. Subjects received the first test

conflict session on the day following the last day of Phase 1 conditioning.

Five minutes into each test conflict session, the experimental subject was presented with the CS, followed 10-sec later by the door opening and the presentation of the US conspecific. During the conflict sessions the US conspecific was free to intrude into the experimental subject's territory (the mesh cage in the stimulus panel having been removed). The US conspecific was permitted access to the subject's territory for a ten min period at which point the session was terminated.

#### Response Specifications

For Phase 1 conditioning and Phase 2 reconditioning sessions, the response specifications were identical to those of Experiment 1. The dependent variables collected were the mean per cent, duration, latency and frequency of frontal display and approach responding. The latency and frequency of biting and tailbeating were also collected. During the test conflicts the latency, frequency and duration of frontal display responding were monitored for both the experimental subject and the US conspecific when

they were in the subject's territory. Conditioned frontal display responding was defined as in Experiment 1 and was monitored for during the single CS-US interval during each test conflict session. Unconditioned frontal display was defined as in Experiment 1 and was measured from US onset. The total numbers of bites inflicted by both the experimental subjects and the US conspecifics were also recorded.

Since successful territorial defense should preclude or at least minimize, the intrusive behaviour of the US conspecific, a number of the US conspecific behaviours were monitored. These included: latency of intrusion, frequency of intrusion, duration of first intrusion and total duration of intrusion. Intrusion by the US conspecific into the experimental subject's territory was determined to have occurred when the US conspecific's head, up to its opercula, had entered the subject's territory.

## Results

The results from Phase 1 conditioning will be presented first, followed by the results from Phase 2 reconditioning,

and finally, those from Phase 2 test conflict sessions. The responses monitored during Phase 1 conditioning and Phase 2 reconditioning were, frontal display, approach, biting and tailbeating. For frontal display and approach the measures taken were: the mean per cent responding and mean duration of responding during each session. For biting and tailbeating only the mean per cent responding was measured.

The data for Phase 1 were analyzed as follows. First the performance for each dependent measure was analysed during the Pre-CS, CS-US and US intervals by means of repeated measures of ANOVA across days for all 16 subjects (Group PF). As noted earlier Group PF was subdivided into two groups with the eight subjects demonstrating the highest levels of conditioned frontal display forming Group P1 and the remaining eight subjects forming Group P2. The daily mean of each response measure was analyzed between Groups P1 and P2 by means of repeated measures mixed effect analysis of variance (ANOVA) and orthogonal components for trend analysis. A priori tests of significance using t-tests were conducted to determine if any differences in performance existed within each group between the Pre-CS and the CS-US intervals. The results will be presented for the frontal

display, approach, biting and tailbeating responses in turn. For each response, the data from the Pre-CS interval will be presented followed by the data from the CS-US and the US intervals.

### Phase 1: Conditioned Responding

#### Phase 1: Frontal Display.

Per Cent Responding. The mean per cent frontal display responding for groups PF, P1 and P2 during the Pre-CS, the CS-US and the US interval can be seen in the upper matrix of Table 6. The Table shows responding for all groups was lowest during the Pre-CS interval and greatest during the US interval. With respect to responding in Groups P1 and P2, it can readily be observed that performance in Group P1 was greater than in Group P2 during all intervals.

The upper panel of Figure 6 depicts the mean per cent frontal display responding during the Pre-CS interval as a function of days for Groups PF, P1, and P2. Frontal display responding during the Pre-CS interval for Group PF and the two subgroups did not change significantly over days. A repeated measures ANOVA between groups P1 and P2 for frontal display responding during the Pre-CS interval failed to

Table 6. The mean per cent and duration for frontal display responding (upper and lower matrix respectively), across days for Groups P1, P2 and PF during the Pre-CS, CS-US, and US intervals.

Frontal Display

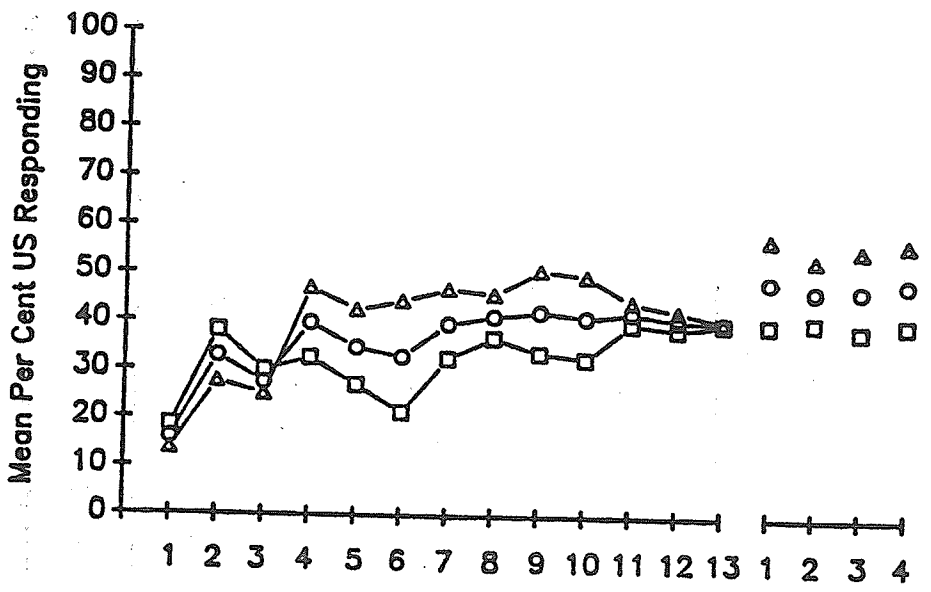
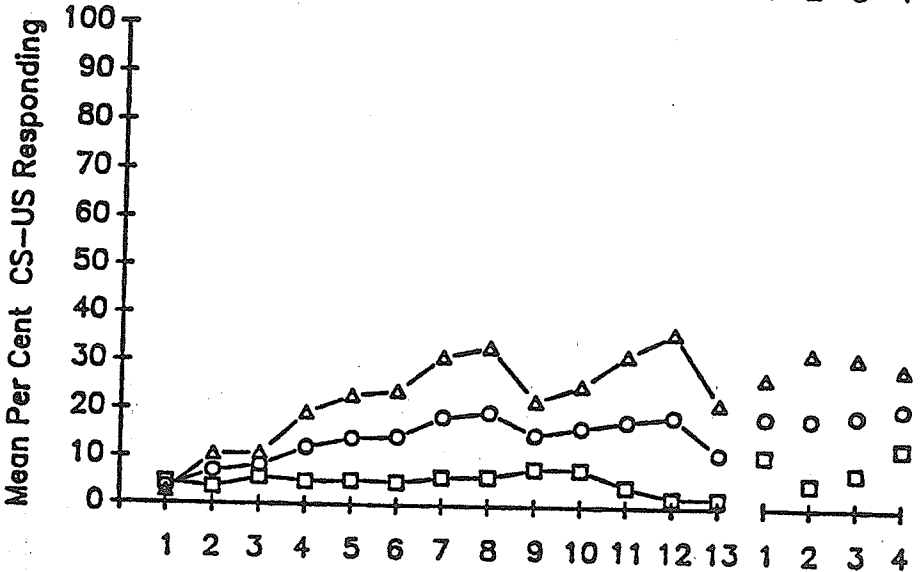
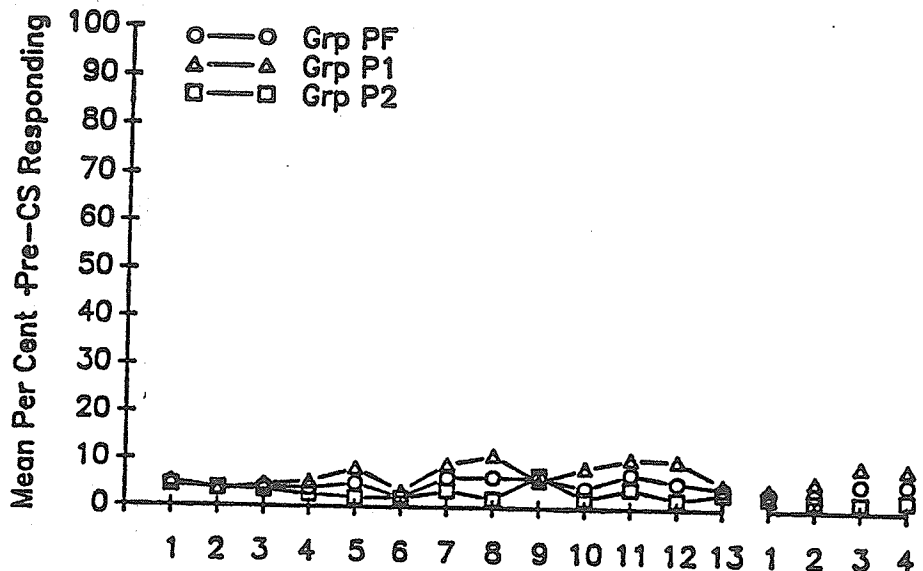
Per Cent Responding

G	I	Pre-CS	CS-US	US
PF		4.9	13.7	36.3
P1		7.0	22.5	40.1
P2		2.9	4.9	32.4

Response Duration (seconds)

G	I	Pre-CS	CS-US	US
PF		1.5	2.0	4.2
P1		1.9	2.7	4.8
P2		1.1	1.4	3.6

Figure 6. Mean per cent frontal display responding during the 13 days of Phase 1 conditioning, and the 4 days of Phase 2 reconditioning, for Groups PF, P1 and P2, during the Pre-CS, CS-US, and US intervals (upper, middle and lower panels respectively).



Days



identify any significant effects. Accordingly, for the mean per cent frontal display during the Pre-CS interval, responding was stable over the course of the experiment and did not differ between groups.

The mean frontal display responding during the CS-US interval for Groups PF, P1, and P2 is depicted in the centre panel of Figure 6. As can be observed responding was greatest in Group P1, and least in Group P2 with group PF falling between them. For frontal display responding in Group PF during the CS-US interval, an ANOVA confirmed the presence of a significant days effect ( $F(12,180)=1.88, p < 0.05$ ). These results indicate that the frontal display responding increased over days in Group PF. An ANOVA between Groups P1 and P2 identified a significant group ( $F(1,14)=8.51, p < 0.01$ ), and days effect ( $F(12,168)=2.01, p < 0.05$ ), as well as a days x group interaction ( $F(12,168)=2.03, p < 0.05$ ). The ANOVA confirmed that the mean frontal display responding during the CS-US interval was greater in Group P1 than in Group P2, and that it diverged from responding in Group P2 over days. Dependent t-tests between frontal display responding during the CS-US and the Pre-CS intervals confirmed that there was a significant difference

in performance for Group PF, ( $t= 7.08$ ,  $df=30$ ,  $p < 0.01$ ), Group P1, ( $t= 7.30$ ,  $df=14$ ,  $p < 0.01$ ), and Group P2 ( $t=2.94$ ,  $df=14$ ,  $p < 0.01$ ) in these intervals. In each group, responding during the CS-US interval was significantly higher than during the Pre-CS responding interval.

The bottom panel of Figure 6 depicts the mean per cent frontal display responding during the US interval for Group PF, P1, and P2. As can be observed, frontal display responding did not appear to differ over days or between groups during this interval. An ANOVA applied to frontal display responding in Group PF during this interval failed to find a change over days ( $F(12,180) = 1.50$ ,  $p \geq 0.05$ ). An ANOVA applied to frontal display responding in Groups P1 and P2 during the US interval determined that no group differences existed. These results indicate that responding during the US interval was stable over days and did not differ between Groups P1 and P2.

Duration. The mean duration of frontal display for each group during the Pre-CS, the CS-US and the US intervals can be seen in the lower matrix of Table 6. As can be observed the duration of frontal display responding during the Pre-CS, the CS-US and the US intervals do not appear to differ

among the three groups. Similarly, the duration of frontal responding does not appear to differ between the Pre-CS and the CS-US interval in any groups.

A repeated measures ANOVA applied to the mean duration of frontal display during the Pre-CS interval for Groups PF confirmed that there was no significant change over days ( $F(12,180) = 0.71$ ). A subsequent comparison of Groups P1 and P2 identified no significant effects. During the CS-US interval, no significant changes were found over days ( $F(12,180) = 1.40$ ) for Group PF. A repeated measures ANOVA applied to the mean duration of frontal display responding during the CS-US interval for Groups P1 and P2 confirmed only that Group P1 had a longer duration of frontal display than Group P2 ( $F(1,14) = 11.41$ ,  $p < 0.01$ ). Dependent t-tests that contrasted the duration of responding during the CS-US and the Pre-CS intervals confirmed that responding was significantly higher during the CS-US interval in Groups PF ( $t = 2.66$ ,  $df = 30$ ,  $p < 0.05$ ) and P1 ( $t = 3.49$ ,  $df = 14$ ,  $p < 0.01$ ), but not in Group P2 ( $t = .96$ ,  $df = 14$ ,  $p > 0.05$ ).

For the US interval no change in the mean duration of frontal display responding in Group PF were identified over days. An ANOVA applied to the mean duration of frontal

display for Groups P1, and P2 during the US interval found neither a group effect ( $F(1,14) = 1.76$ ) nor a days effect ( $F(12,168) = 0.65$ ). The ANOVA did however confirm the presence of a significant days by group interaction ( $F(12,168) = 2.24$ ,  $p < 0.05$ ), with the mean duration of frontal display for Group P1 increasing over days while that of Group P2 remained at a low and stable level.

In summary, for the mean per cent and duration of frontal display, responding was stable across days and did not differ between groups during the Pre-CS and the US intervals. During the CS-US interval the mean per cent responding increased over days. For both the mean percent and the duration of frontal display, responding was greater in Group P1 than P2. Thus splitting Group PF into two halves based on the mean per cent frontal display responding during the CS-US interval yielded statistically different groups.

#### Phase 1: Approach Responding.

Per cent responding. The mean percent approach responding during the Pre-CS, the CS-US and the US intervals for Groups PF, P1, and P2 can be seen in the upper matrix of Table 7.

Table 7. The mean per cent and duration for approach responding (upper and lower matrix respectively), across days for Groups P1, P2 and PF during the Pre-CS, CS-US, and US intervals.

Approach

Per Cent Responding

G	I	Pre-CS	CS-US	US
	PF	30.9	43.1	72.4
	P1	30.7	44.6	68.7
	P2	31.1	41.6	76.1

Response Duration (seconds)

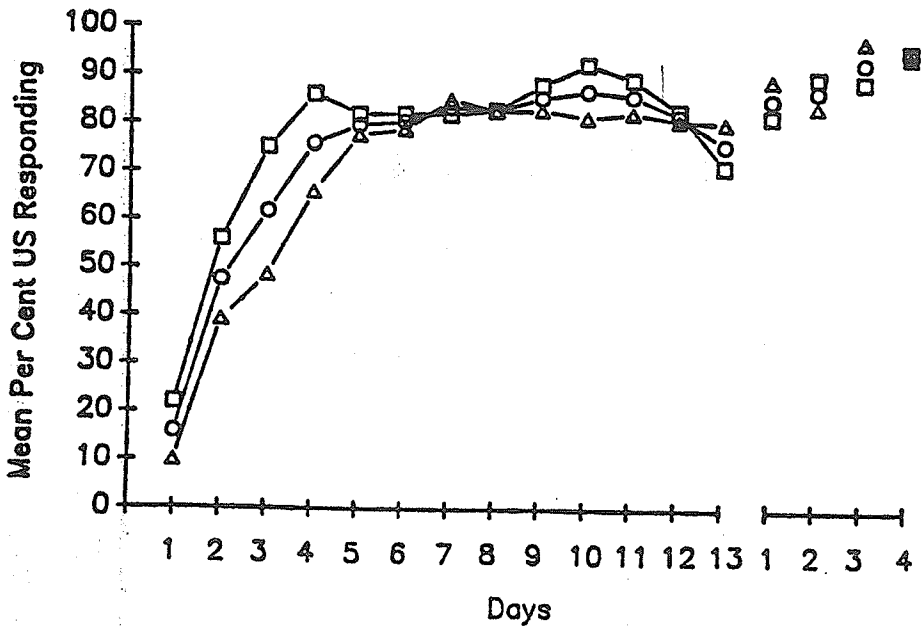
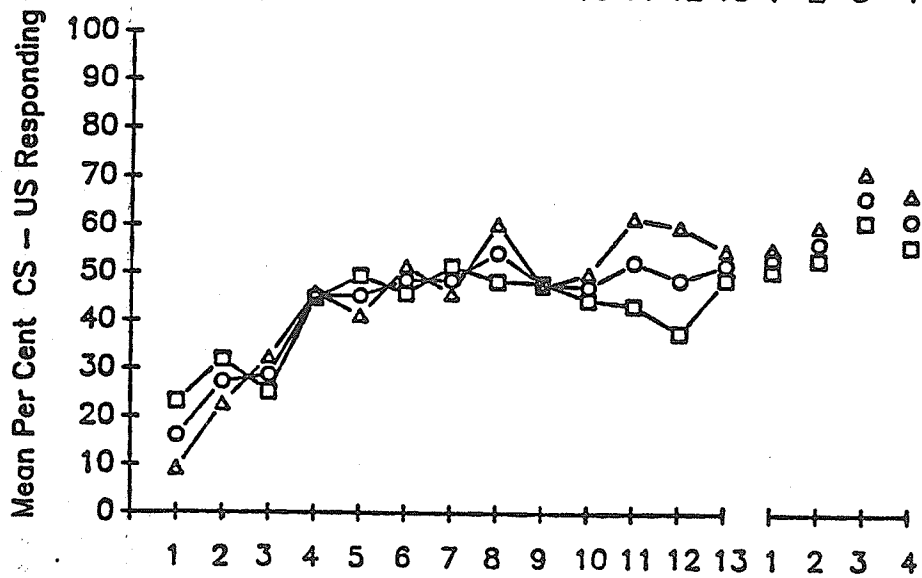
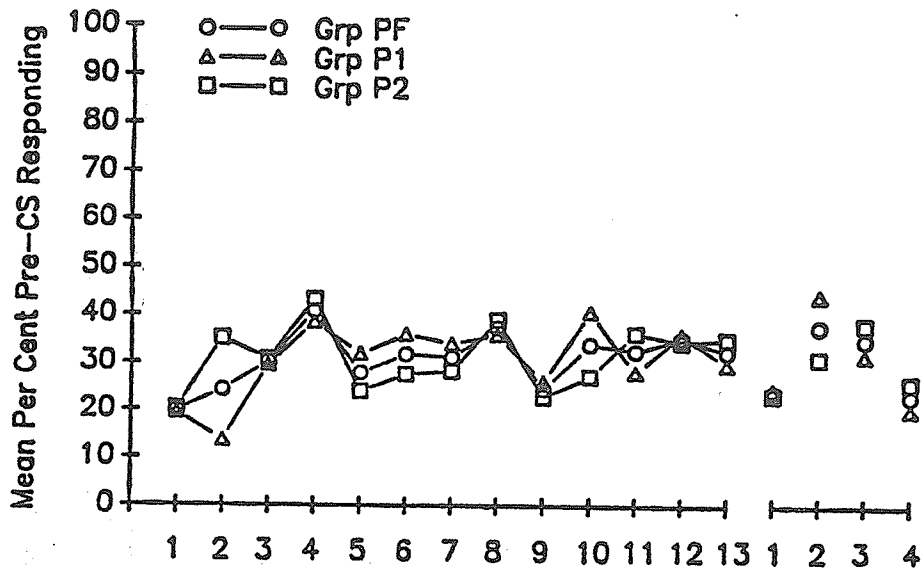
G	I	Pre-CS	CS-US	US
	PF	4.4	4.5	9.1
	P1	4.7	4.7	8.7
	P2	4.2	4.3	9.4

As can be observed no differences appear to exist in overall responding between groups during the Pre-CS, CS-US or US intervals. The per cent approach responding for each group was lowest during the Pre-CS interval and greatest during the US interval.

Figure 7 depicts the mean per cent approach responding during the Pre-CS, CS-US and US intervals for Groups PF, P1, and P2 as a function of days. As can be seen in the upper panel of Figure 7, responding during the Pre-CS interval appears to be stable over days with no apparent differences between groups. A repeated measures ANOVA applied to the mean per cent approach responding during the Pre-CS interval for Group PF confirmed that no significant days effect ( $F(12,180) = 1.72$ ) was present. An ANOVA comparing the responding in Groups P1 and P2 identified no differences.

The middle panel of Figure 7 presents the mean per cent responding for approach during the CS-US interval for all groups. As can be observed responding does not appear to differ between groups but does appear to increase over days. An ANOVA confirmed that performance increased across days in group PF ( $F(12,180) = 5.08, p < 0.01$ ). A repeated measures ANOVA applied to the mean per cent approach responding in

Figure 7. Mean per cent approach responding during the 13 days of Phase 1 conditioning, and the 4 days of Phase 2 reconditioning, as a function of days, for Groups PF, P1, and P2 during the Pre-CS, CS-US and US intervals (upper, middle and lower panels respectively).





Groups P1 and P2 found neither a significant group, nor a days by group interaction.

Dependent t-tests applied to the mean per cent approach responding during the CS-US interval and the Pre-CS interval in each of Groups PF, P1 and P2, confirmed that significant differences existed for Group PF, ( $t = 5.06$ ,  $df < 0.01$ ), Group P1, ( $t = 4.57$ ,  $df = 14$ ,  $p > 0.01$ ), and Group P2, ( $t = 3.72$ ,  $df = 14$ ,  $p < 0.01$ ). In all groups, responding was greater during the CS-US interval than during the Pre-CS interval.

The mean per cent approach responding during the US interval for all groups can be seen in the lower panel of Figure 7, no differences appear to exist between groups although responding does appear first to increase and then decrease over days. For Group PF, a repeated measures ANOVA determined that a significant days effect ( $F(12,180) = 11.50$ ,  $p < 0.01$ ) comprised of a significant linear ( $F(1,15) = 14.38$ ,  $p < 0.01$ ), and quadratic ( $F(1,15) = 53.17$ ,  $p < 0.01$ ) component for trends, was present. A repeated measures ANOVA also revealed that, for the mean per cent approach during the US interval for Groups P1 and P2, no significant differences existed. These results indicate that, for the

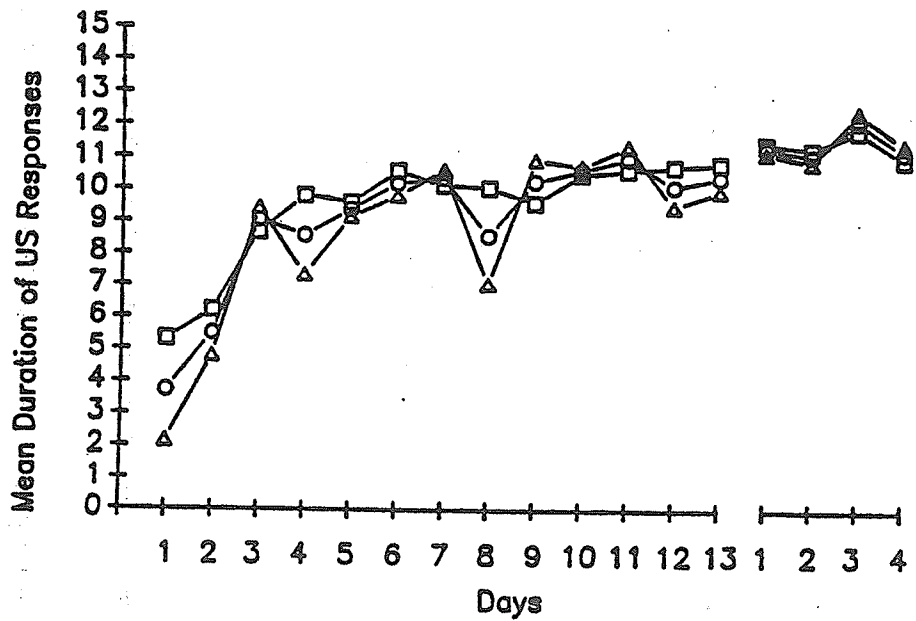
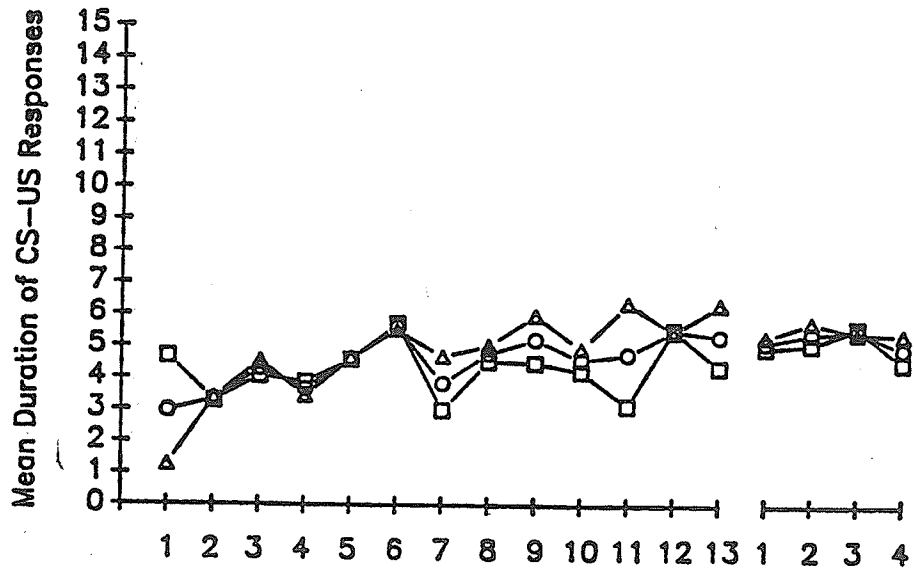
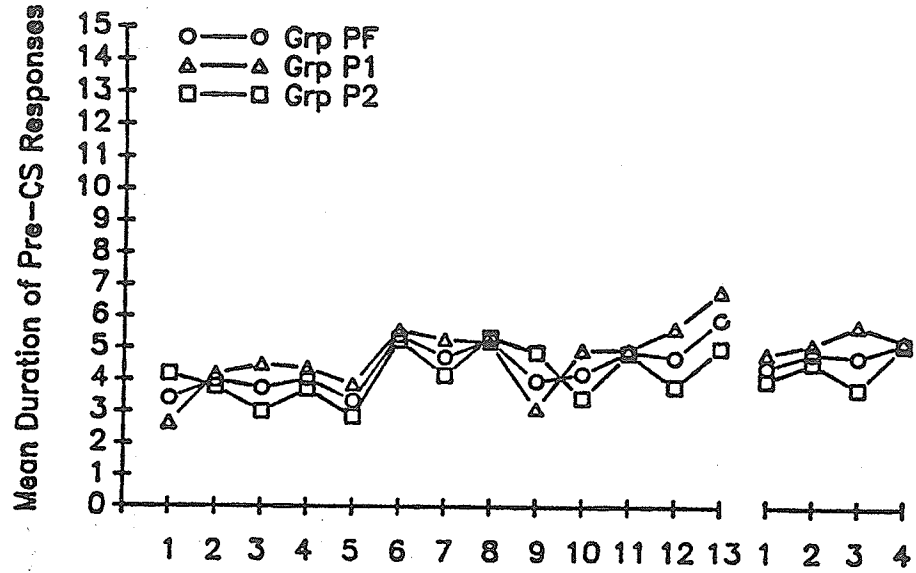
mean per cent approach, responding was stable during the Pre-CS interval but increased over days to an asymptote and began to decline during both the CS-US and US intervals. For Groups P1 and P2 no differences in mean per cent approach responding were observed during any of the intervals.

Duration. The mean duration in the approach area for Groups PF, P1, and P2, during the Pre-CS, the CS-US, and the US intervals can be seen in the lower matrix of Table 7.

Figure 8 presents the mean duration of approach responding, during Phase 1, as a function of days for all groups during the Pre-CS, CS-US and US intervals (upper, middle, and lower panels respectively). No differences for duration in the approach area appear to exist between groups during the Pre-CS, the CS-US or the US intervals. As can also be seen in Table 7, no differences appear to exist within groups between the Pre-CS and CS-US interval for any of the three groups.

A repeated measures ANOVA applied to the mean duration in the approach area during the Pre-CS for Group PF confirmed the presence of a significant days effect ( $F(12,180) = 1.94, p < 0.05$ ), comprised of only a significant

Figure 8. The mean daily duration (in seconds) of approach responding during the 13 days of Phase 1 conditioning for Groups PF, P1 and P2 during the Pre-CS, CS-US, and US intervals (upper, middle and lower panels respectively).



linear trend ( $F(1,15) = 5.51, p \leq 0.05$ ). An ANOVA applied to the mean duration in the approach area during the Pre-CS interval for Groups P1 and P2 found neither a group effect, nor a days  $\times$  group interaction. These results suggest that for duration of approach, responding increased over days but did not differ between groups during the Pre-CS interval.

For the CS-US interval, the mean duration in the approach area increased over days for Group PF, as indicated by a significant days effect ( $F(12,180) = 2.40, p < 0.01$ ). The mean duration of approach during the CS-US interval for Group P1 and P2 was 4.70 sec and 4.25 sec respectively. An ANOVA applied between Groups P1 and P2, confirmed that no significant group effect ( $F(1,14) = 0.94, p > 0.05$ ) existed, however a significant days  $\times$  group interaction was observed ( $F(12,168) = 2.25, p < 0.01$ ). The combined results indicate that the mean duration in the approach area during the CS-US interval increased over days, with Group P1 increasing significantly more than Group P2.

Dependent t-tests comparing the mean duration in the approach area during the Pre-CS and the CS-US interval confirmed that no significant difference existed for Group PF ( $t = 0.11$ ), Group P1 ( $t = 0.4$ ), or Group P2 ( $t = 0.17$ ).

Thus the mean duration of conditioned approach responding was not greater than the mean duration of baseline approach responding for any groups.

The mean duration of approach responding during the US interval is depicted in the lower panel of Figure 8. As can be observed the duration of responding does not appear to differ between groups although it does appear to increase over days. For Group PF, an ANOVA confirmed the presence of a significant days effect ( $F(12,180) = 10.60, p < 0.01$ ). No other comparisons were significant.

In summary, the mean per cent approach responding increased over days for all groups during the CS-US interval and the US interval while the duration of responding increased for all groups in all three time intervals. The mean per cent approach responding was greater during the CS-US interval than during the Pre-CS interval for all groups, while the duration of approach responding did not differ between the CS-US and Pre-CS interval for any groups. For the mean per cent and duration of approach responding, no differences were found between Groups P1 and P2 during any time interval.

Phase 1: Biting and Tailbeating. Biting and tailbeating only occurred during the US interval. The mean percent of trials on which biting occurred during the US interval was 20.5, 13.2 and 27.8 for Group PF, P1 and P2 respectively. The mean per cent of trials during which tailbeating occurred was .14, .26 and .02 for Group PF, P1 and P2 respectively. It should be noted that the means presented are the result of responding in 1 or 2 subjects and should not be construed as reflecting group performance. These data were not amenable to statistical analysis.

Phase 2: Conditioning Responding

The results from Phase 2 reconditioning were analysed following the same procedure used for Phase 1 data. The sole exception was that t-tests were not conducted on performance during the Pre-CS and the CS-US.

Phase 2: Reconditioning, Frontal Display.

Per Cent Responding. The mean per cent frontal display responding for groups PF, P1 and P2 during the Pre-CS, the CS-US and the US intervals can be seen in the upper matrix of Table 8. With respect to responding in Groups P1 and P2,

it can readily be observed that performance in Group P1 appears to be greater than in Group P2 during all intervals. As can also be seen in Table 8, responding for all groups was lowest during the Pre-CS interval and greatest during the US interval. The upper panel of Figure 6 depicts the mean frontal display responding during the Pre-CS interval as a function of days for Groups PF, P1, and P2. As can be observed in Figure 6 and as was confirmed by an ANOVA, frontal display responding during the Pre-CS interval for group PF did not change significantly over days ( $F(4,60) = 0.90$ ,  $p = 0.47$ ). An ANOVA between Groups P1 and P2 for frontal display responding during the Pre-CS interval found no differences.

The centre panel of Figure 6 depicts the mean per cent frontal display responding during the CS-US interval for Groups PF, P1, and P2. For frontal display responding in Group PF during this interval, an ANOVA found no significant days effect ( $F(4,60) = 2.08$ ,  $p > 0.05$ ). The mean per cent frontal display responding for Groups P1 and P2 was 28.7 and 7.53 respectively. An ANOVA between Groups P1 and P2 determined the presence of a significant group effect ( $F$



Table 8. The mean per cent and duration for frontal display responding (upper and lower matrix respectively), across days of Phase 2 reconditioning, for Groups P1, P2 and PF during the Pre-CS, the CS-US, and the US intervals.

Frontal

Percent Responding

G I	Pre-CS	CS-US	US
PF	4.5	18.1	46.4
P1	6.9	28.7	52.8
P2	2.2	7.5	39.9

Response Duration (seconds)

G I	Pre-CS	CS-US	US
PF	1.4	2.4	4.7
P1	2.2	3.3	5.5
P2	0.7	1.4	3.8

(1,14)=5.58,  $p < 0.05$ ), but not a significant days by group interaction ( $F(4,56) = 0.80$ ,  $p > 0.05$ ).

As can be observed in Figure 6 very little difference in responding appears to exist between terminal levels of responding during Phase 1 conditioning and responding during Phase 2. In order to determine if the levels of frontal display responding in Phase 2 reconditioning in Groups P1 and P2 differed from the levels of performance achieved during Phase 1, an ANOVA was conducted to compare the last four days of Phase 1 conditioning with the four days of Phase 2 conditioning. The results from the ANOVA indicated that a significant group difference was present ( $F(1,14) = 5.94$ ,  $p < 0.05$ ) for Groups P1 and P2, but that no days effect ( $F(7,98) = 1.15$ ,  $p > 0.05$ ) or days by group interaction existed ( $F(7,98) = 1.36$ ,  $p > 0.05$ ). In essence, the performance in Groups P1 and P2 during the CS-US interval in Phase 1, was unchanged in Phase 2 reconditioning.

The bottom panel of Figure 6 depicts the mean per cent frontal display responding during the US interval for Group PF, P1, and P2. An ANOVA applied to frontal display responding in Group PF during the US interval confirmed that responding did not change over days ( $F(4,60) = 0.67$ ,  $p >$

0.5). An ANOVA applied to frontal display responding during the US interval between Groups P1 and P2 also found no differences.

Duration. The mean duration of frontal display for each group during the Pre-CS, the CS-US and the US intervals can be seen in the lower matrix of Table 8. As can be observed the duration of frontal display responding during the Pre-CS, the CS-US and the US intervals is least during the Pre-CS interval and greatest during the US interval in all three groups.

A repeated measures ANOVA applied to the daily mean duration of frontal display during the Pre-CS interval for Groups PF found no effects. The mean duration of responding in Groups P1 and P2 was 2.16 sec and 0.68 sec respectively. An ANOVA applied to the mean duration of frontal display in Groups P1 and P2 during the Pre-CS interval confirmed that the mean duration of frontal display in Group P1, was longer than that in Group P2. No other effects were found.

For the duration of frontal responding during the CS-US interval for Group PF a repeated measures ANOVA determined that no significant days effect existed ( $F(4,60) = 1.06, p > 0.05$ ). The duration of frontal display during the CS-US

for Groups P1 and P2 was 3.32 sec and 1.4 sec respectively. A repeated measures ANOVA applied to responding in Groups P1 and P2 confirmed that the mean duration of frontal display was greater in Group P1 (group effect ( $F(1,14) = 8.68$ ,  $p < 0.01$ )).

For the duration of frontal display responding in Group PF during the US interval an ANOVA revealed that a significant increasing effect of days was present ( $F(4,60) = 2.58$ ,  $p < 0.05$ ). An application of an ANOVA to the mean duration of frontal display for Groups P1, and P2 during the US interval found no group effects. Thus the increase over days noted in Group PF was not differentially due to changes in any one subgroup.

In summary, for the frontal display response, the mean per cent and duration of responding during the Phase 2 reconditioning period was stable during all three intervals save for the US interval when duration increased over days. The difference observed between Groups P1 and P2 for mean per cent and duration of frontal display during the CS-US interval in Phase 2 reconditioning reflected the difference observed in Phase 1 conditioning and could not be ascribed to the effect of the interpolated conflict sessions.

Phase 2: Reconditioning, Approach Responding.

Per Cent Responding. The mean percent approach responding during the Pre-CS, the CS-US and the US responding intervals for Groups PF, P1, and P2 can be seen in the upper matrix of Table 9. As can be observed no differences appear to exist in responding between groups during the Pre-CS, the CS-US or the US intervals. The per cent approach responding for each groups was lowest during the Pre-CS interval and greatest during the US interval.

Figure 7 depicts the mean per cent approach responding during the Pre-CS, CS-US and US intervals, as a function of days (upper, middle and lower panel respectively). As can be observed no differences appear to exist between Groups PF, P1 or P2 during the Pre-CS, the CS-US or the US intervals. Figure 7 does show a systematic change over days for all groups during all three time intervals. Mean per cent approach responding appears to decrease during the Pre-CS interval and to increase during the US intervals.

For the Pre-CS interval, a repeated measures ANOVA applied to approach responding during the Pre-CS interval for Group PF confirmed a significant decreasing effect of

Table 9. The mean per cent and duration of approach responding (upper and lower matrix respectively), across days of Phase 2 reconditioning, for Group P1, P2, and PF, during the Pre-CS, CS-US, and US intervals.

Approach

Per Cent Responding

G I	Pre-CS	CS-US	US
PF	30.4	57.7	86.6
P1	30.1	61.5	88.1
P2	30.7	53.8	85.2

Response Duration (seconds)

G I	Pre-CS	CS-US	US
PF	5.0	5.3	11.2
P1	5.6	5.6	11.4
P2	4.5	4.9	11.2

days ( $F(4,60) = 2.69, p = 0.05$ ). An ANOVA applied to the responding in Groups P1, and P2 found no effects.

For the mean per cent approach responding during the CS-US interval, no significant effect of days was found for Group PF ( $F(4,60) = 2.03, p > 0.05$ ). The repeated measures ANOVA applied to the per cent approach responding in Groups P1 and P2 also found no effects.

The mean per cent approach responding during the US interval for Group PF was determined by ANOVA to increase over days ( $F(4,56) = 5.63, p < 0.01$ ). The ANOVA comparing Group P1 and P2 identified no group effects.

Duration. The mean duration in the approach area for Groups PF, P1, and P2, during the Pre-CS, the CS-US, and the US responding intervals can be seen in the lower matrix of Table 9. No significant differences for duration in the approach area appear to exist between groups during the Pre-CS, the CS-US and the US intervals. In addition no differences appear to exist within groups between the Pre-CS and the CS-US intervals.

A repeated measures ANOVA applied to the mean duration in the approach area during the Pre-CS for Group PF confirmed that no significant days effect ( $F(4,60) = 0.88,$

$p > 0.05$ ), was present. An ANOVA applied to the duration in the approach area during the Pre-CS interval for Groups P1 and P2 with means of 5.57 and 4.50 respectively determined that the duration of responding in Group P1 was significantly higher than that in Group P2 ( $F(1,14) = 4.68$ ,  $p < 0.05$ ), but no significant days by group interaction ( $F(4,56) = 0.41$ ,  $p > 0.05$ ) was found.

For the duration in the approach area during the CS-US interval for Group PF, an ANOVA revealed that no significant changes over days ( $F(4,60) = 0.45$ ,  $p > 0.05$ ) occurred. Similarly, an ANOVA applied to Groups P1 and P2, found no significant group effects.

During the US interval, an ANOVA applied to the mean duration in the approach area for Group PF failed to find a significant days effect ( $F(4,60) = 1.19$ ,  $p < 0.05$ ). Comparisons of Groups P1 and P2, also revealed no significant effects.

In summary, the mean per cent approach responding did not differ between groups in any intervals during the reconditioning, but there was a change in responding over days in both the Pre-CS and the US. It appears that the intervening conflict sessions may have had the effect of



decreasing approach during the Pre-CS and increasing approach during the US interval. The mean duration of approach responding during the Pre-CS interval was higher in Group P1 than in Group P2 but did not differ between groups during the CS-US or the US intervals, and did not change over days in any of the intervals.

Phase 2 Reconditioning: Biting and Tailbeating. As in Phase 1, biting occurred only during the US interval. The mean per cent of trials during which biting occurred was 15.0, 9.15 and 20.85 for Groups PF, P1 and P2 respectively. It should be noted that the means for biting are the result of responding in 1 or 2 subjects and are not a reflection of group performance. These data were therefore not amenable to statistical analysis. No tailbeating occurred at all during any intervals.

In summary the data from Phase 2 reconditioning sessions was not notably different from the results during the Phase 1 conditioning sessions. This suggests that the interpolated conflict sessions had limited impact on the conditioning sessions.

Phase 2: Responding During Conflict Sessions

For the conflict sessions, the measures of agonistic responding including the latency, frequency, and duration of frontal display and the latency to and frequency of biting were analysed by means of ANOVAS applied across days in Group PF, and between Groups P1 and P2. These measures of agonistic responding were also taken for the US conspecifics matched to subjects in Groups P1 and P2 and were analysed by means of ANOVA as well.

During the CS presentations in each conflict session, the experimental subjects gave few conditioned responses. This observation is similar to what was observed on the first trial of each conditioning session in Phase 1 and 2. The mean per cent frontal display conditioned responses occurring on the first trial of the last four days of conditioning in Phase 1 and on the first conditioning trial during the four days of Phase 2 reconditioning were 14.7 and 18.0 respectively. Similarly the mean per cent responding on the first trial for the three conflict sessions was equally low at 10.4 per cent. Given the low levels of conditioning during the conflict sessions, no analysis of conditioned responding were undertaken. All measures of

agonistic responding therefore were taken from US onset. The means are presented in Table 10.

For the latency, frequency, and total duration of frontal display, as well as, the latency to bite and number of bites, ANOVAs were conducted in order to determine if any differences in performance existed between 1) the subjects in Group PF and the US conspecifics, 2) the subjects in Groups P1 and P2, and 3) the groups of US conspecifics matched to the subjects in Group P1 and P2.

#### Conflict Sessions: Frontal Display.

Latency of Frontal Display. A mixed effect ANOVA applied to the mean latency to first frontal display during the conflict sessions revealed no significant group effect between experimental subjects and US conspecifics ( $F(1,28) = 3.50, p > 0.05$ ), nor was there a significant effect of days ( $F(2,56) = 2.83, p > 0.05$ ). The ANOVA did reveal the presence of a days x group interaction between experimental subjects and the US conspecifics ( $F(2,56) = 3.96, p < 0.05$ ). The latency to frontal display during all sessions was longer for the experimental group than the US conspecifics. However, latency decreased over days in the experimental

Table 10. Mean intrusive frequency and duration of intraterritorial and intrusive responding for all groups across the three conflict sessions.

Groups Responses	Experimental Subjects		US Conspecifics Matched to		All Experimental Subjects	All US Conspecifics
	P1	P2	P1	P2		
FRONTAL DISPLAY						
Mean Latency (standard dev.)	87.8 (141.2)	45.8 (64.2)	21.0 (30.9)	15.0 (21.1)	66.8 (102.1)	18.0 (26.0)
Mean Frequency (standard dev.)	7.7 (6.1)	8.5 (6.8)	8.5 (5.3)	10.1 (6.8)	8.1 (6.5)	9.2 (6.1)
Mean Duration (standard dev.)	140.1 (169.9)	203.5 (196.0)	156.8 (144.4)	226.1 (160.2)	171.8 (183.0)	191.5 (152.3)
BITING						
Mean Bites (standard dev.)	46.5 (33.1)	46.7 (24.7)	10.3 (22.9)	4.2 (8.1)	46.6 (28.9)	7.3 (18.5)
INTRUSIONS						
Latency (standard dev.)			17 (20.4)	14.9 (19.4)		
Frequency (standard dev.)			10.1 (5.7)	10.2 (4.1)		
DURATION OF						
First intrusion (standard dev.)			156.0 (221.2)	105.3 (107.7)		
Total intrusions			406.0 (146.6)	404.6 (121.5)		

group but not in their conspecifics. For the mean latency to frontal display responding in Groups P1 and P2, an ANOVA revealed that no significant group effect was present, although a significant decreasing effect of days was found ( $F(2,28) = 3.94, p < 0.05$ ) supporting the observation that the latency to frontal display decreased over days. An ANOVA revealed that the latency to frontal display by the US conspecifics matched to subjects in Group P1 and P2 neither differed between groups nor changed over days. Thus, the results indicate that the experimental subjects responded progressively more quickly over days to the sight of the US conspecifics which, which generally gave a frontal display first, and showed no change over days.

Frequency of Frontal Display. For the frequency of frontal display, an ANOVA between experimental subject and US conspecifics found no significant effects. Similarly, an ANOVA comparing Groups P1 and P2 revealed that no significant difference existed in mean frequency of frontal display, nor was there a significant effect of days. However, there was a significant days by group interaction with frequency in Group P1 decreasing and the mean frequency in Group P2 increasing over days ( $F(2,28) = 4.27, p < 0.05$ ).

An ANOVA applied to the performance of the US conspecifics matched to subjects in Group P1 and P2 revealed no significant differences. Thus, the results indicate that the frequency of frontal display decreased over days in the experimental subjects that displayed the highest levels of conditioning (Group P1) during Phase 1 and 2, while the opposite was true for the experimental subjects with the lower levels of conditioning. For the US conspecifics no changes in mean frequency of frontal display were noted.

Total Duration of Frontal Display. For the mean total duration of frontal display responding for experimental subjects and US conspecifics, an ANOVA revealed that only the mean total duration decreased over days of conflict ( $F(2,56) = 3.41, p < 0.05$ ). For comparisons of Groups P1 and P2, the ANOVA revealed no significant differences. For the US conspecifics matched to the subjects in Groups P1 and P2, no significant effects involving groups were found.

However, the mean frontal display duration for the US conspecifics across the three conflict sessions was 256.86 sec., 185.19 secs and 132.38 sec respectively. This decreasing trend produced a significant days effect ( $F(2,28) = 3.73, p < 0.05$ ). The results indicate that the mean

duration of frontal display decreased over days. However the experimental subjects and their US conspecifics did not differ.

Conflict Sessions: Biting. The mean number of bites inflicted on the US conspecifics by the experimental subjects during each of the 3 conflict sessions were 31, 25 and 62, and the mean number of bites inflicted on the experimental subjects by the US conspecifics was 7, 3, and 10 respectively for each of the three sessions. For the total number of bites inflicted by the experimental subjects compared to the US conspecifics, an ANOVA confirmed a significant group effect ( $F(1,28) = 28.03, p < 0.01$ ), as well as a significant days effect ( $F(2,56) = 9.97, p < 0.01$ ) and a days by group interaction ( $F(2,56) = 6.78, p < 0.01$ ). As can be deduced from the group means the experimental subjects inflicted substantially more bites than the US conspecifics and increases in the frequency of biting were also greater for the experimental subjects.

For the subjects in Groups P1 and P2 no significant differences were found in the number of bites inflicted on the US conspecifics during each conflict session. For the

US conspecifics matched to the subjects in Groups P1 and P2, no significant differences were found.

The results indicate that the experimental subjects inflicted substantially more bites than the US conspecifics intruding on their territory, and that prior levels of conditioning in Groups P1 and P2 did not influence the frequency of bites inflicted on the US conspecifics.

The latency to first bite on each session were not amenable to statistical analysis since neither all experimental subjects nor all intruders engaged in biting. Given 16 experimental subjects across 3 conflict sessions, a total of 48 sessions were observed, for the experimental subjects, bites were delivered on 43 of 48 sessions with a mean latency of 145 secs to the first bite. For the US conspecifics, bites were delivered on 10 of 48 sessions with a mean latency to first bite of 278 secs. A greater number of experimental subjects inflicted bites and did so much sooner during the sessions than did the US conspecifics. Over the three conflict session the 8 subjects in Group P1 delivered bites during 21 of 24 sessions with a mean latency to first bite of 124 secs while subjects in Group P2 delivered bites on 22 of 24 sessions with a mean latency of



165 secs. No differences appear to exist between Groups P1 and P2. For the US conspecifics matched to subjects in Groups P1 and P2, only 5 subjects delivered bites in each matched group, with a mean latency of 222 secs and 334 secs respectively. There appears to be little difference in the number of occasions on which bites were delivered and the latency to bite in subjects in Groups P1 and P2, or in the US conspecifics matched to the subjects in Groups P1 and P2.

In summary, there is a clear difference between experimental subjects and US conspecifics in the number of subject inflicting bites and the latency to bite. The experimental subjects inflicted substantially more bites and did so much sooner than the US conspecifics. In terms of conditioning history as reflected in Groups P1 and P2, there appears to be no differences in the number of subjects that delivered bites or the latency to bite.

Conflict Sessions: Intrusive Behaviour of US conspecifics. A number of measures of intrusion by the US conspecifics were also taken during the conflict sessions. It was presumed that the differences in levels of conditioning of the experimental subjects in Groups P1 and P2 could result in some differences in the intrusive

behaviour of the US conspecifics. As such ANOVAs were conducted between the US conspecifics matched with the experimental subjects in Groups P1 and P2. The intrusive behaviour monitored for in the US conspecifics included; 1) latency to enter experimental subject's territory 2) frequency of intrusion, 3) duration of first intrusion, 4) and total duration of intrusion.

The mean latency of first intrusion over the three conflict sessions for rivals matched to subjects in Group P1 and P2, was 17.0 and 14.9 secs respectively. An ANOVA found no significant group differences or changes over days. These results indicate that the differences in level of frontal display conditioning of experimental subjects during Phase 1 did not impact on the latency of intrusions by rivals.

The mean frequency of intrusions of the US conspecifics of subjects in Groups P1 and P2 during each session was 10.1 and 10.4 respectively. Again an ANOVA indicated that no group effect nor days x group interaction was present. However, the ANOVA did confirm the presences of an increasing days ( $F(2,28) = 17.50, p < 0.01$ ) effect. These results again indicate that the prior level of frontal

display conditioning did not influence the experimental subjects capacity to minimize the frequency of intrusions into their territories and that the frequency of intrusions of all US conspecifics increased over time.

The mean duration of first intrusion for each session, of US conspecifics matched to subjects in Groups P1 and P2, was 156.1 and 105.3 secs respectively. Once more the repeated measures ANOVA found no effects.

The mean duration of total intrusion for each session for US conspecifics matched to subjects in Groups P1 and P2 was 406 and 404 secs respectively. An ANOVA found no significant effects. The results indicate that the differences in Phase 1 frontal display conditioning for subjects in Groups P1 and P2 conferred no greater capacity for these subjects to limit either the duration of the first intrusion or the duration of total intrusion into their territory during the conflict sessions.

In summary, the results indicate that the latency, frequency and duration of intrusions by the US conspecifics were not effected by the prior levels of frontal display conditioning of the experimental subjects that the US conspecifics battled. In essence prior level of

conditioning in experimental subjects was not related to success in minimizing or limiting intrusion of the rivals into their territory.

#### Analysis of Correlations

The last stage of analysis in Experiment 2 was a correlational analysis. The variables that were correlated are grouped into three categories in order to facilitate discussion. The categories were conditioning variables, agonistic variables, and intrusion variables. The measures of conditioning included the mean per cent and duration of both frontal display and approach responding during the CS-US interval in Phase 1 and Phase 2. The second group of variables was the measures of agonistic behaviour taken for both the experimental subjects and the US conspecifics during the conflict sessions. This second group of agonistic variables included the latency, frequency and mean duration of frontal display as well as the total number of bites inflicted during the conflict sessions by the experimental subjects and the US conspecifics. Correlations between the agonistic responding of the experimental subjects and the US conspecific were obtained in order to

determine if any patterns existed between the behaviour of the experimental subjects and the US conspecific. The third group of variable monitored was the measures of intrusive behaviour by the US conspecifics. As noted earlier if conditioning had imparted some capacity to the experimental subjects to maximize their capacity to defend their territory we would expect to see differences in the US conspecifics intrusions into that territory as a function of conditioning of the experimental subjects. The third group of variables monitored included latency to first intrusion, duration of first intrusion, total duration and frequency of intrusions.

The correlation matrix is presented in Table 11. The first page of the table presents all the correlations while the second page presents only those that were significant at either the 0.05 or 0.01 level. The purpose of this analysis was four fold: first to determine the relationship between measures of frontal display and approach conditioning, second to determine the relationship between the measures of agonistic behaviour, third to determine the relationship between measures of intrusion and lastly to determine the

Table 11. Correlations between measures of conditioning, intraterritorial conflict and intrusion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21				
1	1.00																								
2	0.74	1.00																							
3	0.89	0.68	1.00																						
4	0.70	0.77	0.84	1.00																					
5	0.32	-0.02	0.10	-0.12	1.00																				
6	0.16	0.14	-0.03	-0.16	0.50	1.00																			
7	0.44	0.00	0.36	0.11	0.79	0.43	1.00																		
8	0.26	0.34	0.14	0.19	0.17	0.51	0.44	1.00																	
9	0.10	0.11	0.23	0.30	-0.14	0.06	0.14	0.30	1.00																
10	0.07	0.11	0.13	0.38	-0.35	-0.10	-0.02	0.34	0.76	1.00															
11	-0.04	-0.01	-0.04	-0.14	-0.17	-0.04	-0.32	-0.39	-0.56	-0.52	1.00														
12	0.06	0.07	0.07	-0.07	0.16	0.25	-0.01	-0.11	-0.01	-0.27	0.55	1.00													
13	0.14	0.00	0.01	-0.15	0.58	0.07	0.44	0.30	-0.32	-0.35	-0.19	0.16	1.00												
14	0.04	0.17	0.00	0.18	-0.41	-0.06	-0.31	-0.01	0.11	0.38	0.45	0.41	-0.34	1.00											
15	0.32	0.39	0.16	0.00	0.06	0.37	-0.08	-0.05	-0.23	-0.32	0.52	0.67	0.10	0.46	1.00										
16	0.08	0.04	0.17	0.19	-0.15	-0.28	-0.25	-0.40	-0.52	-0.34	0.68	0.11	-0.26	0.09	-0.07	1.00									
17	0.11	0.23	0.13	0.35	0.05	0.10	-0.01	0.42	0.35	0.34	-0.14	0.29	0.13	0.12	-0.23	0.09	1.00								
18	0.13	-0.01	0.03	0.21	-0.12	-0.18	0.09	0.26	0.36	0.81	-0.43	-0.45	-0.08	0.26	-0.33	-0.20	0.12	1.00							
19	0.16	0.25	0.03	-0.06	-0.04	0.01	-0.28	-0.42	-0.24	-0.34	0.53	0.57	-0.08	0.50	0.86	0.01	-0.34	-0.32	1.00						
20	0.00	-0.14	-0.12	-0.26	0.10	0.14	0.02	-0.36	-0.04	-0.21	-0.45	0.56	-0.17	0.46	0.52	0.01	-0.19	-0.21	0.69	1.00					
21	-0.07	-0.25	0.17	0.32	-0.15	-0.25	0.28	0.17	0.27	0.51	-0.39	-0.44	-0.16	-0.28	-0.70	0.09	0.20	0.43	-0.69	-0.36	1.00				

critical values for 15 df @  
 p < 0.01 = 0.61  
 p < 0.05 = 0.49

Table 11. Correlations between measures of conditioning, intraterritorial conflict and intrusion.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1																					
2	0.74																				
3	0.89	0.68																			
4	0.70	0.77	0.84																		
5																					
6					0.50																
7					0.79																
8						0.51															
9																					
10								0.76													
11								-0.56	-0.52												
12										0.55											
13					0.56																
14																					
15																					
16										0.52	0.67										
17									-0.52	0.68											
18																					
19									0.81												
20										0.53	0.57			0.50	0.86						
21										0.51					0.52				0.69		
															-0.70					-0.69	

critical values for 15 df @  
 p < 0.01 = 0.61  
 p < 0.05 = 0.49

Table 11. (cont) Correlations between measures of conditioning, intraterritorial conflict and intrusion.

1 Frontal display Per cent responding Phase 1 cond: mean across 13 days	5 Approach responding Per cent responding Phase 1 cond: mean across 13 days	9 Latency of frontal display for residents
		10 Latency of frontal display for rivals
		11 Total duration of frontal display for residents
2 Frontal display Duration of responding Phase 1 cond: mean across 13 days	6 Approach responding Duration of responding Phase 1 cond: mean across 13 days	12 Total duration of frontal display for rivals
		13 Latency to bite for residents
		14 Total number of bite by residents
3 Frontal display Per cent responding Phase 2 reconditioning: mean across 4 days	7 Approach responding Per cent responding Phase 2 reconditioning: mean across 4 days	15 Total number of bites by rivals
		16 Frequency of frontal display for residents
		17 Frequency of frontal display for rivals
4 Frontal display Duration of responding Phase 2 reconditioning: mean across 4 days	8 Approach responding Duration of responding Phase 2 reconditioning: mean across 4 days	18 Latency to first intrusion by rival
		19 Duration of first intrusion by rivals
		20 Total duration of intrusion by rivals
		21 Frequency of intrusion by rivals



relationship between the measures of conditioning, measures of agonistic behaviour and measures of intrusion.

Correlations for Frontal Display and Approach

Responding. A number of significant correlations were found between measures of conditioned frontal display and approach responding during Phase 1 and the mean per cent frontal display during Phase 2. As can be observed in Table 11, the mean per cent and duration of frontal display and approach responding were correlated both within and between Phase 1 and 2. For frontal display and approach responding, the mean per cent and duration of responding were correlated both within and between phases. No measures of frontal display in either Phase 1 or 2, however, were correlated with approach responding, suggesting that these two response systems are distinct.

Correlations for Frontal Display and Biting During

Conflict Sessions. During the intraterritorial conflict a number of significant relationships between the various measures of agonistic behaviour or territorial defense were obtained. As expected, measures of latency, duration and frequency of frontal display in the experimental subjects

were correlated. However this was not the case for the US conspecifics.

The general absence of significant correlations between the various measures of conditioned frontal display during the conflict and biting during the conflict were surprising. For the experimental subjects there was absolutely no relationship between measures of frontal display during the intraterritorial conflict and biting. Frey and Miller (1972) noted that the best predictor of bout winners was biting and that frontal display was the initial behaviour of losers. In light of Frey and Miller's (1972), it is not surprising to discover a lack of relationship between any measures of frontal display and biting in the experimental subjects. For the US conspecifics frequency of biting was related only to the duration of frontal display in both the experimental subjects and US conspecifics.

The relationships between the agonistic behaviour of the two rivals were also obtained. In terms of frontal display, the correlations revealed a strong relationship between the latency and duration of frontal display but not frequency of display. It was also observed that no

relationship was found between the biting behaviour of the two rivals.

Correlations for Measures of US Conspecific Intrusion.

In terms of measures of intrusion, the total duration of first intrusion correlated directly with total duration of intrusion ( $r=0.69$ ,  $p < 0.01$ ) and inversely with the frequency of intrusion ( $r = -0.69$ ,  $p < 0.01$ ). It is interesting to note that the latency to enter the experimental subject's territory was not related to the duration of intrusion.

Correlations for all Response Measures Between Phases.

In examining between phase correlations, it is important to note that no measures of conditioned frontal display responding in the experimental subjects were related to measures of agonistic behaviour during the intraterritorial conflict of either the experimental subjects or the US conspecifics. In addition, none of the measures of frontal display conditioning correlated with measures of intrusion by the US conspecifics. Of the measures of approach responding, only one was related to a territorial defense measure. The mean per cent approach responding during Phase 1, was positively related to the latency to bite in the experimental subjects. In contrast, no measure of

approach conditioning was related to any measure of intrusion by the US conspecifics. These results indicate that neither the conditioning of frontal display or approach responding had a major impact on the agonistic behaviour of the experimental subjects or their matched US conspecifics during the intraterritorial conflicts, nor on the intrusive behaviour of the US conspecifics as measured in this study.

As noted earlier, Frey and Miller (1972) state that biting is likely the best predictor of successful territorial defense. The correlation matrix indicates that conflict biting indices were not correlated with either the levels of prior conditioned frontal display or approach responding or any measures of intraterritorial conflict. Furthermore, the levels of conditioned frontal display and approach responding reached by the experimental subjects was not related to the total number of bites inflicted on them by their US conspecifics. Thus conditioning measures failed to correlate with the best index of territorial defense (Frey and Miller, 1972).

The measures of territorial defense did show some relationships with measures of intrusion. It was of particular concern to determine if any measures of behaviour

in the experimental subjects were related to measures of intrusion by the US conspecifics. The correlation matrix indicated that the total number of bites and duration of frontal display by the experimental subjects was directly related to the duration of first intrusion by US conspecifics.

The agonistic behaviours of the US conspecifics also correlated with their intrusive behaviour. The latency to frontal display was directly related to latency of first intrusion and the frequency of intrusion or the frequency of exit and reentry. These results indicate that the longer it took for a US conspecific to give a frontal display the longer it took for it to intrude and the more it exited and reentered the experimental chamber. The relationship between the latency to frontal display and the latency to intrusion is not surprising since frontal display could not occur before intrusions. It may however be readily suggested that both measures of latency reflect, to some extent, aggression.

In summary, the results from the analysis of correlations contain two important findings. The first is that neither the mean per cent nor the duration of frontal

display or approach responding are related in any significant way to measures of territorial defense or intrusion. While the mean per cent approach responding during Phase 1 is related to the latency to bite in the experimental subjects during the conflict sessions, the relationship is positive and indicates that increases in conditioned responding are related to increases in latency to bite. The second finding related to the patterns of relationships between the measures of agonistic responding or territorial defense taken for both experimental subjects and US conspecifics during the conflict sessions. As expected measures of frontal display such as latency, frequency and duration were related in both the experimental subjects and US conspecifics. The high correlation between latency, and duration of frontal display in the experimental subjects and the US conspecifics suggests that behaviour of both the experimental subjects and the US conspecific during the conflicts are to some degree the results of an interactive process. The relationships in the behaviour of US conspecific also revealed some patterns, for example, the latency and duration of frontal display in US conspecifics

was closely related to the total duration of intrusion and the number of bites inflicted by the US conspecific.

#### Discussion

The purpose of Experiment 2 was to answer two questions. First, is the frontal display response common to all Trichogaster trichopterus when presented with a US conspecific? And second, is there a relationship between levels of conditioned agonistic responding, particularly frontal display, and measures of territorial defense and intrusive behaviour?

In order to assess the degree of variability in unconditioned and conditioned responding 16 fish were monitored. In terms of mean percent unconditioned frontal display and approach responding across days, responding varied substantially. For unconditioned frontal display the daily means ranged between 1.60 and 70.80 and the overall mean was 36.26 per cent. For unconditioned approach the means ranged between 36.90 and 94.10 per cent with an overall mean of 72.4 per cent. In terms of conditioned frontal display responding the means across days ranged from

0.00 to 61.60 per cent with an overall mean 13.70 per cent. For approach conditioning, the range was from 16.00 to 65.20 per cent with an overall mean of 43.10 per cent. These results replicate those found in Experiment 1.

Thus, the results of the present experiment answer the first question in the negative. Neither unconditioned or conditioned reactions occurred reliably in Trichogaster trichopterus. Instead, subjects demonstrated wide differences in their reactivity to a male conspecific. The observation that within this sample, substantial differences in reactivity existed is consistent with Miller's (1964) conclusion of minimal and selective intraspecific aggression in male Trichogaster trichopterus.

Three major observations impact on the second question concerning the relationship between conditioning and conflict resolution. First, the levels of conditioned frontal display and approach responding were not related to measures of agonistic responding during actual conflict sessions. In particular, no relationship was found between conditioned frontal display and biting which is the best predictor of bout outcome (Frey and Miller, 1972). Second, the levels of conditioning had no impact on the intrusive



behaviour of the US conspecifics. And finally, the levels of conditioning of frontal display and approach were not influenced by the interpolation of intraterritorial conflict sessions. Each of these observations is consistent with the conclusion that there is no relationship between conditioning and conflict resolution.

The observation that neither conditioned frontal display or approach responding was related to agonistic responding during the conflict session presents some concern in light of Hollis's (1984) results. Hollis (1984) found that fish who had, been given Pavlovian conditioning and acquired a conditioned frontal display response, entered their rival's territory more often and inflicted more bites than did their rivals. The present study found that subjects that had received Pavlovian conditioning also inflicted more bites on their rivals. However, both conditioned subjects that gave few frontal display response and those that gave frontal display responses both inflicted more bites on their rivals than they received. In addition, there were no differences between the two subgroups. These results indicate that no relationship exists between conditioned frontal display responding and biting.

Hollis (1984) measured successful territorial defense by assessing the level of aggression that the experimental subjects displayed. Successful territorial defense was measured by frequency of biting and also by the capacity of the experimental subjects to intrude into a rivals territory. In the present study, territorial defense was measured by assessing the capacity of the experimental subjects to minimize intrusion by the rivals. We therefore monitored measures of intrusion of the rival in order to assess the capacity of the experimental subject to defend its territory. It was observed that the level of frontal display conditioning in the experimental subjects in groups P1 and P2, while significantly different, did not result in a difference in the experimental subject's capacity to limit intrusion in their matched rivals. In addition, correlations between levels of frontal display and measures of intrusions were nonsignificant. These results do not support Hollis's (1984) observations that frontal display conditioning impacts on successful territorial defense.

It was also interesting to observe that no relationship was found between conditioning indices during Phase 2 reconditioning and the interpolated conflict sessions. The

reconditioning essentially appears to be a continuation of performance established during Phase 1 conditioning. The absence of any relationship between boundary behaviour and intraterritorial behaviour supports Miller's (1964), and Frey and Miller's (1972) assertions that boundary behaviour and intraterritorial behaviour differ with respect to their controlling variables.

## General Discussion

Hollis's (1982, 1984) prefiguring hypothesis was an attempt at identifying the adaptive significance of conditioning. The hypothesis has two central assumptions. First, it was assumed that a CR is the result of S-S associations formed by repeated presentation of a neutral event, the CS, and a biologically significant event, the US. And second, it was assumed that the function or purpose of the CR was to allow an organism to deal more effectively with an upcoming biologically significant event and thereby maximize inclusive fitness.

To test the prefiguring hypothesis, Hollis (Hollis, 1984; Hollis et al, 1989), adopted a set of assumptions concerning both her experimental species, Trichogaster trichopterus, and how the prefiguring hypothesis would apply to intraspecific territorial interactions. Her assumptions were as follows. First, she assumed that all male Trichogaster trichopterus are territorial and exhibit intraspecific aggression to a male conspecific. Second, she assumed that a male conspecific could serve as a US in the conditioning of intraspecific conflict and that a frontal

display response would index conditioned intraspecific aggression. Third, she assumed that levels of conditioned aggression are related to successful territorial defense. And, finally, she assumed that successful territorial defense is a "currency" of reproductive gain and hence inclusive fitness.

In support of the prefiguring hypothesis Hollis (1984), Hollis et al (1984) and Hollis et al (1989) demonstrated that all Trichogaster trichopterus that had received pairings of a light CS and a US conspecific demonstrated conditioning of a frontal display. In addition, she demonstrated that conditioned fish upon presentation of the light CS, were more aggressive and defended their territory more effectively than their rivals which had not received the light CS in the conflict situation.

However, Hollis did not determine that the mechanism of association was S-S. Given that no explicit tests were undertaken to determine that pairings of a light CS and a US conspecific necessarily yield S-S associations, the assumption is tenuous. Nor did Hollis convincingly demonstrate that conditioning resulted in better territorial defense. Aggression was measured by intrusions into the

opponent's territory, and frequency of biting during the ensuing conflict. It might be argued that leaving a territory unattended and aggressing into an opponent's territory does not constitute better defense.

When the territory is unattended, there is no defense possible against intrusion by other fish.

The present studies attempted to clarify the ambiguities in Hollis's work. Experiment 1 was designed to determine the nature of the associations established during conditioning of frontal display responding in Trichogaster trichopterus. And, Experiment 2 was designed to evaluate the contribution of conditioning to territorial defense by assessing the capacity of the conditioned subjects to prevent intrusions into their territory.

Three important conclusions can be derived from the results of the present experiments. First Experiment 1 showed that when conditioning occurred, it appeared to be predominantly the result of S-S associations, although the variability in responding permits this to be only a tentative conclusion. Second, the observation that there existed a substantial variability in the degree of frontal display and approach responding demonstrated by male

Trichogaster trichopterus in the presence of another male conspecific indicated that the occurrence of aggression is not as robust as initially hypothesized. And finally, there appeared to be limited concordance between levels of conditioning and either measures of agonistic responding during the conflict or effectiveness of territorial defense. Each of these observations will be discuss in the paragraphs that follow.

#### Mechanism of Conditioning

The major observation derived from the Experiment 1 was that when conditioning occurred it appeared to be predominantly under the control of S-S associations. This conclusion is made on the basis of significantly greater conditioning in the Paired group relative to the Omission group, coupled with the absence of differences between the Omission and the Yoked groups. It should be noted however, that the variability of unconditioned and conditioned responding in the present studies and the low levels of conditioned responding seriously limited the effectiveness of the omission procedure. Consequently, conclusions concerning the absence of R-S learning must be viewed as

tentative. Caution is warranted because of the evidence from studies using Betta splendens by Murray (1973). Murray (1973) carried out a negative automaintenance procedure with subjects selected for vigorous agonistic responding. The selection of aggressive subjects ensured elevated levels of baseline unconditioned responding, such that an effective omission procedure was implemented. While Murray's (1973) results are restricted to the aggressive members of the species the results indicated that when agonistic behaviour occurred, both S-S associations and R-S associations control it.

This outcome is not surprising. The paradigms labelled classical and operant conditioning, which are said to yield S-S and R-S associations, are paradigms devised by researchers. In nature, it is probable that most learned behaviour is the result of an interaction between classical and operant conditioning paradigms and the associative mechanisms that underlie them. It is also possible that some as yet undiscovered paradigms interact to yield the complex behaviour patterns observed in the various organisms in nature.



Invoking the operation of two learning processes, or Pavlovian conditioning, in the situation conveys a flexibility to the subject that either alone does not provide. The S-S learning provides the subject with information concerning the impending occurrence of a particular class of biological significant environment event; the R-S component guides the subjects' reaction to the event. Either process acting alone would lead to a rigidity of acquired behaviour, because the same reaction would occur to all exemplars of a class of biologically significant events. Thus for example, if aggression is the reaction to intrusion, then preparing for aggression is the only option available. On the other hand, the two processes acting together provide an open system that can react to localized effects. For example, intrusion by a larger dominant fish might better be dealt with by avoidance rather than fighting, with the reverse true when a less dominant fish intrudes. In this case the S-S component is used to identify the difference in impending situations and the R-S component differs between the situations.

Variability in Unconditioned and Conditioned Reactions

In Experiment 1 and 2, the presentation of a US conspecific to the male experimental subject did not reliably elicit either unconditioned or conditioned agonistic responses in all experimental subjects. For example, unconditioned frontal display responding ranged from 1.6 to 70.8 per cent while conditioned responding ranged from 0.0 to 61.6 per cent. These results differ substantially from those found by Hollis who reported very high levels of both unconditioned and conditioned frontal display responding.

As noted earlier the variability may to some degree be explained in terms of the random sampling procedure used to select subjects in the current study. However, sampling procedures alone do not account for the differential outcomes in the present studies and Hollis's work. A methodological difference may also have also contributed to the differential outcomes.

Procedurally, a major difference between the two research programs existed in how the US conspecific was presented to the experimental subjects. In Hollis's studies, the US conspecific was isolated from the subjects

by being presented in a glass jar (Hollis, 1984; Hollis et al 1984). Whereas, in my study, the US conspecific was separated from the experimental subjects only by a mesh grid. While it may appear that the isolated presentation and the mesh cage presentation of the US are equally realistic, the physical isolation that occurs when the US is presented in a glass jar disrupts the interactive behavioural sequences between the two fish by preventing the occurrence of significant cues which that occurs between conspecifics. Some of these cues may include: the aversive stimulation which results from tail beating or strikes being directed at the rival, as well as chemical cues that are emitted by the conspecific and are waterborne. That the preclusion of such cues by the presentation procedure impact on the level of aggression in Trichogaster trichopterus has not been established. However, evidence from a closely related species strongly suggest that the presentation procedure does alter cues that are relevant to aggressive interactions.

Lobb and McCain (1976) found, in Betta splendens, that a dominant-submissive relationship was established between rivals when a wire mesh separated the subjects, and that the

dominant conspecific continued to display while the submissive subject did not. However, when a glass wall was used the dominant-submissive relationship was not established and both subjects continued to engage in frontal display behaviour. The difference between wire mesh and glass walls was not restricted to the elicitation of frontal display. Lobb and McCain (1976) further demonstrated that a significant amount of avoidance of the rival occurs in the submissive fish when a wire mesh separation is used, but not when the rival are separated by a glass wall. And finally, Lobb and McCain (1976) suggested that the difference between the isolated presentation and the wire mesh may alter, if not preclude, the establishment of the natural sequential relationship in the agonistic behaviour of the rivals.

In the present studies, if the wire mesh permitted the establishment of dominant-subordinate relationships in pairs of rivals it would be expected that only some (one half by chance) of the subjects would become the dominant one of the interacting pairs. In as much as some of my experimental subjects would not be the dominant fish of the pair, agonistic behaviours would not be observed in all subjects. This would increase the between subject variability in

responding that was noted in Experiment 1 and 2. Thus, with the wire mesh cage used in the present study, the differential contribution to responding of dominant and submissive subject would occur with the subsequent increase in between subject variability. The glass enclosure used by Hollis would preclude or at least slow the development of submissive/dominant relationship and prolong responding. Both outcomes would tend to homogenize performance in her experiment.

A second class of cues that are precluded by glass chambers, were also assumed to impact on aggressive responding. These cues are the waterborne chemicals emitted by the fish. In a normal interaction, and also with the wire mesh procedure, the exchange of water between the areas around the rivals results in any waterborne chemical emitted being detected by the rivals.

The general importance of chemically induced reactions in fish behaviour is well documented. Pfeiffer (1963a; 1963b) noted that a number of species of fish respond strongly to waterborne alarm substances from conspecifics that are under attack. These alarm substances serve as cues for danger when released from the damaged skin of a

conspecific under attack. Cheal and Davis (1974), Lee and Ingersoll (1979), Piccolo (1964), Pollak, Becker & Haynes (1978) and observed that chemical cues can serve to modulate nest building and social behaviour in Trichogaster trichopterus. In addition, Hara (1971) stated that chemoreception is also relevant to sex discrimination, and parental behaviour. For example, Baeninger (1968) and Ingersoll, Bronstein and Bonventre (1976) observed that Betta splendens curtailed their aggressive activity when placed in water in which either a pair of conspecifics had just fought or where a nondisplaying conspecific had been. If chemicals modulate behaviour and are part of the signalling required for the development of effective interactions between conspecifics, then the use of a mesh grid versus a glass jar would allow the signalling to occur much as it would in nature, whereas the latter would not.

The elicitation and subsequent habituation of agonistic behaviour is also a function of the nature of the agonistic stimulation. Dore, Lefebvre and Ducharme (1978) found in Betta splendens, the rate of habituation of that agonistic responding by a male was faster to presentations of an actual opponent than to a conspecific behind glass, which in

turn was faster than to a mirror presentation. Baenninger (1966) demonstrated that the tendency for Betta to view a conspecific also habituated faster than their tendency to view a mirror image. Similarly, Peeke, Herz and Gallagher (1970) showed that presentation of a conspecific minimized habituation of aggressive responding in cichlids (*Cichlasoma nigrofasciatum*). Baenninger (1970), Clayton and Hinde (1968) and Rhoad, Kalat and Klopfer (1975) also found that habituation of aggressive responding in Betta splendens was greatest when the eliciting stimulus was a conspecific as opposed to a mirror or a model. It appears that responding habituates most effectively to the actual presentation of a conspecific and least effectively to the visual representations of the conspecific in the absence of other possible cues. These results suggest that the visual presentation of a US conspecific differs substantially in stimulus properties from a natural presentation and results in the maintenance of responding beyond what would occur in a natural setting. The differences in responding to mirror images or models may be related to the lack of physical and chemical cues. While the reasons for the differences cannot be completely specified, the observation of differences

supports the notion that isolated presentation of the US conspecific may elicit an unnatural response pattern.

The above observations suggests that the method of US conspecific presentation used by Hollis (1982, 1984) may have distorted the intraspecific dynamics of the interacting fish. While such distortions may be acceptable for studying learning processes (because variability between subjects can be reduced), the distortions limit the ecological validity of the outcomes. With limited ecological validity, the extension of the results to evolutionary issues, such as the adaptive value of the learning, is questionable. Separating rivals by a grid, while still precluding some of the natural interactions, allows for a far broader range of actions, and is, consequently, a better approximation to the natural situation for the fish.

The results of both Experiment 1 and 2 indicated that the presence of a male conspecific does not always elicit frontal display or approach responding. Therefore, the presentation of a male conspecific can not be defined as a reliable unconditioned stimulus for these responses. Given that the reliable occurrence of the US-UR is a requirement



for classical conditioning, it is not surprising that pairings of a CS with a US conspecific did not support the conditioning of a frontal display or approach responding in all male Trichogaster trichopterus.

The variability in unconditioned and conditioned agonistic response is problematic for the prefiguring hypothesis. For fish that showed limited unconditioned agonistic reactions, the prefiguring assumption that aggression is an evolutionary currency leads to the conclusion that this proportion of the species did not evidence inclusive fitness. For fish that showed limited conditioned agonistic reactions, the assumption that conditioning facilitates aggression and hence enhances inclusive fitness, leads to the conclusion that there is not adaptive significance to learning for these fish. The coupling of the present results with the prefiguring assumptions leads to the conclusion that only a small proportion of the subjects (i.e. the aggressive ones) demonstrated a currency of inclusive fitness and that conditioning augmented fitness in only a few individuals. This conclusion has two problems. First, it reduces the realm of the prefiguring hypothesis to a subset of the

population, without providing an a priori specification for identifying that subset. Bounding the hypothesis in this fashion undermines its purpose which is to identify the adaptive significance of learning. And second, the conclusion has the net effect of applying the concepts of fitness and adaptive significance to attributes of an individual rather than to the species as a whole. This is an inappropriate application of the evolutionary powers.

#### Conditioning and Function

In Experiment 2 it was noted that: no measure of conditioned or unconditioned agonistic behaviour correlated to measures of conflict; that fish that demonstrated conditioned agonistic responses were not more aggressive in the conflict situation than those that did not demonstrate conditioned responses; and, that fish that demonstrated conditioned responses did not have an advantage in limiting intrusion by rivals. These results are not consistent with the observations of Hollis (1982, 1984). Furthermore, the results refuted the major prediction of the prefiguring hypothesis which states that conditioned responding augments aggression with the consequence of enhanced inclusive

fitness. The lack of support for the prefiguring hypothesis leaves open the question of the relationship between conditioning and the function of conditioned behaviour. Given the present results two possibilities appear to exist. The first of the possibilities is that there is no adaptive significance to learning in terms of territorial defense. Or, the strategies of territorial defense require a far more flexible system than posited by Hollis.

The first alternative arises when the observation that the behaviour patterns during conditioning don't appear to be correlated to actual conflict, and would suggest that any advantages conferred on an organism during conditioning during boundary conflicts does not carry over into intraterritorial battles. As noted earlier, Miller (1964) and Frey and Miller (1972) found little relationship in conflict patterns between intraterritorial conflicts and boundary conflicts. Without crossover between the two situations, the adaptive significance of a conditioned reaction within one of these types of conflicts is at best restricted to that conflict, and the adaptive significance must be identified within the same type of conflict.

Neither Hollis nor the present student studies meet these conditions.

The second alternative, that a more flexible system is needed to deal with the situation can be derived from Dawkins (1986). Dawkins (1986) noted that it would not be useful for a species to have an aggressive or Hawkish strategy. If all members of the species were required to engage in aggressive interaction in order to ensure reproductive success, the species would breed forwards to generate a very aggressive population. Eventually, this strategy would become less effective since reproductive success would require a battle wherein one or both conspecifics would be seriously injured.

Doves or less aggressive fish would, at this point, for a period of time have the advantage, ultimately neither strategy would be stable. By stable it is meant that the strategy would be one which, if adopted by the population would result in a higher reproductive success. In our example, the Hawk or Dove strategy is only effective providing their frequency is low, yet in as much as they were successful in reproduction would cause them to increase in frequency and thereby lose their competitive edge.

A more effective strategy would be one wherein the membership had a representation of both Doves and Hawks. This would be a mixed evolutionarily stable strategy (ESS). A mixed ESS could come about in two ways: by having two forms of individuals, Hawks and Doves, each pursuing a particular strategy; or, by having one type of individual pursuing at random either a Hawkish or Doveish strategy. If the individual pursuing a mixed ESS undertakes to respond in a Hawkish or Dovish mode in other than a random fashion the ESS is no longer a mixed one but rather can be viewed as a pure conditional strategy.

A conditional ESS involves the animals selecting cues to determine whether a Hawkish or Dovish approach ought to be taken when confronted with a conspecific or a particular situation. As noted in the section on conditioning mechanisms, the two process approach (S-S and R-S) provides an effective mechanism for organisms that use a conditioned mixed ESS strategy. For example in a conflict with conspecifics of differing size the strategies for each conspecific would differ based on the following condition, be a Hawk if larger than rival and a dove if smaller.

Size presents a fairly good predictor of ultimate outcome of battles and is a good basis for not undertaking to war with a larger conspecific. A number of other cues may be used that are more vulnerable to cheating or that predict less accurately the ultimate outcome of further escalation of the battle. Obviously cues or signals that accurately predict outcomes of escalation of conflict are difficult to determine and require testing to some degree. It is at this point that the R-S component of Pavlovian conditioning comes into play, the outcomes of particular behaviour in the presence of given cues will begin to influence subsequent behaviour of the conspecific when presented again. When cues associated with an aversive outcome for a given behaviour are present, the probability of that behaviour would be decreased and the likelihood of some other strategy increased. Alternative might include escalation to battle from frontal display or submission and retreat. This opened program concept was suggested by Lorenz (1969). The response actually engaged in on any occasion would depend on the prior history of reinforcement in the presence of similar stimuli, in a similar context. The flexibility of this interaction would permit a

synergistic interplay of cues and responses between the two rivals that might minimize actual combat by incorporating the prior history of each subject into the situation. Male conspecifics may acquire or lose territories without serious battles taking place but as a result of these rituals.

Finally, it should be noted that Hollis's assumption that aggression in territorial defense can serve as a currency for inclusive fitness has not been shown. While the present study does not address this issue, the assumption that aggression is a currency should not be accepted without evidence. Bateman (1948) originally observed that the variance in male offsprings in the fruitfly was quite large, and suggested that this variance in offspring was a function of the male's capacity to defend a territory and attract a mate, in essence, the result of competition between males for a mate. However, Sutherland (1985) has since shown that this is not quite accurate, and that Bateman's (1948) results may be the result of no more than random effects. Sutherland further stated that the time required for offspring production in males is lower than in females, and therefore the opportunity for reproductive attempts is higher in males. Consequently,

difference in lifespan breeding opportunity for males may be the main basis for the variance in reproductive success. Indeed, it appears that the number of matings in damselflies for example, depend essentially on its life span the duration of which is random (Dawkins, 1986).

To the extent that these results generalize to fish, and that fact has not yet been established, however, the assumption that the variance in the number of a male's offspring results from differentially effective territorial defense, may be more intuitively appealing than accurate. Given this observation, Hollis (1984) assertion that territorial defence is the basis for sexual selection can not be used as a currency for reproductive success without reservations. If territorial defense is to be used as a currency for inclusive fitness an empirical relationship between territorial defense and life time reproductive success must be demonstrated.

In summary, the present research has raised several difficulties for Hollis's prefiguring hypothesis. On reflection, the difficulties appear to be the result of a tacit assumption made in the field. That assumption is that a behavioural currency is an index of genotypes. This



assumption is pervasive, unproven, and probably rarely correct. Often the currency established, which is presumed to reflect differences genotypic differences, reflect only the reproductive success of a phenotype.

Examining genetic variability in learning and aggression and possible evolutionary change can only occur with a range of variants in genotypes. Neither current or earlier work has done this. However, the present study could be viewed as a first approximation to this task because we have identified ranges of variation. Whether this variation is genetically determined or not, can not be ascertained. To discuss adaptation it must be assumed that different phenotypes reflect different genotypes. This is gratuitous because phenotypes have an ontological as well as a phylogenetic history. Differences in phenotypes could reflect either of the two histories. Consequently, caution must be exercised until the phylogenetic component is isolated.

Given that a genetic component to an observed phenotype can be identified, Dawkins (1986) has identified four strategies to confirm the adaptive significance of that genetic component. The first strategy involves comparing

the reproductive success of behavioural variants currently found in the population. The second strategy requires comparing artificially produced variations to the actual variant, and observing "survival rate". This strategy is used if only one variant can be isolated in a population. The third method would see the reproductive success of closely related species in different environments compared in order to identify evolved differences of an attribute. And finally, Dawkins suggests making comparisons between observed "design features" in the species and the presumed ideal design. In as much as the designs are similar, the selected design is assumed to be the result of natural selection. The first and third are direct procedures because they examine the existing variants, while the second and fourth procedure are indirect because inferences are based on exclusionary data. Future research efforts must adopt these strategies if the question of the adaptive value of conditioning is to be unravelled.

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