CONTIGUITY AND INFORMATIONAL VARIABLES IN CLASSICAL CONDITIONING

by

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--Short Title--

CONTIGUITY AND INFORMATIONAL VARIABLES IN CONDITIONING

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This thesis investigates the role of the animal's uncertainty about the time of presentation of unconditioned stimuli (UCS) in the development and maintenance of the responding established with classical conditioning procedures. This question was examined through an analysis of anticipatory conditioned licking when the thirsty rat is, or is not, given information about the exact time of water deliveries. Less conditioned licking and longer response latencies to a temporally prior conditioned stimulus (CS) were observed when a second, brief (0.5 sec) marker stimulus coincided with the onset of water presentation during conditioning trials. It was shown that the presentation of the marker stimulus at unpredictable times during conditioning trials did not result in any general disruption of or interference with conditioning to the CS. Moreover, no evidence was found that the attenuation of conditioned licking was attributable to the development of inhibition to the CS. Rather the findings supported the hypothesis that the reduction in responding to the CS was a consequence of the more precise information that the marker stimulus gives about the time of UCS presentation. These results are discussed in terms of the Rescorla-Wagner and selective attention models of conditioning, as well as in terms of the view that the rate of responding depends on the <u>relative</u> informational significance of conditioned stimuli present at the time.

CONTIGUITE ET VARIABLES D'INFORMATION DANS LE CONDITIONNEMENT CLASSIQUE

Paula E. Pasquali

Le but de cette thèse est d'investiguer le rôle de l'incertitude de l'animal en ce qui concerne le temps de présentation de stimuli inconditionnels (UCS) dans le développement et le maintien de réponses établies par des procédures de conditionnement classique. Cette question fut examinée par une analyse de lappement conditionnel d'anticipation lorsqu'un rat assoiffé est, ou n'est pas, informé du temps exact des présentations d'eau. Moins de lappement conditionnel et de plus grandes latences de réponse à un stimulus conditionnel antérieur furent observés lorsqu'un second stimulus de courte durée (0.5 sec) coincidait avec le début de la présentation d'eau, durant les essais de conditionnement. Il fut démontré que la présentation du stimulus marqueur à des moments imprédictibles durant les essais de conditionnement ne produit pas de dérèglement ou d'interférence avec le conditionnement au CS. De plus, qu'une diminution du lappement conditionnel soit attribuable au développement d'une inhibition au CS ne fut pas démontré. Au contraire, les résultats confirment l'hypothèse selon laquelle la réduction de réponses au CS est une conséquence de l'information plus précise que le stimulus marqueur donne concernant le temps de la présentation de l'UCS. Ces résultats sont discutés en termes des modèles de conditionnement de Rescorla-Wagner et de l'attention sélective, aussi bien qu'en termes de la position selon laquelle le taux de réponse dépend de la signification relative de l'information concernant les stimuli conditionnels présent à ce moment.

TABLE OF CONTENTS

Page

PREFACE i

INTRODUCTION

Historical Background 3
Meanings of Temporal Contiguity 7
Informational Variables in Conditioning 15
Theoretical Formulations 21
Temporal Variables in Conditioning 29
Anticipatory Conditioned Responding and Temporal Uncertainty 37
General Statement of the Problem 39

DESCRIPTION OF THE BASIC FINDINGS

Experiment 1 42
Experiment 2 49
Discussion of Experiments 1 and 2 58

THE INTERFERENCE HYPOTHESIS

Experiment 3 60
Experiment 4 64
Discussion of Experiments 3 and 4 66

THE INHIBITION HYPOTHESIS

Experiment 5 68

THE INFORMATION HYPOTHESIS

Experiment 6 77
Experiment 7 80
GENERAL DISCUSSION 85
REFERENCES 97
APPENDICES 109

PREFACE

This thesis investigates the behavioural outcome of classical conditioning procedures in terms of the informational role of conditioned stimuli. The methodology developed in this series of experiments demonstrates the animal's sensitivity to and knowledge of the temporal specificity of the predictive relations between stimuli in the experimental situation. Further, the results obtained using this conditioning procedure question the use of overall changes in response rate as the primary measure of the efficacy of various conditioning procedures and allow for some tentative conclusions to be made concerning the structure of the knowledge acquired by the organism about temporal relations between stimuli in its environment.

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INTRODUCTION

The doctrine of associationism has played a pivotal role in the evolution of modern psychological thought. Perhaps in no field within psychology has the impact of associationism been greater than in the study of learning and the related phenomena of memory. It has often been assumed that the basis of learning is the formation of associations between certain classes of entities. Although the limitations of this approach have been fully exposed (e.g., Köhler, 1925; Tolman, 1932), associative models of conditioning have yet to be rejected as wholly untenable or successfully challenged by any comprehensive "cognitive" model. Thus, the belief that learning consists of the establishment of associative connections continues to be the working hypothesis of many psychologists seeking general principles of learning.

Two broad questions have been addressed by investigators working within the associationistic tradition in psychology. The first concerns the nature of the entities that enter into associations. With few exceptions, early psychological theorists (e.g., Guthrie, 1935; Hull, 1943; Pavlov, 1927; Skinner, 1938; Thorndike, 1932; Watson, 1916) were in general agreement that learning involved the establishment of new sensori-motor neural connections, or less precisely, stimulus-response associations. Recently, however, the Tolmanian view that learning might be better described in terms of the formation of associations between stimuli has received considerable support (e.g., Bindra, 1974; Bolles, 1972; Estes, 1969; Hearst, 1978; Rescorla, 1978). But the attempts to demonstrate empirically that associations involved in various phenomena of learning are exclusively of one form or the other have failed to produce a generally acceptable conclusion. Indeed, a common eclectic position (e.g., Bolles, 1972; Estes, 1969; Rescorla, 1975) is that both stimulus-response and stimulus-stimulus associations may be involved in all learning phenomena. Rescorla and his colleagues (Holland & Rescorla, 1975; Rizley & Rescorla, 1972; Rescorla, 1975) have found that the extent to which each type of association participates in learning may differ according to the task demands.

The second, not unrelated, question concerns the conditions under which associations are likely to be established. In all traditional associationistic models of conditioning, the _principle of association by temporal contiguity_ assumes fundamental importance (Carr, 1931). The precedence of association by temporal contiguity over other conditions of association can be found in the philosophical, as well as psychological, literature. Moreover, temporal proximity between the associated entities continues to be regarded as a fundamental condition of learning by present-day theorists (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972).

This thesis re-examines the role of temporal contiguity between events in the establishment of classically conditioned responding. As such, a brief review of the importance of the principle of temporal contiguity in modern learning theory will be useful. Of particular interest is the possibility that temporal contiguity, as a condition of association, might be understood within the larger context of the informational value of the conditioned stimulus in classical conditioning.

Historical Background

The wide acceptance of the principle of association by temporal contiguity in learning theories can perhaps be best appreciated by first examining its precedence in the philosophical treatment of associationism.

British Empiricism

The doctrine of associationism was an aspect of an epistemological system that stressed the empirical origin of knowledge. This system was elaborated by a group of philosophers of the 17th and 18th Centuries who are collectively referred to as the British Empiricists. Among them, David Hartley (1705-1757) is distinguished for having developed associationism into a viable psychological theory. Unlike his predecessors, Hartley assumed the validity of association as the process underlying human understanding; his rigorous and systematic treatment of association was thus intended as an analysis of the whole range of human activities--from emotion to voluntary movement--in terms of the formation of associations. It is Hartley's version of associationism which is most clearly reflected in 20th Century psychology (Warren, 1921). The most general statement of the principle of association is given by Hartley as:

> "If any sensation A, idea B or muscular motion C, be associated for a sufficient number of times with any other sensation D, idea E or muscular motion F, it will, at last, excite d, the simple idea belonging to the sensation D, the very idea E or the very muscular motion F." (from <u>Observations on Man</u>, 1749, as quoted in D. Robinson, 1976).

Acceptance of the associative process as the means by which sensory, ideational and motoric activity become integrated necessitates a description of the conditions conducive to the establishment of associations and an enumeration of the factors that affect the strength of association. Despite considerable variability in the laws postulated by various members of the British Empiricist school, similarity and temporal contiguity of the entities to be integrated are most often recognized as the relations critical in the formation of associations (Warren, 1921).

Intuitively, the law of association by similarity would seem to refer to the ease or likelihood of forming an association as a function of the similarity of the to-be-associated entities. However, as noted by Carr (1931), Köhler (1941), Asch (1969) and, most recently, Rescorla (1978), historically the law of similarity was most often applied to the <u>activation</u> of previously formed associations, rather than the establishment of new associations. Illustrative of this usage is Bain's statement of the law of similarity: "Present actions, sensations, thoughts, or emotions tend to revive their <u>like</u> among previous associations." (from <u>Senses and Intellect</u>, 1855, as quoted in Warren, 1921). Within an associationistic framework, similarity has been commonly attributed to the common elements of complex experiences which are composed of prior multiple associations. Thus conceived, it is a simple exercise in logic to show that the associative activation of similar entities may be understood in terms of the formation of associations based upon temporal contiguity. A distinct principle of association formation based upon similarity is required if it is meant that similar entities are more readily associated than are dissimilar entities. Notwithstanding the lack of any universally acceptable definition of similarity, it should be clear that the formation of associations based upon similarity cannot be subsumed under the law of contiguity which is intended as a statement of the conditions under which any two entities might become associated.

In its most general form, the law of temporal contiguity states that an association is likely to be formed between two entities, be they sensations, ideas or movements, when they occur contemporaneously or in immediate succession. Simultaneity and succession, however, as different arrangements of temporal contiguity between entities, have not received comparable consideration in either the philosophical or psychological literature, with succession emphasized to the near exclusion of simultaneity (Warren, 1921).

Based upon the writings of the British Empiricists, the principle of association by temporal contiguity should be considered the mainstay of association theory. While it is undeniable that factors such as the frequency, salience, and hedonic quality of the associated entities influence the strength of associations, they can only do so provided the necessary condition for establishing an association, namely temporal contiguity between the to-be-associated entities, is satisfied. Empirical verification of the principle of association by contiguity was to come from the laboratory of Russian physiologist Ivan Pavlov.

The Basic Phenomenon of Classical Conditioning

Pavlov's basic experiment consisted of presenting a small amount of food powder to a hungry dog, a procedure which was guaranteed to elicit copious salivation. When the presentation of the food powder was repeatedly preceded by some initially neutral stimulus (such as a light or tone), *that* stimulus soon acquired the ability to elicit salivation. Pavlov termed such a stimulus a *conditional* stimulus (CS) to emphasize that its response-eliciting properties were strictly dependent ("conditional") upon the subsequent presentation of food. This general finding was systematically replicated by Pavlov and his co-workers, using a number of different *unconditional stimuli* (UCS), each eliciting some characteristic (unconditional) response. Although Pavlov confined his work to reflexive response systems, it is now well established that classical conditioning procedures can modify complex, voluntary responses such as directed approach and contact (e.g., autoshaping, see Brown & Jenkins, 1968) and the performance of instrumental responses such as lever-pressing (e.g., conditioned emotional response [CER] procedure, see Estes & Skinner, 1941).

Based upon the results of many experiments that systematically varied the temporal relation between the CS and UCS, Pavlov (1927) concluded that the necessary condition for the establishment of conditioned responding is that the conditional stimulus "....must overlap in point of time with the action of an unconditional stimulus" (p.26). In the absence of strict contiguity between the CS and UCS, Pavlov assumed that conditioned responding could only be established if some neural trace of the CS outlasted the actual presence of the CS and persisted until the time of UCS presentation. This is not inconsistent with his observation that conditioned responding was difficult, if not impossible, to establish using procedures that did not make the CS presentation overlap in time with the response elicited by the unconditional stimulus. Thus for Pavlov, as for the British Empiricists, the main condition necessary for establishing an association was temporal contiguity between the to-be-associated entities. But it soon became apparent that even when this condition obtained, the different ways of arranging temporal contiguity between the CS and UCS were not functionally equivalent.

Meanings of Temporal Contiguity

The development and maintenance of conditioned responding to a CS is facilitated when that stimulus is paired with the UCS in a forward manner so that the onset of the CS precedes the presentation of the UCS. The efficacy of this temporal arrangement contrasts sharply with the inability to obtain reliable conditioned responding when the CS is not the temporally prior stimulus. For example, Pavlov (1927) observed that the presentation of the CS following the UCS (the backward conditioning procedure) resulted in a conditioned response which was "of small magnitude and short-lived" (as translated by Razran, 1956). These observations suggest that the temporal contiguity of the CS and the UCS is not a sufficient condition for association but that, in addition, the CS must precede the UCS. This has encouraged the view that the CS participates in an association because it signals the occurrence of the UCS. Contiguity may thus be important in classical conditioning because it insures that the temporally prior CS is a good signal for UCS occurrence.

The adequacy of this signalling interpretation can be evaluated by comparing conditioning to a CS when it is temporally related to the UCS in other than a forward manner. A survey of the recent experimental literature shows that such conditioning procedures have been reported by different experimenters to yield excitatory and inhibitory, as well as neutral, CSs (Mackintosh, 1974). Three methodological and conceptual inconsistencies in this literature have undoubtedly contributed to this confusion.

Classification of Conditioning Procedures

First, the slight, but potentially important, procedural differences across experiments have largely been overlooked, indicating a failure to consider seriously the precise relation between the onsets and terminations of both the CS and UCS. In this discussion, simultaneous, embedded, cessation and backward conditioning procedures will be operationally defined so as to clearly differentiate four temporal relations between the CS and UCS; this classification is consistent with, but not identical to, those that have appeared in the literature thus far (e.g., Heth & Rescorla, 1973; Plotkin & Oakley, 1975; Razran, 1956). The defining characteristic of the simultaneous conditioning procedure is that the onsets of the CS and UCS be synchronous; the CS and UCS may or may not be coextensive. In both the embedded and cessation conditioning procedures, CS onset follows UCS onset. In the embedded procedure the CS terminates during the UCS presentation whereas the CS terminates with the UCS in the cessation procedure. Finally the use of the term backward conditioning procedure should be reserved for those cases in which UCS termination precedes CS presentation so that the CS and UCS are never concurrently present. Admittedly, these procedural distinctions are most pertinent when relatively long UCSs are used--it would not be expected, for example, that simultaneous and backward fear conditioning procedures would differ substantially if a 0.5-sec shock UCS were used. Notwithstanding this disclaimer, the usefulness of this classification will depend upon whether the systematic variation in the CS-UCS temporal arrangement which characterizes these procedures is reflected in behaviour.

Assessment of Conditioning to the CS

The second methodological problem concerns the techniques used to assess conditioning to the CS. Clearly no meaningful measure of conditioned responding to the CS can be obtained on reinforced trials when the CS is presented during or following UCS onset since responding elicited by the UCS will contaminate measurement of the conditioned response (CR). One obvious, but inadequate, method of assessing conditioning would be to present the CS without the UCS on test trials. But with repeated testing, rapid extinction of conditioned responding would ensue. Even if nonreinforced test trials were interspersed with reinforced training trials in order to prevent extinction, such a testing procedure would introduce a second source of variation in conditioned responding due to the partial reinforcement of the CS. A more important consideration is that when the onset of the CS coincides or follows the onset of the UCS on training trials, the absence of the UCS on test trials could serve as a discriminative cue (Heth & Rescorla, 1973). In this case, the presentation of the CS alone necessarily constitutes an extinction trial and weaker conditioned responding to the CS would be expected on that basis.

Tests of secondary, or conditioned, reinforcement may provide a more sensitive measure of conditioning to a CS that has been paired with a UCS in other than a forward manner. In these tests, the extent to which a CS can serve as a reinforcer of instrumental responding is assessed. These tests successfully circumvent the problem of the unavoidable discrimination between reinforced (CS+) and nonreinforced (CS-) trials encountered when conditioning is evaluated by the direct measurement of conditioned responding to a CS which coincides or follows UCS presentation.

The Associative Outcome of Conditioning Procedures

Lastly, and most importantly, is the consideration that the procedures of classical conditioning must be distinguished from the associative mechanism presumed to underlie conditioned responding. As Razran (1956) writes "....backward conditioning should not be a priori bracketed with 'backward association'...." (p. 56). In the earlier investigations, the selection of techniques that measure only excitatory conditioning may indicate a failure to make this distinction. Various authors have since argued that in backward and cessation procedures, in particular, the CS may become associated with UCS termination rather than UCS onset as in forward conditioning procedures (Barlow, 1956; Goodson & Brownstein, 1955; Mowrer & Aiken, 1954) or with the succeeding reinforcer-free period (Moscovitch & LoLordo, 1968; Plotkin & Oakley, 1975). In either case, the conditioned responding elicited by the CS would be antithetical to that observed when the CS and UCS are paired in a forward manner. By definition, such a CS is a conditioned inhibitor (Rescorla, 1969a) and so appropriate techniques for assessing conditioning to the CS would be those that can detect inhibitory, as well as excitatory, response tendencies.

The Efficacy of Different Conditioning Procedures

Conditioning to a CS paired with a shock UCS in either forward, simultaneous, embedded, cessation or backward conditioning procedures has been directly compared in two studies (Heth & Rescorla, 1973; Mowrer & Aiken, 1954). In both studies, conditioning to the CS was assessed using a test for conditioned punishment; in this procedure, the strength of conditioning is indicated by the extent to which response-contingent presentations of a CS previously paired with an aversive UCS suppress instrumental responding for food. The results of these experiments were consistent and unequivocal: the effectiveness of a CS as a conditioned punisher of barpressing was greatest when the CS had been paired with shock in a forward manner; in nonforward procedures, suppression of baseline responding decreased systematically as the interval between UCS onset and the presentation of the CS increased, with little or no suppression observed following conditioning with the backward procedure. These results suggest that the strength of excitatory conditioning may decrease as the onset of the CS occurs progressively later in time relative to UCS onset.

The possibility that the excitatory conditioned effects observed when nonforward conditioning procedures are used are transitory has been examined by varying the number of conditioning trials during training. Excitatory responding to a CS paired with shock in a backward manner has been found to decrease as a function of training in experiments using the conditioned salivary procedure with dogs (Pavlov, 1927), the CER procedure with rats (Siegel & Domjan, 1971, 1974) and the conditioned eyeblink procedure with rabbits (Siegel & Domjan, 1971, 1974). Similar findings have been reported by Heth (1976), who assessed the effects of a cessation conditioning procedure following 0, 10, 30, or 160 trials using the conditioned punishment test. These results are consistent with Pavlov's (1927) suggestion that extended training with these procedures may establish the CS as a conditioned inhibitor of responding. However, following extensive training with a CS paired with shock in a simultaneous or forward manner, Sherman and Maier (1978) found roughly equal diminution of suppression in tests of conditioned punishment. Moreover, following Heth (1976), Sherman and Maier showed that this effect is not due to the habituation to shock but depends upon the continued pairing of the CS with shock. These investigators suggest that extended training enables the subject to better discriminate the training situation (in which shocks occur) from the shock-free testing situation. As such, the more rapid extinction of conditioned punishment may be viewed as an artifact of the measurement technique and not the outcome of prolonged experience with some particular temporal arrangement between the CS and UCS. These considerations make it unlikely that the decline in CS effectiveness with extended training is attributable to a weakening of the underlying associative mechanism.

Several studies have shown that backward conditioning procedures produce an inhibitory effect. The development of excitatory responding is more retarded following training with a backward conditioning procedure than following appropriate control procedures (e.g., pre-exposure to the CS or UCS alone and uncorrelated presentations of the CS and UCS) in CER conditioning (Siegel & Domjan, 1971) and eyelid conditioning (Plotkin & Oakley, 1975; Siegel & Domjan, 1971). Similarly, Moscovitch and LoLordo (1968) found that when a CS paired with shock in either a cessation or backward procedure was subsequently superimposed on an unsignalled shock avoidance schedule, there occurred a reliable decrease in the rate of avoidance responding. Although in their experiment, more suppression was observed during the backward CS, the response rate immediately following CS termination and the gradual recovery of responding to pre-CS rates were similar for the cessation and backward conditioning groups. In a second experiment, these investigators showed that the necessary condition for establishing such inhibition to a backward CS is not that the CS be contiguous with shock termination but rather that the CS precede a shock-free period of time and so may be considered a "safety signal" when the UCS is an aversive event. Thus, this experiment is a convincing demonstration that backward conditioning procedures do not result in the formation of a backward association; rather a CS so trained may become associated with the succeeding shock-free period. This result raises the possibility that the backward conditioning procedure with one UCS may, in fact, be a forward conditioning procedure with another, usually unspecified, event (e.g., a shock-free period) and thus yield excitatory responding appropriate to the latter. This would be less likely to occur in cessation conditioning procedures, when the CS and UCS terminate at the same time, since the CS does not uniquely signal the subsequent UCS-free period. In fact, Heth (1976) found no evidence that the cessation conditioning procedure establishes the CS as a conditioned inhibitor using the summation test for inhibition (Rescorla, 1969a).

In summary, there is now considerable evidence that simultaneous, embedded, cessation and backward, as well as forward, conditioning procedures can make the CS effective in producing some reliable change in behaviour, thus confirming the importance of the temporal contiguity of the CS and UCS in classical conditioning. But the very fact that these procedures do not produce the same behavioural outcomes means that temporal contiguity alone does not provide an adequate account of classically conditioned responding. A signalling role for the CS is implicated when the CS is paired with the UCS in either a forward or backward manner; excitatory conditioning to the CS is strongest when the CS is temporally prior to the UCS, whereas inhibitory conditioning may require that the CS precede a UCS-free period. Thus the differences in the form of the conditioned responding established using forward and backward conditioning procedures may be explicable in terms of differences in the nature of the signalled event. Whether the CS also serves as a signal in simultaneous, embedded and cessation conditioning procedures remains to be investigated.

Informational Variables in Conditioning

The signalling interpretation of the differential responding observed in forward and backward conditioning procedures has encouraged the more general view that conditioning depends upon the information that the CS gives about the occurrence and nonoccurrence of the UCS. This possibility has been evaluated by examining the effects of the CS-UCS contingency on the form and strength of conditioned responding.

CS-UCS Correlation

In traditional views of classical conditioning, the number of co-occurrences, or pairings, of the CS and UCS was considered to be the primary determinant of the strength of association. But when the CS and UCS are always presented contiguously, the effects of pairing the CS with the UCS are confounded with the effects of arranging a positive contingency (or correlation) between the CS and UCS. If conditioning is, in fact, a function of the CS-UCS correlation (that is, of the conditional probability of UCS occurrence given the CS), then procedures which degrade this correlation (e.g., the unpaired presentation of CSs or UCSs or both) should attenuate the strength of the classically conditioned association, even when the CS and UCS frequently co-occur.

The first experiment to assess directly the relative importance of pairing and contingency in classical conditioning was conducted by Rescorla (1966). Three conditioning treatments, characterized by different CS-UCS relations, were administered to independent groups of dogs. For one group, the CS and UCS were positively correlated so that a tone CS was always followed by a shock within 30 seconds. In the uncorrelated treatment, the number and temporal arrangement of the CS-UCS co-occurrences were the same as in the positive correlation but in addition, unpaired CSs and UCSs were presented at random times during the intertrial interval so that overall, the CS had no consistent relation with the UCS. Finally the dogs in the negatively correlated, or explicitly unpaired, treatment were given the same sequence of unpaired CSs and UCSs as subjects in the uncorrelated condition but for this third group, all CS-UCS pairings were omitted. Following training, the CS was presented while the animals were responding on a free-operant unsignalled shock avoidance schedule and changes in response rate during and immediately following CS presentation were noted. The CS that had always been followed by shock accelerated the avoidance response rate, whereas the CS that had never been paired with shock had an inhibitory effect and depressed responding below baseline levels. Most interestingly, the uncorrelated CS had _no_ measurable effect on responding, despite the same number of pairings with the UCS as in the positively correlated treatment condition: the differential responding to the CS shown by these two groups strongly supports the contention that it is the positive contingency between the CS and UCS, and not temporal contiguity alone, that determines the strength of conditioned excitatory responding. Moreover inhibitory conditioning appears to require that the CS reliably precede a period of time in which UCS presentation is improbable. As such, backward conditioning procedures may be viewed as a special case of a negative correlation between the CS and UCS.

In a subsequent study with rat subjects, Rescorla (1968) showed that the degree of conditioned suppression to a CS paired with shock increased as a function of the _relative_ probability of UCS occurrence during or immediately succeeding the CS; that is, given a fixed probability of reinforcement on CS trials, the conditioning of fear to the CS decreased as the number of unsignalled shocks during the intertrial interval increased. In the limiting case where the occurrence of shock was equiprobable in the presence and absence of the CS (i.e., there was no correlation between the CS and UCS), no suppression of bar-pressing during the CS was observed, regardless of overall shock density. Thus the occurrence of excitatory conditioning seems to require that the likelihood of UCS presentation be greater during and immediately after the CS than at any other time during the experimental session; and the strength of conditioned responding depends upon the difference in the probability of UCS occurrence when the CS is, and is not, present.

The establishment of conditioned inhibition has been found to be directly related to the probability of UCS occurrence in the absence of the CS (Rescorla, 1969b). When the CS is presented in an experimental situation so that shock UCSs never occur within two minutes of CS termination, the strength of conditioned inhibition, as assessed by both the retardation of excitation and the summation tests (Rescorla, 1969a), is a function of shock density during the intertrial interval.

These results demonstrate that, at least in certain situations, organisms are sensitive to contingencies between events in their environment and that conditioned responding to a CS varies systematically as the correlation between the stimulus and some UCS varies. Excitatory responding to the CS is observed when the CS and UCS are positively correlated and inhibitory conditioning occurs when this interevent correlation is negative. Thus both the form and strength of conditioned responding to a

CS can be said to depend upon the information that the CS provides about the occurrence and nonoccurrence of some UCS.

Blocking

Several studies have demonstrated that the ease of conditioning of a given CS with some UCS may depend on the prior conditioning of *other* conditioned stimuli with that UCS. When a compound CS (say *AB*) consisting of two coextensive salient stimuli (e.g., a tone and a light) is reinforced by the presentation of a UCS, both stimuli elicit substantial, though not necessarily comparable, conditioned responding when tested in isolation. However, when training with the compound CS is preceded by reinforced trials with one of the elements (say *A*), then the other element, *B*, fails to elicit conditioned responding when presented alone despite considerable training with the compound CS (Kamin, 1968). This so-called "blocking" of conditioning to the superimposed element is a robust effect and has been widely documented. Though the original study and most subsequent investigations have used a CER procedure with rat subjects, blocking has also been reported using appetitive conditioning procedures such as discrete-trial barpressing for food (Neely & Wagner, 1974) and autoshaped keypecking (Hall, Mackintosh, Goodall & dal Martello, 1977; Leyland & Mackintosh, 1978). Moreover, the blocking of inhibitory conditioning can be obtained using an analogous procedure (Suiter & LoLordo, 1971).

The original interpretation of the blocking phenomenon given by Kamin (1968, 1969a, b) was that the added element fails to gain control over responding because the UCS occurrence is already fully predicted by the pretrained CS; more generally, Kamin argued that conditioning to any stimulus occurs only insofar as it provides information about the occurrence of an unexpected or "surprising" UCS. It follows from this view, that if the UCS used on compound trials is different from that used to condition the initial element, blocking of conditioning to the added element should be attenuated.

The most obvious test of this idea would be to withhold the UCS on compound conditioning trials. This corresponds to the procedure used by Pavlov (1927) to establish conditioned inhibition; the nonreinforced presentation of a neutral CS in compound with a known excitor establishes the added stimulus as a conditioned inhibitor of responding. More subtle, yet equally effective, experimental manipulations which cause the added element to become excitatory include changing the intensity or magnitude of the UCS (Kamin, 1968,1969b; Neely & Wagner, 1974) and increasing the number of UCS presentations on each compound conditioning trial (Kamin, 1969b; Dickinson, Hall & Mackintosh, 1976). In like manner, conditioning to the added element in a CER procedure is obtained when the time of occurrence of an expected shock is delayed or when one of two expected shocks is omitted following the presentation of the compound CS (Dickinson, Hall & Mackintosh, 1976). If responding to the initial element is extinguished prior to, but not after, training with the compound CS (Kamin, 1968) or if the schedules of reinforcement in effect during the conditioning of the element and compound CSs are different, conditioned responding to the added element is observed (Neely & Wagner, 1974;

Hall, Mackintosh, Goodall & dal Martello, 1977). Thus, conditioning to the superimposed element occurs when that stimulus gives new or more reliable information about reinforcement than the pretrained element.

Theoretical Formulations

It is clear that the occurrence and form of conditioned responding to a CS depends upon the present correlation between the CS and UCS, as well as the prior correlation of other stimuli with that UCS. Having made these observations, the problem becomes one of specifying a mechanism by which organisms could learn such correlations. Rescorla and Wagner (1972) and Mackintosh (1975) have provided accounts of these results which preserve the principle of association by temporal contiguity but abandon the assumption of traditional models of conditioning (e.g., Guthrie, 1935; Hull, 1943) that all stimuli acting upon the organism's sensorium independently enter into associations. These newer theories hold that the conditioning of any particular stimulus is jointly determined by the current sensory input and the presently activated, but previously formed, associations. By providing means by which the formation of associations can be selective, both models can successfully accommodate the "informational" variables in classical conditioning described above.

The Rescorla-Wagner Model

Rescorla and Wagner propose that the change in associative strength of any given stimulus is determined by the discrepancy between the maximum level of conditioning which can be supported by the UCS (λ) and the sum of the associative strengths of all stimuli present during the conditioning trial (ΣV_i). Formally, the change in the associative strength of some stimulus A can be expressed as:

$$\Delta V_A = \alpha_A \beta_1 (\lambda_1 - \Sigma V_i)$$

In this equation, α and β are fixed parameters associated with the CS and UCS, respectively; they are meant to convey only that the ease with which an association is formed or strengthened is, in part, determined by the relative salience of the CS and UCS. Increments in the associative strength of any stimulus can occur on reinforced trials since $\lambda > 0$, whereas nonreinforcement, which is equated with $\lambda = 0$, can reduce associative strength under certain circumstances.

An important added assumption of the Rescorla-Wagner model is that background stimuli, which consist of static apparatus cues as well as random stimulus changes which occur during the experimental session that are not under the experimenter's control, are conditionable in precisely the same manner as discrete experimenter-manipulated CSs. In order to quantify the effects of the usually unspecified, and more often unspecifiable, background stimuli, the intertrial interval is divided into consecutive unmarked "trials" having the same duration as the discrete CS. Usually the value of α associated with background stimuli is taken to be less than that of discrete CSs. This assumption is not unreasonable, for determining which stimuli can function as effective conditioned stimuli depends upon the extent to which they can be distinguished from the context.

A standard conditioning session in which a UCS reliably follows each presentation of stimulus A can be said to consist of reinforced CS-plus-background AX+ trials alternating with strings of nonreinforced trials in which only the background stimuli, X, are present. With training, V_A will approximate λ whereas V_X will approach 0 due to the combined effects of reinforcement and nonreinforcement on AX and X trials, respectively. Nonreinforcement of a compound CS can produce conditioned inhibition to one of the elements ("negative" associative strength) if ΣV_i is greater than λ. This condition is satisfied when the CS and UCS are negatively correlated in time; in this case, the UCSs are presented only in the absence of the CS and so the associative strength of the background stimuli will gradually increase; ΔV_A on nonreinforced CS-plus-background trials will thus be proportional to $-\Sigma V_i$, thereby establishing A as a conditioned inhibitor of responding. It should be apparent that for CS-UCS correlations that lie between 1.00 and -1.00, the associative strengths of the CS and the background will be a function of the likelihood of reinforcement on CS-plus-background and background-only trials. Excitatory responding to the CS should be seen whenever the probability of UCS occurrence is greater in the presence, than absence, of the CS; conversely, attenuation of excitatory responding during the CS should be observed when the likelihood of reinforcement is greater in its absence. In the special case when reinforcement is as likely in the presence of the CS as it is in its absence, the CS should be associatively neutral and should have no measurable effect on behaviour.

Several predictions derived from this model concerning the conditions necessary to establish conditioned excitation and inhibition agree well with empirical investigations of how the CS-UCS correlation maps onto behaviour (Rescorla, 1966, 1968, 1969b). Moreover, this model can account for the "blocking" phenomenon by assuming that the associative strength of the pretrained element is close to the theoretical asymptote, λ, when the compound conditioning trials are given. Since $(\lambda-\Sigma V_i)$ will be close to zero, only minimal associative strength can accrue to the added element on the reinforced compound trials. Accordingly, conditioning to the added element would be predicted in all cases where $(\lambda-\Sigma V_i)>0$. This condition is met when the associative strength of the initially trained element is preasymptotic. Alternatively excitatory responding to the added element should be observed when the value of λ is increased by using a more potent UCS and inhibitory conditioning should occur when $\lambda=0$ due to the nonreinforcement of the compound CS. Many of the experimental treatments which attenuate blocking satisfy precisely these conditions.

Three major empirical objections to the Rescorla-Wagner model can be raised. First, the model specifies that the conditions for establishing conditioned inhibition to a CS are symmetrically opposite to those necessary for the establishment of conditioned excitation. However, in contrast to the finding of excitatory conditioning when the correlation between the CS and UCS is positive but less than 1.00, the establishment of conditioned inhibition when a CS-UCS correlation of -1.00 is degraded by the occasional presentation of a CS and UCS in a paired manner has not been demonstrated. Further, experimental manipulations such as the nonreinforcement of a conditioned inhibitor presented alone (Zimmer-Hart & Rescorla, 1974) or in compound with a neutral stimulus (A. Baker, 1974) fail to produce behavioural effects opposite to those observed when the CS is a conditioned excitor. Although these findings pose problems for the model as originally stated, possible modifications have been proposed which successfully accommodate the demonstrated asymmetry of conditioned inhibition and excitation (see Zimmer-Hart & Rescorla, 1974).

Second, the prediction that a CS uncorrelated with reinforcement should be associatively neutral would appear to be inconsistent with reports of excitatory responding to a CS related in this manner to a UCS (e.g., Benedict & Ayres, 1972; Kremer, 1971; Kremer & Kamin, 1971; Quinsey, 1971). However, analysis of the exact sequence of CS and UCS presentations showed that such excitation, though associative, was an artifact of a positive correlation between the CS and UCS early in training, resulting from either a disproportionate number of chance CS-UCS pairings (Benedict & Ayres, 1972; Kremer, 1971) or the failure to condition the background stimuli to asymptote (Ayres, Benedict & Witcher, 1975; Keller, Ayres & Mahoney, 1977; Kremer, 1974).

A more serious threat to the adequacy of the Rescorla-Wagner model is the finding that pre-exposure to the uncorrelated procedure interferes with the subsequent conditioning of that CS. The acquisition of autoshaped keypecking (Gamzu & Williams, 1973; Mackintosh, 1973), conditioned licking (Mackintosh, 1973), conditioned emotional response (A. Baker, 1976; Mackintosh, 1973), and signalled punishment (A. Baker, 1976) is slower following uncorrelated CS and UCS presentations than following pre-exposure to either stimulus alone. Similarly, prior experience with the uncorrelated treatment retards the development of conditioned inhibition to a CS (A. Baker & Mackintosh, 1977). This interference effect could be accounted for within the Rescorla-Wagner model by the "blocking" of conditioning to the CS by the background stimuli if it is assumed that pre-exposure to the uncorrelated procedure makes the context somewhat excitatory. Although there is some empirical support for a mediational role of background stimuli in the interference effect (e.g., Dweck & Wagner, 1970; Tomie, 1976), A. Baker and Mackintosh (1979) have found slower acquisition of suppression to a CS which had previously been presented in an uncorrelated manner with shock, even when conditioning to the background is prevented by signalling all shocks with a second CS. This finding points to the inadequacy of the hypothesis that the interference effect can be fully accounted for by the prior conditioning to the background stimuli.

A final objection is that many of the manipulations that produce conditioning to the added element in the "blocking" procedure would not be expected to increase the value of λ (e.g., changing the time of an expected shock UCS or omitting one of two expected shocks). Even a brief (0.5 sec) reinstatement of the compound CS following UCS termination reliably attenuates the blocking effect (Gray & Appignanesi, 1973). Results such as these are more easily accounted for by the modified selective attention theory proposed by Mackintosh (1975).

Mackintosh's Selective Attention Model

Like traditional theorists, Mackintosh assumes that the increment in associative strength of some stimulus A following a conditioning trial is a function of the current level of conditioning to that stimulus; that is,

$$\Delta V_A = \alpha_A(\lambda - V_A)$$

Although the initial value of α_A is determined by the physical properties of the CS, Mackintosh proposes that this value is modified by the history of reinforcement associated with A. More specifically, it is assumed that when some stimulus A better predicts the outcome of a trial than any or all of the stimuli concurrently present (including contextual cues), collectively denoted as X,α_A will increase, i.e.,

$$\alpha_A \uparrow \text{ if } \quad |\lambda - V_A| < |\lambda - V_X|$$

In the event that A provides less information or no new and better information about the trial outcome, α_A will decrease, i.e.,

$$\alpha_A \downarrow \text{ if } \quad |\lambda - V_A| > |\lambda - V_X|$$

The effects of the CS-UCS correlation on the form and strength of conditioned responding are easily accounted for in terms of the relative informativeness of the discrete CS. The increase in α_A (and consequently, the rate of change in the associative strength of A) will depend upon the extent to which A predicts either the occurrence or nonoccurrence of the UCS better than the contextual cues. Excitatory conditioning is expected when the CS is more informative than background stimuli about reinforcement whereas inhibitory conditioning occurs when the CS is more informative about nonreinforcement. The analysis of the blocking phenomenon within this framework is also straightforward; if the outcome of of the AB trial is already well predicted by the pretrained element A, α_B will decrease and little conditioning to B will result, despite a considerable number of reinforced presentations. On the other hand, conditioning to element B would be expected in *all* cases when the outcome of the compound trial is in any respect different from the outcome of the trials with the previously trained element. Thus the numerous and seemingly unrelated procedures which attenuate blocking are presumed to do so, according to the attentional model, because each prevents the diminution of α_B following the transition from A to AB trials.

Although this selective attention theory could be compared with the Rescorla-Wagner model on empirical grounds based upon the differential predictions that they make in certain experimental situations, the important point at present is that both versions of the associative process admirably account for most of the data which imply an informational role for the CS in classical conditioning. Both models must thus be considered valid, if not fully complete, explanations of the informational variables in classical conditioning. Although Mackintosh postulates an attentional process that modulates the strength of conditioning to the CS, nevertheless his model, like that of Rescorla and Wagner, asserts that conditioned responding reflects the current associative strength of the CS and moreover, that the conditions which underlie the establishment of associative bonds ultimately involve instances of temporal contiguity between various stimuli in the conditioning situation.

Temporal Variables in Conditioning

Both the experimental results and the theoretical formulations thus far discussed are concerned primarily with the information the CS provides about the probability of UCS occurrence. Estimates of the conditional probability of UCS presentation in the presence and absence of the CS are derived from frequency counts of UCS occurrence in consecutive temporal intervals throughout the experimental session in which the CS may, or may not, be present; as such, conditional probability does not reflect the assumed time base (usually taken to be the duration of the discrete CS). The description of the CS-UCS relation in terms of conditional probability is convenient in that it allows for the comparison of results from experiments involving disparate response systems with markedly different temporal parameters. Such an analysis, however, would tend to obscure the potentially important effects of time base within, as well as between, response systems.

Absolute and Relative Time of UCS Presentation Following the CS

For most response systems, an inverted U-shaped function best describes the relation between the absolute time from CS onset to UCS presentation (i.e., the CS-UCS interval) in forward conditioning procedures and the strength of excitatory conditioning. Comparable results have been found for the development of conditioned inhibition. Weisman and Litner (1971) exposed rats to two, initially neutral, stimuli which were explicitly unpaired with shock-reinforced presentations of a third CS; all stimuli were subsequently presented while the subjects were responding on an unsignalled shock avoidance schedule. The extent to which the stimuli negatively correlated with shock decreased responding was a function of the duration of the ITI following CS- trials during the conditioning phase.

Even when the CS-UCS interval is constant, the development of conditioned responding may vary according to the relative time of UCS occurrence following presentation of the CS. For example, faster acquisition of autoshaped keypecking to a light CS of fixed duration is observed as the duration of the ITI is lengthened (Perkins, Beavers, Hancock, Hemmendinger, Hemmendinger, & Ricci, 1975; Terrace, Gibbon, Farrell, & Baldock, 1975). Moreover, the rate of acquisition has been found to be proportional to the ratio of the durations of the CS and ITI when both are varied in a factorial design (Gibbon, Baldock, Locurto, Gold & Terrace, 1977).

Bindra (1976) has provided a means by which both the temporal and probabilistic aspects of the CS-UCS relation can be expressed within a single term referred to as the predicted imminence of the UCS following the presentation of the CS. This value is calculated by comparing the average time interval between the onsets of the CS and UCS with the average time between UCS presentations. When the estimated time of UCS presentation given by CS occurrence is less than the average interreinforcer interval (IRI), excitatory conditioned responding should be observed. Conversely, the CS should attenuate responding when the average CS-UCS interval exceeds the average IRI. Of particular interest is the implication that when the UCS reliably follows the CS by a fixed amount of time, the predicted imminence of the UCS is inversely related to the length of the ITI. This feature is consistent with the observed interaction between trial and intertrial durations in the acquisition of autoshaped keypecking. On the other hand, when the value of predicted imminence is fixed, the probabilistic and temporal aspects of the CS-UCS relation are reciprocally related. Whether this tradeoff is also reflected in conditioned responding remains an empirical question.

Several other aspects of temporal relations between stimuli in conditioning situations have also received some attention. Rescorla (1972) has distinguished two aspects of the temporal relation between the CS and UCS within the conditioning trial that might reasonably be expected to influence conditioning: absolute and relative temporal priority of the CS.

Absolute Temporal Priority of the CS

Unquestionably the strongest excitatory conditioning is seen when the CS precedes the UCS. However, as summarized earlier, the temporal priority of the CS is not a necessary condition for establishing responding to a CS, for simultaneous and cessation conditioning procedures have been shown to support reliable, albeit weaker, conditioned responding. These results, in conjunction with the evidence that backward conditioning procedures may endow the CS with inhibitory properties, suggest that the absolute temporal relation between the contiguous CS and UCS may determine the nature and strength of conditioned responding, but not the presence or absence of conditioning. In agreement with the tentative conclusions of Heth and Rescorla (1973), it is suggested that "variations in the US-CS delay can be interpreted as continuous manipulations of some underlying variable sufficient for conditioning." (p. 441).

Relative Temporal Priority of the CS

Of immediate concern to the present thesis is the possibility that when more than one CS is present in the conditioning situation, the *relative* temporal proximity to the UCS may determine the strength of conditioning to the individual stimuli. In principle, serial conditioning procedures, in which two or more discrete stimuli are presented sequentially, provide an opportunity to assess such effects. However, even a cursory examination of the relevant experimental literature reveals a number of methodological considerations which prevent any straightforward evaluation of the effects of relative temporal proximity to the UCS on conditioning to the individual components of a serial CS.

The temporal arrangement of the components. T. Baker (1968) has noted that the components of a serial CS might themselves be related temporally in one of two ways. When the termination of the temporally prior component coincides with the onset of the succeeding stimulus, the components of the serial CS may be described as *nonoverlapping* in time. This is to be contrasted with the partially *overlapping* arrangement in which the temporally prior stimuli continue as the later components are presented and all stimuli terminate together. The use of both arrangements in serial conditioning procedures has been indiscriminate, yet the functional equivalence of these stimulus configurations with respect to the temporal proximity of the components to the UCS remains to be established. In the nonoverlapping procedure, it is clear that the last component is most proximal to the UCS. However, when the components are partially overlapping and terminate together, no one component can be said to be closest to the time of UCS presentation.

At least part of the ambiguity concerning the relative effectiveness of the components of a serial CS to serve as secondary reinforcers may be explained by appealing to this procedural difference. In the original test of the information hypothesis of conditioned reinforcement (Egger & Miller, 1962), rats were pretrained with a partially overlapping two-component serial CS paired with food. In a subsequent test, response-produced presentations of the temporally prior component increased resistance to extinction of barpressing more than response-produced presentations of the second component of the CS. Analogous results have been reported by Seligman (1966) using a test of conditioned punishment following serial conditioning with a shock UCS. However, using similar parameters, Ayres (1966) found comparable suppression to both components when they were presented individually on a baseline of barpressing for food. On the other hand, a different pattern of results is obtained when the components of a serial CS are arranged in a nonoverlapping manner. The last component of a serial CS has been found to be the more effective secondary reinforcer following both aversive (Scheuer & Keeter, 1969) and appetitive (Thomas, Berman, Serednesky & Lyons, 1968) conditioning procedures.

A direct comparison of the conditioned reinforcing strength of component stimuli following appetitive conditioning with either a nonoverlapping or partially overlapping serial CS was made by T. Baker (1972). As would be expected from comparison of the results across experiments, the last component of a nonoverlapping serial CS and the first component of an overlapping serial CS were found to be relatively more effective secondary reinforcers of barpressing following a brief amount of conditioning. These results were generally replicated in a recent study conducted in this laboratory using a slightly different testing procedure (Pasquali, 1978). Both experiments show that, at least under certain circumstances, overlapping and nonoverlapping stimulus presentations are not functionally equivalent even when the time between the onsets of successive components and the UCS presentation is equated in the two procedures.

Amount of training. A second important consideration is the amount of training given with the compound serial CS. As Rescorla (1972, 1973) has pointed out, the temporally prior stimuli might benefit from higher-order conditioning once first-order conditioning to the stimulus most proximal to the UCS has been established. Evidence for such "spread of effect" was obtained in the studies conducted by T. Baker (1972), Pasquali (1978) and Thomas et al., (1968). Presumably a prerequisite for this effect is that the components of the serial CS be differentiated by the subject at the outset of training. Indeed Dubin and Levis (1973) found that when a serial CS consisting of two auditory stimuli that differed only in frequency was paired with shock, the degree of conditioned suppression to the initial component was positively related to the similarity of the two tones.

Alternatively, in the absence of component differentiation, comparable responding to all components would be expected early in training, with a reduction in responding to the temporally prior components as training continues (perhaps through the development of inhibition of delay). This possibility is supported by the finding that uniform suppression to both components of a serial CS paired with shock in a CER procedure was followed by a gradual loss of suppression to the initial stimulus with training (Brahlek, 1968; Scheuer & Keeter, 1969). Cautious interpretation of the data is particularly warranted when tests of secondary reinforcement are used since an interaction between temporal proximity to the UCS and length of training is difficult to detect when conditioning to the components is assessed offbaseline. Moreover, T. Baker (1972) found that length of training may also interact with the number of test sessions.

Confounding of relative temporal priority with the CS-UCS interval. Lastly, and most importantly, is the confounding of relative temporal priority with the absolute time between the onset of the component and the UCS presentation (Rescorla, 1972). It may be that conditioning to any one component of a serial CS depends upon the extent to which the absolute time from the onset of that component to UCS presentation deviates from the optimal CS-UCS interval. The contribution of the absolute time to UCS presentation to the conditioning of the individual components can be assessed if for each component-UCS interval, a control group is trained with a delay conditioning procedure.

Conditioning to the components of a serial CS. There is ample empirical support that conditioning to the components of a serial CS cannot be considered independently and without regard to the total duration of the conditioning trial. For example, Kehoe, Gibbs, Garcia, and Gormezano (1979) found that when both components of a serial CS were of fixed duration and separated by an empty interval of either 0, 500, 1000 or 2000 msec, the percentage of eyeblink response to the first and second components was inversely related, with greater responding to the second component as the time from the onset of the first component to UCS presentation increased. These results show that responding to the component most proximal to the UCS is not necessarily independent of the preceding stimuli. Moreover, in a second study, conditioning to the temporally prior component of the serial CS was greater than conditioning to a trace CS having the same temporal relation to the UCS. Similar findings have been reported by Wickens, Nield, Tuber and Wickens (1973). They trained cats with a partially overlapping serial CS that terminated with the administration of shock to the forepaw. For all subjects, the duration of the second component was constant but the duration of the temporally prior stimulus was varied between groups. Both the latency to paw flexion and GSR to the components presented individually on test trials were found to be U-shaped functions of the total CS duration but within each group, responding to the components was reciprocally related.

Conditioning to serial versus nonserial CSs. An alternative approach to the study of serial conditioning procedures is to consider the serial CS as a unit and assess conditioning to this complex stimulus, rather than to the individual components. When a serial CS is compared to a simple delay CS of the same duration, better temporal control (i.e., increased responding as the time of UCS presentation nears) is seen in autoshaped keypecking (Newlin & LoLordo, 1976; Ricci, 1973), conditioned salivation (Williams, 1965), conditioned suppression (Brahlek, 1968) and conditioning of the nictitating membrane response (Kehoe et al., 1979). Similarly latency to respond in a signalled avoidance task is greater when a serial CS is used; in this case, the avoidance response is usually made immediately following the onset of the last component (Levis, 1970; Levis & Dubin, 1973; Levis & Stampfl, 1972). And finally, the acquisition of the conditioned eyeblink response (in terms of the percentage of trials with a CR) is strictly a function of the duration of the last component, although the latency to initiate the response, but not the time of the peak response, is affected by the total CS duration (Frey, Englander & Roman, 1971). Thus when the time of UCS presentation is better indicated by events that occur within the CS (such as the onsets of successive components) rather than CS onset, the maximum rate of conditioned responding is likely to be delayed until a time which more closely approximates the time of UCS presentation.

Anticipatory Conditioned Responding and Temporal Uncertainty

These findings are consistent with Sheffield's (1966) proposal that the development and maintenance of conditioned responding to a CS is facilitated in situations where the animal is uncertain about the exact time of UCS presentations. Two observations initially made by Pavlov (1927) and subsequently replicated by Sheffield were crucial to this proposal.

Pavlov and Sheffield observed that with extended training, the magnitude of the salivary response to a CS paired with food in a forward manner decreased as the latency to respond upon CS onset increased until salivation in advance of UCS presentations disappeared entirely. Moreover, when an expected food presentation was now omitted, salivation was observed at the time food would normally have been delivered. Thus, "...conditioned salivation is present (italics in the original) ...but it is no longer anticipatory." (Sheffield, 1966, p. 119). Anticipatory responding could be re-established and maintained if the interval between CS onset and UCS presentation was periodically lengthened, thereby making the time of UCS presentation unpredictable from trial to trial. This observation suggests that conditioned responding in advance of UCS presentation is a function of the animal's uncertainty about the exact time of UCS occurrence; initial CS-UCS pairings may establish the CS as an accurate indicator of whether a UCS is likely to be delivered soon. With extended training, however, the subject is better able to predict exactly when UCS presentations will occur following CS onset; consequently the appearance of conditioned responding comes to approximate the time of UCS presentation.

If uncertainty about the time of UCS presentation is critical for the development of anticipatory conditioned responding, then conditioning procedures which minimize or eliminate this uncertainty should prevent or reduce responding to a CS in advance of UCS presentations. This can be accomplished by providing a salient event to mark the precise time of UCS presentation. And indeed when the CS terminates with the onset of UCS presentation so that the CS and UCS are never concurrently present (the nonoverlapping procedure), the strength of anticipatory conditioned responding is less than that observed in the overlapping procedure when the CS continues through the UCS presentation (Pavlov, 1927; Sheffield, 1966; Williams, 1965). In both procedures, CS onset signals the imminence of UCS occurrence and therefore may be considered to be more informative than background or intertrial temporal cues which may also signal UCS presentations. However, in the nonoverlapping procedure, CS termination which is synchronous with the onset of UCS presentation may be said to further reduce the animal's uncertainty because the time of UCS presentation can now be precisely predicted. Thus the weaker anticipatory responding is understandable when the CS precedes UCS delivery but does not overlap with it.

General Statement of the Problem

This thesis investigates the informational role of a stimulus which is synchronous with the onset of UCS presentations. In particular, the hypothesis that anticipatory conditioned responding occurs only to the extent that the animal is uncertain about the exact time of UCS occurrence following CS onset is examined. The experimental approach to this problem involves an analysis of conditioned responding when the thirsty rat is, or is not, given clear information about the exact time of water deliveries. In the series of experiments to be reported, water deliveries always occurred at a fixed time during conditioning trials in a standard delay conditioning procedure. Differences in conditioned licking during the CS were examined when the time of water presentation was better indicated by a second stimulus which was synchronous with water onset.

DESCRIPTION OF THE BASIC FINDINGS

If the development of anticipatory conditioned responding is promoted by temporal uncertainty, then conditioning procedures in which the onset of UCS presentation is precisely indicated should reduce or prevent anticipatory responding. Less conditioned responding to a CS which precedes, but does not overlap with, the UCS would thus be expected because in this case the time of UCS presentation is marked by the termination of the CS. An alternative explanation for this finding, however, is that the associative bond critical for the elicitation of conditioned responding is weak because the to-be-associated events are never concurrently present; when the CS and UCS are nonoverlapping, the CS is never present during the presentation of the UCS and it may be that this temporal relation between the CS and UCS is less than optimal for the establishment of the critical association. It follows then that the lower rate of anticipatory conditioned responding should be considered a direct consequence of the weaker associative strength of the CS rather than a function of the informational value of CS termination.

If stronger associative bonds are established when the CS and UCS overlap in time, then reinstatement of the CS, after a brief delay following its termination with UCS delivery, should increase responding to that CS. In this case the CS and UCS overlap, but the time of UCS presentation is also precisely indicated by the discontinuity in the CS. If anticipatory responding occurs only to the extent that the animal is uncertain about the exact time of UCS presentation, then this procedure, like the nonoverlapping procedure, should produce little conditioned responding to the CS. On the other hand, if the concurrent presence of the CS and UCS is essential for the appearance of strong conditioned responding, then this manipulation should restore responding to the CS.

Experiment 1

The purpose of Experiment 1 is to establish whether the difference between the nonoverlapping and overlapping conditioning procedures is attributable to the subject's greater certainty about the time of UCS occurrence following CS onset in the nonoverlapping procedure. This possibility was examined using a conditioned licking procedure with rat subjects. CS presentations were paired with water deliveries and anticipatory licking at the water spout during CS presentations in advance of water delivery was recorded and compared to an estimate of the baseline rate of licking in the absence of the CS. A measure of approach to the water spout upon CS onset was also obtained. This was done for two reasons: (1) several investigators (e.g., Pavlov, 1932; Sheffield, 1966; Zener, 1937) have reported that motor responses such as orientation towards the food magazine during CS presentations can occur independently of anticipatory conditioned salivation, and (2) approach behaviour can be used as a second measure of the subjects' use of the CS as a signal for the upcoming water delivery.

Method

Subjects. Twenty-four experimentally naive male Sprague-Dawley rats, initially weighing 275-300 g, served as subjects. The subjects were housed individually with Purina Lab Chow available ad lib. Prior to the onset of experimentation, all subjects were adapted to a water deprivation schedule that allowed 45 min of unrestricted access to water daily. This deprivation schedule remained in effect for the duration of the experiment with water being available immediately following each experimental session.

Apparatus. The experiment was conducted in two identical conditioning chambers measuring 32 x 30 x 36 cm (inside dimensions) located in a sound- and light-attenuating cubicle. The front wall of the test chamber was glass; the remaining walls were constructed of wood. The floor was made of 1.3 cm^2 wire grid. In a recessed alcove measuring 7.5 x 6.5 cm centered in the right wall, a brass drinking spout measuring 0.5 cm in outer diameter, was mounted 7 cm above floor level. The drinking spout protruded 0.75 cm into the alcove and was connected to a drinkometer circuit. Time spent in the area of the drinking spout was measured using a photocell circuit located 3 cm into the alcove, 4.5 cm above floor level. Water was delivered at a rate of 15 drops per min by a solenoid valve enclosed in an adjacent sound-attenuating chamber. The CS was a 2000-hz tone delivered through a loudspeaker located in the center of the ceiling of each experimental chamber. Ventilation and masking noise were provided by fans attached to the test chambers.

Scheduling and data recording equipment, which included a PDP-11 digital computer, was located in an adjacent room.

Procedure. The subjects were randomly assigned to one of three treatment conditions. For all subjects, tone onset was followed 10 sec later by a water presentation which lasted 10 sec and consisted of 2-3 drops. In the Overlap condition, the tone remained on throughout the water presentation and terminated with the cessation of water delivery. For the remaining two groups, the tone terminated with the onset of water delivery. In the Non-overlap treatment, the CS was never present during the water presentation. For the Gap group, the CS terminated upon water delivery but was reinstated following a 0.5-sec delay and remained on throughout the remainder of water delivery. These three procedures are diagrammed in Figure 1.

Daily experimental sessions lasted 25 min and consisted of 10 tone-water trials, occurring at fixed intertrial intervals of 120 sec. The experiment terminated after 12 sessions. The mean number of licks and time spent in the water alcove during the CS and the 10-sec Pre-CS period were recorded daily.

Results

For each subject, a difference score (number of licks during the CS minus number of licks during the Pre-CS period) was calculated in order to assess conditioning to the tone on the four 30-trial (3-session) blocks. Conditioning to the tone, as measured by the number of licks, is illustrated in Figure 2. The asymptotic level of conditioned licking was greatest in the Overlap

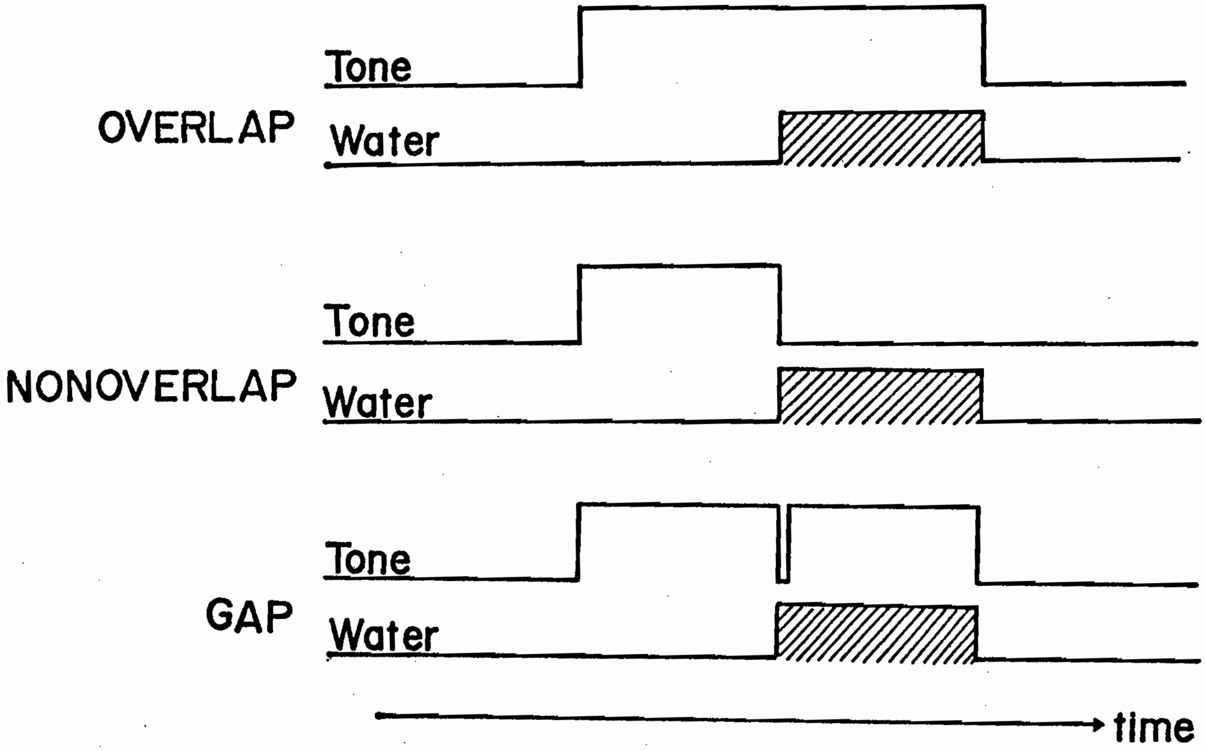

Figure 1. Schematic representation of the Overlap, Nonoverlap and Gap conditioning procedures used in Experiment 1.

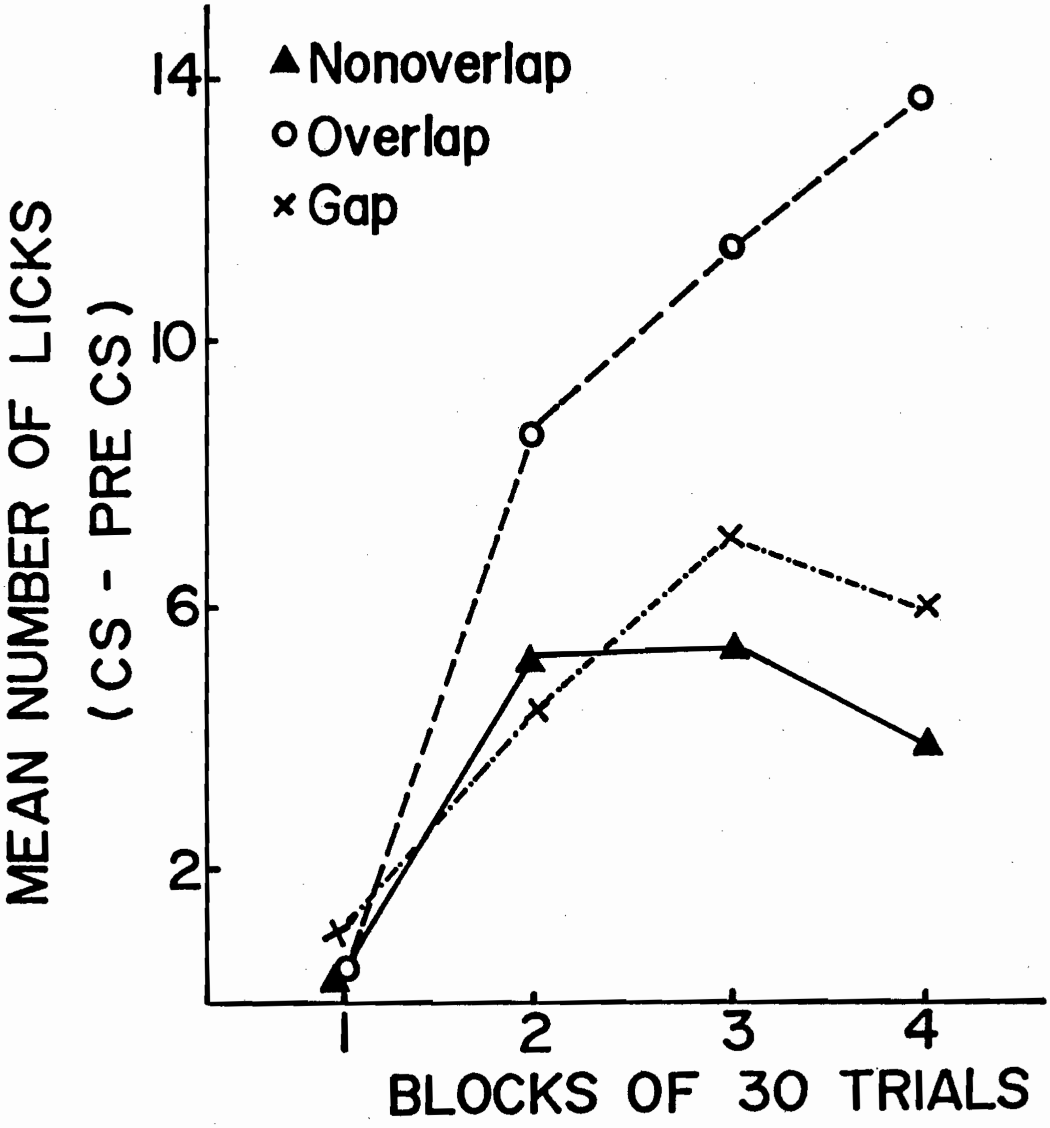

Figure 2. Mean conditioned licking scores of the Nonoverlap, Overlap and Gap groups as a function of blocks.

group. A two-way analysis of variance (treatment x block) is presented in Table 1. Conservative degrees of freedom, given in parentheses, were used to test all main effects and interactions involving repeated measures (Winer, 1962). This analysis yielded reliable main effects of treatment, $F(2,21)=7.29$ and block, $F(1,21)=43.75$, as well as a reliable treatment x block interaction, $F(2,21)=6.22$, all p's $< .01$. Tests of simple effects, using a pooled error term and Satterthwaite's approximation of the degrees of freedom (Winer, 1962), were performed to further evaluate this interaction. Although no reliable differences between groups were found on the first block of trials, $F(2,51)=0.06$, $p > .05$, a reliable effect of treatment was found on each of the subsequent blocks [Block 2, $F(2,51)=3.32$, $p < .05$; Block 3, $F(2,51)=6.65$, $p < .01$; Block 4, $F(2,51)=17.40$, $p < .01$]. On Block 2, the largest difference in conditioned licking was between the Overlap and Gap groups; however, this comparison was not statistically reliable using the Newman-Keuls method of multiple comparisons, $Q(3,51)=3.40$, $p > .05$. The results of this analysis for Blocks 3 and 4 are shown in Table 2. On both blocks of trials, the Overlap condition produced stronger anticipatory conditioned licking than either the Nonoverlap or Gap condition (all p's $< .01$) but these latter groups did not differ from each other (both p's $> .05$). These differences in the conditioning scores are not attributable to differences in the baseline rate of licking since analysis of the rate of licking during the Pre-CS period failed to find any statistically reliable effects (see Appendix A).

TABLE 1

A two-way analysis of variance comparing the effects of CS-UCS temporal relation and amount of training on anticipatory conditioned licking

Source of Variation	Sum of Squares	df^a	Mean Square	F
Treatment (T)	421.64	2	210.82	7.29 **
S(T)	607.28	21	28.92	
Block (B)	854.88	3(1)	284.96	43.75 **
TB	243.03	6(2)	40.51	6.22 **
BS(T)	410.39	63(21)	6.51	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

TABLE 2

Newman-Keuls tests comparing differences in conditioned licking on Blocks 3 and 4 by the Nonoverlap (I), Gap (II), and Overlap (III) groups

	Block 3		Block 4	
	II	III	II	III
I	1.39	5.00**	2.07	8.03**
II		3.61*		5.96**

* $p < .05$

** $p < .01$

$df_{error} = 51$

The probability that at least one lick occurred during the 10-sec CS presentation was also examined because it appeared that the Nonoverlap treatment had reduced the likelihood of contacting the water spout during the CS. However, a two-way analysis of variance (treatment x block) failed to confirm either a reliable main effect of treatment, $\underline{F}(2,21)=2.71$, or a reliable treatment x block interaction, $\underline{F}(2,21)=1.23$, both $\underline{p}$'s $> .05$. Thus the differences in the asymptotic rate of conditioned licking cannot be attributed to differences in the overall probability of licking during the CS since the groups did not differ on this measure. This analysis did yield a statistically reliable effect of block, $\underline{F}(1,21)=56.53$, $\underline{p} < .01$, $\underline{MS}_{error}=.0185$. The percentage of trials in which at least one lick was made was 41.9, 78.3, 82.5 and 86.0% for Blocks 1-4, respectively. Newman-Keuls tests indicated that subjects were more likely to contact the spout during the tone on Blocks 2, 3 and 4 than on the first block of trials (all $\underline{p}$'s $< .01$); no other differences were statistically reliable (see Appendix B).

It is possible that the obtained differences in conditioned licking are consequences of different latencies to approach the water spout upon tone onset. Latency to approach upon CS onset was not directly measured in this experiment; however, if the treatments resulted in different approach latencies then the absolute amount of time spent in the alcove during CS presentations would be expected to differ between groups. The mean number of seconds in the alcove during the tone are plotted as a function of blocks in Figure 3. Table 3 presents the results of a two-way

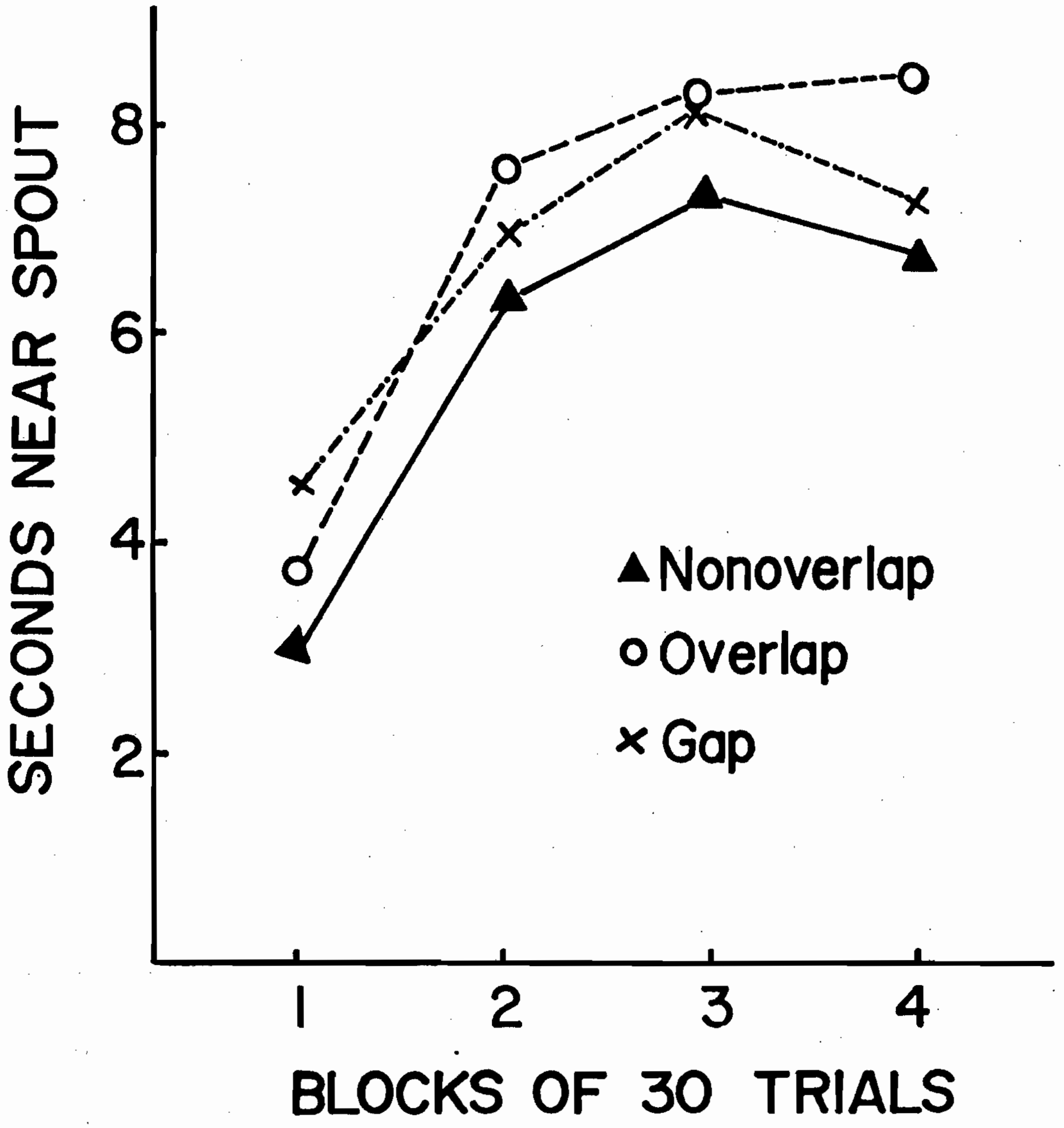

Figure 3. Time spent in the water alcove during CS presentations.

TABLE 3

Two-way analysis of variance (treatment x block) on the time spent in the water alcove during CS presentations

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	20.28	2	10.14	6.32 **
S(T)	33.69	21	1.60	
Block (B)	250.73	3(1)	83.58	101.44 **
TB	8.56	6(2)	1.43	1.73
BS(T)	51.91	63(21)	0.82	

** $\underline{p} < .01$

[a] conservative degrees of freedom are given in parentheses

analysis of variance (treatment x block) performed on these data; statistically reliable main effects of treatment, $\underline{F}(2,21)=6.32$ and block, $\underline{F}(1,21)=101.44$, were obtained, both $\underline{p}$'s $< .01$. The means for the Nonoverlap, Overlap, and Gap groups were 5.80, 6.86 and 6.66 sec, respectively. As indicated by Newman-Keuls tests, the subjects in the Nonoverlap group spent less time in the water alcove than did subjects in the Gap group, $\underline{Q}(2,21)=3.84$, $\underline{p} < .05$, or the Overlap group, $\underline{Q}(3,21)=4.73$, $\underline{p} < .01$. However, these latter groups did not differ from each other, $\underline{Q}(2,21)=0.89$, $\underline{p} > .05$, indicating that differential rates of conditioned licking are not fully accounted for by differences in the time spent near the spout. It is likely that the lower time score of the Nonoverlap group is attributable to a longer latency to approach the water spout upon tone onset rather than to any overall difference in baseline behaviour, for the time spent in the vicinity of the water spout during the Pre-CS period did not differ between groups ($\underline{p} > .05$). Analysis of this estimate of baseline responding is presented in Appendix C. For all groups, however, the time spent in the water alcove during CS presentations increased with training. A comparison of the mean time scores for each block of trials, using Newman-Keuls tests, is presented in Table 4. This analysis indicates that the time spent in the alcove increased up to Block 3 when subjects spent approximately 7.5 sec (of the possible 10 sec from CS onset to water delivery) in the alcove.

Discussion

The results of this experiment lend support to Sheffield's suggestion that the development of anticipatory conditioned responses

TABLE 4

Newman-Keuls tests comparing the time spent in the water alcove during CS presentations on successive blocks of trials (I: Block 1; II: Block 2; III: Block 4; IV: Block 3)

	II	III	IV
I	18.21 **	20.17 **	21.50 **
II		1.96	3.28 *
III			1.33

* $\underline{p} < .05$

** $\underline{p} < .01$

$df_{error} = 63$

is promoted when the animal is not certain about the exact time of UCS presentation; when the termination of the CS is synchronous with the onset of water delivery, anticipatory conditioned licking was dramatically reduced. Moreover, it was shown that reinstatement of the CS during UCS presentations does not result in recovery of the licking response. The finding that the Nonoverlap and Gap groups differ in the time spent in the water alcove, but not in anticipatory licking, during the CS suggests that differences in <u>approach</u> latencies cannot fully explain the depressed rate of conditioned licking seen in both groups. The possibility that the differences in anticipatory conditioned licking arise from different latencies to <u>lick</u> the water spout upon CS onset remains to be investigated.

The overlapping of the CS and UCS in time does not guarantee the appearance of strong anticipatory conditioned licking. Rather the development and maintenance of such responding may, to a great extent, depend upon the animal's uncertainty about the exact time of UCS presentations. As Sheffield proposed, it appears that the strength of anticipatory conditioned responding is maximized in procedures which make the time of UCS arrival ambiguous. In the present experimental situation, when CS termination provides information about when water will be available following CS onset (as in the Nonoverlap and Gap treatments), the vigor of conditioned responding to that CS is reduced. This may be because the appearance of conditioned responding is delayed until it more closely approximates the time at which a UCS presentation will occur.

In all treatment conditions of this experiment, tone onset always indicated that a water presentation would begin in 10 sec. The finding that anticipatory licking is markedly reduced when the termination of the tone provides information about the time of UCS arrival may necessitate a more precise specification of the stimuli which control an animal's behaviour. Typically in classical conditioning experiments, only the presence and absence of the CS are recognized as major determinants of conditioned responding and thus the strength of conditioning is assessed by comparing the changes in responding during the CS with baseline responding in the absence of the CS. Although this approach has yielded many important and interesting results, it probably represents an overly simplistic view of which stimuli come to be important in the control of behaviour. It has already been suggested that the onset, termination and duration of conditioned stimuli should be distinguished (Bindra, 1976; Rescorla, 1973). The data from the present experiment show that, under certain conditions, CS termination can serve as an effective signal.

Experiment 2

This experiment was conducted in order to reconfirm, using a different experimental procedure, the finding of Experiment 1 that a stimulus synchronous with UCS onset can greatly reduce anticipatory conditioned responding. In this experiment, during conditioning trials with a tone, a light was presented so that it was synchronous with the onset of water presentation. This procedure was analogous to the Gap treatment of the previous experiment except that the onset of water delivery was now marked by a

0.5-sec light flash instead of a gap in the tone of that duration. It was expected that this procedure would provide another condition in which subjects could make use of an event (namely the light flash) which is a better discriminative stimulus for the time of water presentations than tone onset; learning about the light would be reflected in reduced responding to the tone as compared to the responding of control subjects.

The reversibility of this effect was also examined. Once responding of both the experimental and control groups had stabilized, the treatments were reversed. It was expected that subjects initially trained with the Tone-Light procedure would begin to show increased responding to the tone when the light is omitted because the animals would now have to use tone onset as the discriminative stimulus for the time of UCS presentations. Conversely, when given the opportunity to learn about the more informative light, the control subjects should begin to show less anticipatory conditioned licking to the tone because the onset of water presentation would now be marked by the concomitant light flash.

Method

Subjects. Twenty-four experimentally naive male Sprague-Dawley rats, initially weighing 275-300 g, served as subjects. The rats were housed in pairs with standard lab chow available ad lib. All subjects were adapted to and maintained on a water deprivation schedule identical to the one described in Experiment 1.

Apparatus. The apparatus used in this experiment was different from that used in Experiment 1 and consisted of four identical conditioning chambers, each enclosed in a sound- and light-attenuating shell. The test chambers measured 20.5 x 20.5 x 30.5 cm (inner dimensions) and were constructed of 0.75 cm thick Plexiglas. The front wall of each chamber was transparent, the remaining three walls were black and the ceiling was opaque. The grid floor consisted of steel bars, 0.3 cm in diameter, spaced 1.0 cm apart. The drinking spout was constructed by inserting a brass tube, measuring 0.5 mm in outer diameter, in a 1.0 x 1.1 x 0.7 cm piece of black Plexiglas. The spout was centered in the right wall of each chamber, 3.2 cm above floor level, and was connected to a drinkometer circuit. Water was delivered by a Cole-Parmer variable speed hydraulic pump located outside the sound-attenuating chambers. A loudspeaker was centered 9.5 cm above the water spout on the right wall of each experimental chamber. A 25-watt, 120-volt picture light bulb, 11.5 cm in length, was mounted 0.75 cm above the ceiling of each test chamber, 1.75 cm from the right wall. Ventilation and masking noise were provided by fans attached to each outer shell. Scheduling and recording equipment was located in an adjacent room.

Procedure. The subjects were assigned to one of two treatment conditions. Conditioning sessions began on the day after a 30-min habituation session which consisted of ten 20-sec water presentations. All subjects then received 10 conditioning trials at intervals averaging 3 min (range: 2-4 min) daily. The experimental and control groups received training with a tone CS having the same temporal relation with UCS presentations. For both groups, onset of a 30-sec tone was followed 10 sec later by a water delivery which lasted 20 sec. For the experimental group (Tone-Light), a 0.5-sec light was presented simultaneously with the onset of water delivery. Following 12 conditioning sessions, the treatments were reversed; the experimental group received 6 additional sessions of conditioning to the tone with the onset of water presentations no longer signalled by the light. The control animals were now trained with the Tone-Light compound CS for 6 sessions.

Throughout the two phases of the experiment, the probability of licking and the number of licks were recorded during the CS and Pre-CS period. In addition, the temporal course of anticipatory licking was examined by recording the number of licks which occurred in the 10 consecutive 1-sec bins of the 10-sec CS. Finally the latency of the first lick after tone onset was also measured.

Results

Acquisition. The mean difference scores were computed as in the previous experiment for each of 4 consecutive 30-trial (3 session) blocks. The mean conditioned licking scores of the Tone and Tone-Light groups during acquisition are shown on the left side of Figure 4. The compounding of the tone CS with a 0.5-sec light that was synchronous with the onset of water delivery greatly reduced conditioned responding during the tone. The results of a two-way analysis of variance (treatment x block) performed on these data are shown in Table 5. As expected, the difference in the rate of responding shown by subjects in the Tone and Tone-Light

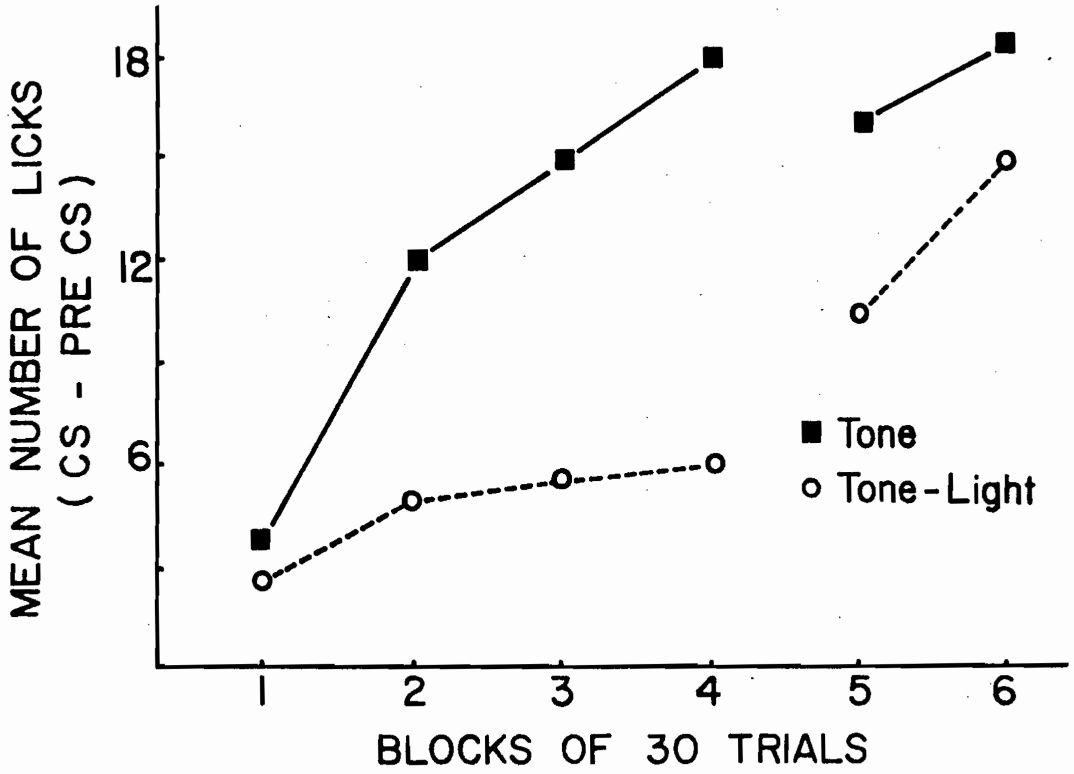

Figure 4. Mean conditioned licking scores of the Tone and Tone-Light groups during the acquisition (Blocks 1-4) and reversal (Blocks 5-6) phases of Experiment 2.

TABLE 5

Two-way analysis of variance comparing the conditioned licking of the Tone and Tone-Light groups as a function of blocks

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	151741.6	1	151741.60	9.81 **
S(T)	340241.6	22	15465.52	
Block (B)	112452.2	3(1)	37484.07	15.92 **
TB	34299.5	3(1)	11433.16	4.86 *
BS(T)	155371.8	66(22)	2354.12	

* $\underline{p} < .05$

** $\underline{p} < .01$

[a] conservative degrees of freedom are given in parentheses

groups was significant, $F(1,22)=9.81$, $p < .01$. In addition, a reliable effect of block, $F(1,22)=15.92$, $p < .01$ and treatment x block, $F(1,22)=4.86$, $p < .05$, was found.

The interaction between treatment and block was further analyzed using tests of simple effects to compare the responding of subjects in the two treatment conditions on each block of trials. Only on the first block of trials was the responding of the Tone-Light group not different from that of control subjects, $F(1,43)=0.47$, $p > .05$. The control animals trained with the tone alone as the CS showed reliably greater anticipatory responding on all subsequent blocks [Block 2, $F(1,43)=6.12$, $p < .05$; Block 3, $F(1,43)=10.06$, $p < .01$; Block 4, $F(1,43)=16.38$, $p < .01$]. These differences are a function of differential response rates during the tone and not differences in the baseline rate of licking; analysis of the responding of the two groups during the Pre-CS period failed to find either a main effect of treatment, $F(1,22)=0.75$, or an interaction between treatment and block, $F(1,22)=0.40$, both p's $> .05$ (see Appendix D). Subsequent analysis of the reliable block effect, $F(1,22)=5.73$, $p < .05$, using Newman-Keuls tests indicated that the baseline rate of licking was greater during the first block of trials than on all subsequent blocks (all p's $< .01$); no other pairwise comparisons were reliable (all p's $> .05$). A summary of these results is presented in Appendix E.

The mean latency to lick upon tone onset on each of the four blocks of trials is shown in Table 6. The pattern of results for this measure was similar to that obtained for response rate. The latency scores of subjects in the Tone and Tone-Light groups were

TABLE 6

Mean latency to lick following CS onset for Blocks 1-4

	Uncorrected Latency		Corrected Latency	
	Tone	Tone-Light	Tone	Tone-Light
Block 1	5.4	6.9	3.4	4.2
Block 2	4.0	6.6**	3.4	5.3**
Block 3	3.7	6.6**	3.3	5.7**
Block 4	3.5	6.6**	3.0	5.8**

**$p < .01$

submitted to a two-way analysis of variance with repeated measures on blocks. As summarized in Table 7, this analysis yielded reliable main effects of treatment condition, $F(1,22)=12.29$, and block, $F(1,22)=9.50$, both p's $< .01$, as well as a reliable interaction, $F(1,22)=4.35$, $p < .05$. Tests of simple effects revealed that on Block 1, the latency to lick following tone onset did not differ between groups, $F(1,29)=3.71$, $p > .05$. However, on Blocks 2-4 subjects trained with the compound CS exhibited longer latencies to lick upon CS onset than did subjects in the Tone group, $F(1,29)=11.08$, 13.66, and 16.09, respectively, all p's $< .01$.

It is important to note that in the calculation of the mean latency, the failure to respond during a trial was entered as a score of 10 sec (i.e., the time from tone onset to water delivery). This would tend to inflate the difference in mean response latencies of the Tone and Tone-Light groups if subjects in the latter group were less likely to lick during the CS. Comparison of the probability of licking during the CS as a function of treatment, using a two-way analysis of variance (treatment x block), confirmed that the subjects in the Tone-Light group were less likely to respond during the CS ($M=0.67$) than were subjects in the Tone group ($M=0.84$), $F(1,22)=4.99$, $p < .05$. But the effect of treatment did not vary with block, $F(1,22)=0.30$, $p > .05$. (The complete analysis of variance table is shown in Appendix F.)

An adjusted latency score, using only those trials in which at least one response was made, was calculated. Analysis of these adjusted latencies, which are shown in Table 6, was consistent with that obtained using the uncorrected latencies. As can be seen

TABLE 7

Two-way analysis of variance on the uncorrected latency to respond upon tone onset by subjects in the Tone and Tone-Light groups

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	153.85	1	153.85	12.29 **
S(T)	275.31	22	12.51	
Block (B)	20.28	3(1)	6.76	9.50 **
TB	9.29	3(1)	3.10	4.35 *
BS(T)	46.97	66(22)	0.71	

* $\underline{p} < .05$

** $\underline{p} < .01$

[a] conservative degrees of freedom are given in parentheses

in Table 8, a reliable interaction between treatment and block was obtained, F(1,22)=6.79, $p < .05$. Tests of simple effects indicated that on Block 1, the latency to lick was not reliably different for the Tone and Tone-Light groups, F(1,36)=2.13, $p > .05$ but the time until the first lick following tone onset was greater in the Tone-Light group on Blocks 2-4, F(1,36)=12.10, 17.12 and 23.98, all p's < .01.

The temporal course of anticipatory conditioned licking shown by subjects in the Tone and Tone-Light groups is strikingly different. Figure 5 illustrates the distribution of licking during the tone on the last block of trials. Anticipatory conditioned licking by subjects trained with the tone begins soon after tone onset; the rate of licking rapidly increases to a high asymptotic level which is maintained for the remainder of the CS. In contrast, licking by the Tone-Light group is seen at a later time during the CS and very slowly increases up to the time of UCS presentation. The percentage of total conditioned responding that occurred during the first 5 sec of the CS was 39.5 and 12.2% for the Tone and Tone-Light groups, respectively; this difference was statistically significant, t(22)=5.46, $p < .01$. Thus not only the degree of conditioned responding, but also the distribution of licking is altered when the onset of water deliveries is precisely signalled.

Reversal. Conditioned licking to the tone following treatment reversal is shown on the right side of Figure 4. The two-way analysis of variance (treatment x block) presented in Table 9 shows that the two groups no longer showed differential rates of conditioned licking during the tone [treatment: F(1,22)=0.85;

TABLE 8

Two-way analysis of variance on the corrected latency to respond upon tone onset of subjects in the Tone and Tone-Light groups

Source of Variation	Sum of Squares	df^a	Mean Square	F
Treatment (T)	94.15	1	94.15	16.06 **
S(T)	129.00	22	5.86	
Block (B)	7.73	3(1)	2.58	4.17
TB	12.58	3(1)	4.19	6.79 *
BS(T)	40.75	66(22)	0.62	

* $p < .05$

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

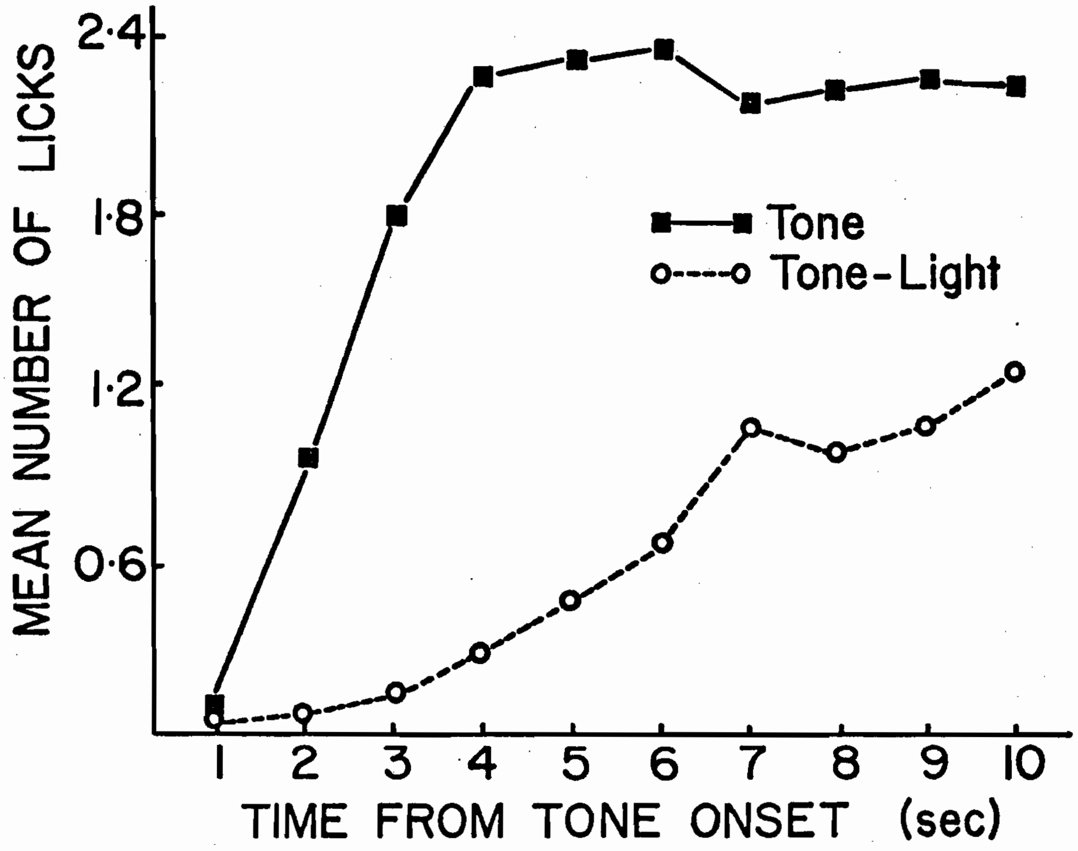

Figure 5. Distribution of conditioned licking, in terms of the number of licks per sec, from tone onset to water presentation.

TABLE 9

Analysis of variance (treatment x block) on the conditioned licking scores during the reversal phase of Experiment 2

Source of Variation	Sum of Squares	df	Mean Square	F
Treatment (T)	18080.80	1	18080.80	0.85
S(T)	470059.00	22	21366.32	
Block (B)	15165.63	1	15165.63	8.14 **
TB	1548.14	1	1548.14	0.83
BS(T)	40973.06	22	1862.41	

** $p < .01$

treatment x block, $F(1,22)=0.83$, both p's $> .05$]. The higher level of conditioned licking on the second block of trials yielded a reliable main effect of block, $F(1,22)=8.14$, $p < .01$.

As predicted the Tone-Light group showed enhanced conditioned responding when the onset of UCS presentation was no longer accompanied by a light flash. The mean increase in responding from Block 4 of acquisition to the first reversal block was 4.80 licks per CS. This difference is reliably greater than zero, $t(11)=3.50$, $p < .01$, and may be accounted for by the small, but reliable, decrease of 0.7 sec in the latency to lick upon CS onset, $t(11)=2.77$, $p < .05$.

On the other hand, subjects initially trained with the tone only did not show a reliable decrease in conditioned responding when the tone was presented in compound with a light synchronous with the onset of UCS presentation, $t(11)=0.78$, $p > .05$, even though the latency to lick upon tone onset reliably increased by 1.0 sec, $t(11)=2.65$, $p < .05$. While the omission of a light which signals UCS onset results in an increase in conditioned responding to the tone, the addition of a light which better indicates the time of UCS presentation than tone onset does not substantially modify previously established conditioned responding to the tone.

Discussion

This experiment corroborates and extends the findings of the previous experiment. Recall that in Experiment 1, decreased anticipatory conditioned responding was obtained when the termination of a CS or a brief gap in an otherwise continuous CS was synchronous with UCS onset. The present experiment shows that this effect is also seen when a second stimulus (a light flash) that is synchronous with UCS presentation is superimposed on a tone CS which precedes and overlaps with the entire water presentation. These findings support the view that an event that is synchronous with the onset of UCS presentation may enable the animal to better estimate or predict the exact time of UCS presentation during conditioning trials.

Moreover, it was found that subjects trained with the tone-light compound showed longer latencies to lick upon tone onset than control subjects. But the reduction in anticipatory conditioned licking is not only a function of response latency. If it were, the temporal course of licking following initial contact with the water spout during the CS would not be different; but in fact when tone onset best indicated the time of UCS presentation, the rate of conditioned licking sharply attained a high asymptotic level shortly after CS onset. In contrast, when there is a signal that is synchronous with UCS onset, not only is the appearance of conditioned licking delayed but the rate of licking increases only gradually as a function of the time remaining until the water delivery. Thus increased latency to contact the spout upon CS onset is insufficient to account for the observed differences in the amount and time course of anticipatory conditioned licking.

Finally, the finding that subjects initially trained with the tone failed to show decreased conditioned responding to it when the light was subsequently introduced is noteworthy. Procedurally and effectively this manipulation resembles experiments on the "blocking" phenomenon. In the present experiment, the prior conditioning of the tone may have prevented learning about the light which would have been evidenced by decreased responding to the tone. It should be noted, however, that the appropriate control group, trained with the compound CS throughout the experiment, is not available for purposes of comparison; nevertheless the present findings encourage future research on "blocking" using the methodology developed in the present experiment.

Discussion of Experiments 1 and 2

The results of these two experiments can be taken as support for Sheffield's hypothesis that the strength of anticipatory conditioned responding is a function of the animal's uncertainty about the exact time of UCS occurrence. It was shown that when the time of water delivery is marked by a salient event, conditioned licking to a preceding CS is severely reduced. The termination of the CS, a discontinuity in an otherwise continuous CS, or the presentation of a second brief stimulus can serve as an informative stimulus when its occurrence is synchronous with the onset of UCS presentation.

Two alternative explanations for the reduction in anticipatory conditioned responding when the onset of the UCS is marked can be given. Experiment 1 was conducted in order to evaluate the possibility that the difference in conditioned responding when the overlapping and nonoverlapping procedures are compared is due to a difference in the strength of the association critical for the elicitation of conditioned licking. Specifically, it was suggested that the lack of concurrence between the CS and UCS in the nonoverlapping procedure results in less associative strength to that CS. The finding that reinstatement of the CS following its termination with UCS onset does not enhance conditioned responding suggests that the lack of concurrence per se is not responsible for the lower conditioning scores when the presentations of the CS and UCS are successive but not overlapping. Nevertheless it is possible that <u>any</u> abrupt stimulus change during a conditioning trial interferes with the formation of the critical association. If this were true, then weak conditioned responding should be observed even when the stimulus change does not provide information about the exact time of UCS occurrence.

A second interpretation, which is not incompatible with the informational account, is suggested by the temporal course of conditioned responding seen when UCS onset is marked by a synchronous stimulus. In this case, responding to the CS increases gradually as the time of UCS presentation nears. This may be because the initial portion of the CS has become inhibitory. The development of inhibition of delay would result in less anticipatory conditioned licking as well as longer latencies to respond upon tone onset, as was observed in Experiment 2.

The adequacy of the interference, inhibition and information hypotheses are evaluated in the following experiments.

THE INTERFERENCE HYPOTHESIS

This section describes two experiments which were conducted to evaluate the adequacy of a simple interference account of the reduced anticipatory conditioned responding observed when procedures which mark the exact time of UCS onset are used. In both experiments, a 0.5 sec light presentation occurred during each tone-water trial, but the time of light presentation varied from trial to trial so that it was not always synchronous with UCS onset. It was reasoned that if light presentations have a general disruptive effect so that the conditions for learning the relation between the tone and water are rendered less than optimal, then subjects in the experimental groups should show weak conditioned responding to the tone regardless of the time of light occurrence. On the other hand, if the reduced anticipatory responding to the tone depends upon the information the light provides about the time of UCS occurrence, no reduction should be observed when the presentation of a light during a conditioning trial does not reliably indicate the time of UCS onset.

Experiment 3

Two of the groups in this experiment were given the same treatment as the Tone and Tone-Light groups of Experiment 2. In addition, a third group of rats received the light at random times during an interval ranging from 3 sec prior to UCS onset to 3 sec following UCS onset. If the information hypothesis is correct, more anticipatory responding should be observed in this Tone-Light Variable group than in the Tone-Light group, for the light in the former group does not accurately indicate the time of UCS onset.

Method

Subjects and apparatus. Thirty-six male Sprague-Dawley rats, initially weighing 275-300 g, were subjects in this experiment. Housing and maintenance conditions were like those described in the previous experiment. The apparatus was the same as used in Experiment 2.

Procedure. Following one habituation session in which 10 unsignalled water deliveries occurred, the subjects were randomly assigned to one of three treatment groups. For all subjects, 10 30-sec tones were presented during each conditioning session; water was always delivered during the last 20 sec of the tone. This completely describes the treatment administered to subjects in the Tone group. The Tone-Light treatment was identical to that described in the previous experiment; a 0.5-sec light was presented 10 sec after tone onset, synchronous with water onset. In the Tone-Light Variable treatment, the light presentation and water onset were asynchronous; the time elapsed from tone onset to the presentation of the light varied from 7 to 13 sec, with a mean of 10 sec.

Licking during the first 10 sec of the tone was recorded and compared to licking during the 10-sec Pre-CS period. The experiment was terminated after 15 sessions.

Results

Differences in conditioned licking to the tone in advance of water presentation were assessed on each of the 5 30-trial blocks. The mean difference scores of the three treatment groups are shown in Figure 6 as a function of training. As expected, anticipatory

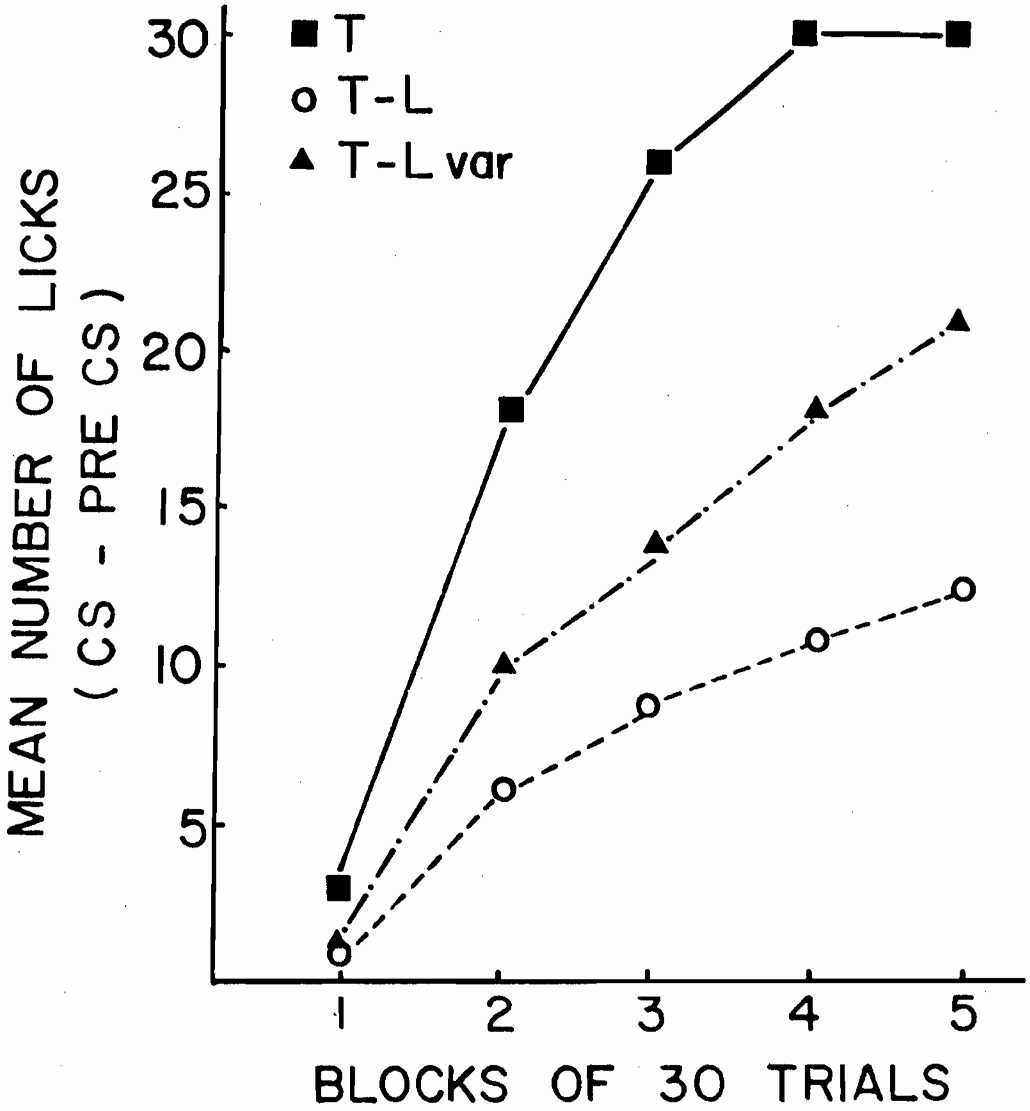

Figure 6. Development of conditioned licking in the Tone, Tone-Light and Tone-Light Variable groups of Experiment 3.

conditioned licking was greatest in the Tone group and least in the Tone-Light group; the responding of the Tone-Light Variable group reached asymptote at an intermediate level. As shown in Table 10, a two-way analysis of variance (treatment x block) on the mean difference scores revealed statistically reliable main effects of treatment, $\underline{F}(2,33)=4.54$, $\underline{p} < .05$, and block, $\underline{F}(1,33)=51.93$, $\underline{p} < .01$, as well as a reliable interaction, $\underline{F}(2,33)=3.51$, $\underline{p} < .05$. As in the previous experiment, the baseline level of responding, estimated by the number of licks during the 10-sec Pre-CS period, was found to differ according to blocks, $\underline{F}(1,33)=8.55$, $\underline{p} < .01$, but not treatment, $\underline{F}(2,33)=2.45$, $\underline{p} > .05$; moreover the effect of block did not interact with treatment condition, $\underline{F}(2,33)=1.40$, $\underline{p} > .05$ (see Appendix G).

The reliable interaction between treatment and block on conditioned licking was submitted to tests of simple effects. This analysis yielded a reliable effect of treatment on Blocks 3-5, $\underline{F}(2,52)=5.74$, 6.72 and 6.24, all $\underline{p}$'s $< .01$; no group differences were found on the first 2 blocks of trials, $\underline{F}(2,52)=0.08$ and 2.81, both $\underline{p}$'s $> .05$. The difference in the conditioned responding of the Tone and Tone-Light groups found in Experiment 2 was replicated; the presentation of a light synchronous with water onset produced less conditioned responding to the tone on Blocks 3-5, $\underline{Q}(3,52)=4.69$, 5.11 and 4.99, respectively, all $\underline{p}$'s $< .01$. Contrary to the informational hypothesis as stated, the Tone-Light Variable treatment did not produce reliably greater responding to the tone than the Tone-Light treatment, $\underline{Q}(2,52)=1.51$, 1.78 and 2.35, for Blocks 3-5, respectively, all $\underline{p}$'s $> .05$. Whereas stronger

TABLE 10

Two-way analysis of variance (treatment x block) on the mean conditioned licking difference scores

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	564309.8	2	282154.90	4.54 *
S(T)	2049176.0	33	62096.25	
Block (B)	896887.3	4(1)	224221.80	51.93 **
TB	121105.8	8(2)	15138.23	3.51 *
BS(T)	569902.2	132(33)	4317.44	

* $p < .05$

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

conditioned responding was seen in the Tone group as compared to the Tone-Light Variable group on Blocks 3 and 4, $Q(2,52)=3.18$ and 3.32, respectively, both p's $< .05$, the responding of these two groups was not reliably different on the last block of trials, $Q(2,52)=2.65$, $p > .05$.

Discussion

Although the ordering of group means was in accordance with the prediction of the informational hypothesis, statistical analysis of the conditioned licking scores failed to provide support for the claim that a stimulus synchronous with UCS onset reduces anticipatory conditioned responding because it is informative with respect to the time of UCS occurrence. On all but the last block of trials, the responding of the Tone-Light Variable group was reliably less than that of the Tone group. Moreover, rejection of the interference hypothesis is not warranted in view of the failure to find reliably greater anticipatory conditioned licking when the light does not consistently indicate the time of UCS delivery than when the light is always synchronous with UCS onset.

That the light was not a reliable indicator of UCS onset in the Tone-Light Variable procedure does not necessarily mean that the light provided no information about UCS occurrence. It should be recalled that the light was presented on *average* 10 sec after tone onset (the time at which water deliveries always began) and that on approximately 60% of the trials, the light either slightly preceded or was synchronous with UCS onset. The failure of the Tone-Light Variable treatment to produce more vigorous anticipatory licking to the tone in this experiment may be because this procedure did not make the light sufficiently uninformative with respect to the time of UCS occurrence.

Experiment 4

Experiment 4 was designed to circumvent the methodological problem encountered in the previous experiment by making the light completely uninformative with respect to the time of water onset. This was accomplished by presenting the light at any time during the tone-water trial. This procedure should insure that the light provides less information about the time of UCS occurrence than does tone onset and consequently a higher level of conditioned licking to the tone would be expected.

Method

Subjects and apparatus. Thirty-six experimentally naive male Sprague-Dawley rats were used in this experiment. Adaptation to a regime of restricted water availability was carried out prior to the onset of experimentation. The apparatus was the same as that used in previous experiments.

Procedure. The subjects were randomly assigned to one of three treatment conditions. The Tone and Tone-Light control procedures were identical to those described in the preceding experiments. For the experimental group, a single light presentation occurred at random times during the conditioning trial; that is, on each trial a 0.5-sec light was presented once during the interval which began with tone onset and ended with the simultaneous termination of the tone and water.

Conditioning began on the day following an habituation session in which 10 water deliveries occurred. All subjects received 10 conditioning trials daily (average intertrial interval: 3 min, range: 2-4 min) on 12 consecutive days. Conditioned licking to the tone was measured and compared with the baseline rate of licking during the 10-sec Pre-CS period.

Results

As illustrated in Figure 7, the strength of conditioned licking to the tone exhibited by subjects in the experimental group was comparable to that of subjects who received the same number of tone-water pairings but had no exposure to the putative distractor. Two-way analyses of variance (treatment x block) were performed on the data from each of the four consecutive blocks of 30 trials. As in the previous experiments, there was no effect of treatment on the baseline rate of licking [treatment: $\underline{F}(2,33)=0.69$ and treatment x block: $\underline{F}(2,33)=0.93$, both $\underline{p}$'s $> .05$] although the total number of licks during the Pre-CS period did vary according to block, $\underline{F}(1,33)=8.69$, $\underline{p} < .05$ (see Appendix H).

As shown in Table 11, analysis of conditioned responding to the tone indicated that both the main effect of treatment, $\underline{F}(2,33)=5.50$ and block, $\underline{F}(1,33)=46.77$, were reliable, both $\underline{p}$'s $< .01$. In this experiment, the effect of treatment did not vary as a function of blocks, $\underline{F}(1,33)=2.53$, $\underline{p} > .05$. Overall group means were compared using the Newman-Keuls method of multiple comparison. Less conditioned licking was observed in the Tone-Light group than in either the Tone, $\underline{Q}(3,33)=4.18$, $p < .05$, or Tone-Light Variable, $\underline{Q}(2,33)=3.94$,

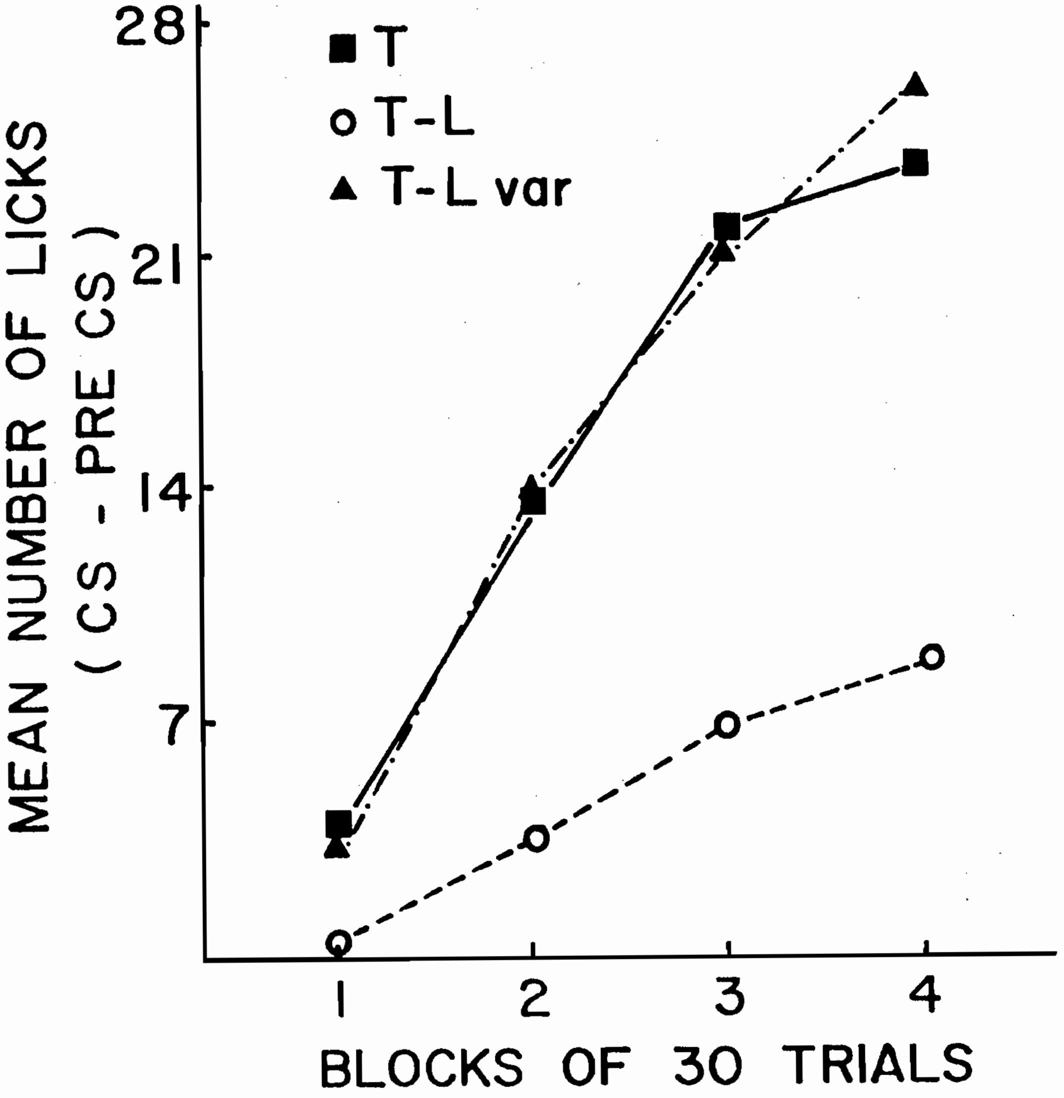

Figure 7. Mean conditioned licking scores of the Tone, Tone-Light and Tone-Light Variable groups in Experiment 4 as a function of training.

TABLE 11

Two-way analysis comparing the effects of treatment and block on anticipatory conditioned licking

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	438957.3	2	219478.60	5.50 **
S(T)	1316686.0	33	39899.59	
Block (B)	622822.4	3(1)	207607.50	46.77 **
TB	67415.0	6(2)	11235.83	2.53
BS(T)	439419.0	99(33)	4438.58	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

$p < .01$, groups. The presentation of the light stimulus at random times during conditioning trials did not interfere with conditioned responding to the tone because the Tone-Light Variable group was not different from the Tone group, $Q(2,33)=0.24$, $p > .05$.

Discussion

When a light signal is presented during tone-water conditioning trials in such a manner that its occurrence bears no relation to the time of UCS presentation, the development of conditioned responding to the tone is unimpaired. But when a light synchronous with water onset is added, anticipatory responding is dramatically reduced. The results of this experiment indicate that the light does not act as a distractor or interference agent, for when the light was made uninformative, as in the experimental condition, strong conditioned licking to the tone was observed.

Discussion of Experiments 3 and 4

Taken together, the results of Experiments 3 and 4 suggest that anticipatory conditioned responding to the tone increases as the information value of the light is degraded relative to tone onset. These results therefore make any simple interference account of the decreased anticipatory conditioned responding when the UCS is marked by a synchronous stimulus untenable. In these experiments, the information value of the light was manipulated by varying both the absolute and relative temporal relation between the light presentation and water onset; the extent to which each of these aspects of the CS-UCS relation influences the information value of the light could be further investigated in a series of parametric studies.

THE INHIBITION HYPOTHESIS

The differences in the latency and time course of conditioned responding observed in Experiment 2 raised the possibility that marking the onset of water with a synchronous stimulus facilitates the development of inhibition of delay to the CS. Inhibition of delay is characterized by (1) a progressive decline in the rate of conditioned responding during the early portion of the CS as a function of training; (2) the appearance of strong conditioned responding at a time that more closely approximates the time of UCS presentation; and (3) the ability of the early portion of the CS to inhibit responding to a previously established conditioned excitor as demonstrated using a summation test for inhibition (Rescorla, 1967). In Experiment 2, there was no evidence that subjects in the control group learned to delay licking following the onset of the tone; after 120 tone-water pairings, the asymptotic level of responding was reached within 2-3 sec of tone onset and this rate was maintained for the remainder of the CS. On the other hand, the distribution of licking during the CS shown by subjects in the Tone-Light group was precisely what would be expected if the early part of the CS was inhibitory. The gradual increase in the rate of conditioned licking as the time of water presentation nears resembles the temporal topography of conditioned salivation during a relatively long CS (Pavlov, 1927; Williams, 1965) and the changes in the rate of free-operant avoidance responding during successive portions of a CS that had previously been paired with shock (Rescorla, 1967). The purpose of Experiment 5 was to determine if the depressed rate of conditioned licking following CS onset in the Tone-Light group was due to the development of inhibition to the early portion of the tone.

Experiment 5

In this experiment, unlike the previous ones, the experimental treatment consisted of marking the onset of water delivery with a 0.5-sec tone during conditioning trials with a light CS. As a control procedure, a second group of rats received training with a light which had the same temporal relation to water, but the tone was not used to indicate water onset. This phase of the experiment thus provided an opportunity to extend the basic finding of reduced conditioned responding to a visual CS when UCS onset is signalled by the presentation of an auditory stimulus.

A longer latency to lick upon CS onset by subjects in the experimental group could mean that for this group, the early portion of the light had become inhibitory. If this were so, then the establishment of this CS as a conditioned inhibitor of responding might be facilitated. This possibility was examined using a standard Pavlovian conditioned inhibition procedure in which reinforced presentations of a previously established conditioned excitor are interspersed with nonreinforced presentations of that excitor with the to-be-established conditioned inhibitor. In the present experiment, the ease with which the two groups of rats pretrained with the light CS learned to inhibit responding to a nonreinforced clicker-light compound CS was compared to the performance of a third group of animals that had no prior experience with the light.

Longer response latencies and less total licking to the compound CS would be expected if the experimental procedure had endowed the early portion of the light CS with inhibitory properties.

Method

Subjects and apparatus. Thirty experimentally naive male Sprague-Dawley rats, initially weighing 275-300 g, served as subjects in this experiment. The apparatus and housing conditions were identical to those described in previous experiments.

Procedure. In Phase 1, following adaptation to a water deprivation schedule, the subjects were assigned to one of three treatment conditions and given 10 unsignalled water presentations in the conditioning chamber. On the next day, two groups of rats were conditioned to a light CS paired with water. For both the Light and Light-Tone groups, water was delivered during the last 20 sec of each of 10 daily 30-sec light presentations; in the Light-Tone treatment, water onset was signalled by a 0.5-sec tone. Subjects assigned to the third, Original Learning, group remained in their home cages throughout the 12 days of this phase.

During Phase 2, all subjects received 10 identical conditioning trials with a 50-hz clicker CS on each of nine consecutive days. As in Phase 1, the 20-sec water delivery began 10 sec after CS onset and terminated with the CS.

In order to determine whether the intervening training with the clicker had any effect on conditioned responding to the light, the Light and Light-Tone groups were tested with 10 reinforced light and light-tone trials, respectively. On this day, subjects in the Original Learning group were given 10 nonreinforced (habituation) trials with the light.

Phase 3 consisted of 8 sessions of discrimination training; on each day, all subjects were given 5 reinforced clicker trials and 5 nonreinforced clicker-light trials in random order.

All experimental sessions lasted approximately 35 min. The latency to respond upon CS presentation, as well as the number of licks during the 10-sec periods immediately preceding and succeeding CS onset, were recorded throughout all phases of this experiment.

Results

Phase 1. The mean conditioned licking difference scores of the Light and Light-Tone groups are shown as a function of blocks in Figure 8. Throughout this phase, the Light group showed consistently greater anticipatory responding to the light CS than did the Light-Tone group. The results of a two-way analysis of variance (treatment x block) performed on these data are presented in Table 12. Both main effects, treatment, $F(1,18)=8.60$ and block, $F(1,18)=25.22$, both p's $< .01$, and the treatment x block interaction, $F(1,18)=6.01$, $p < .05$, were statistically reliable. Although the conditioned licking scores were not different on the first block of trials, $F(1,31)=0.30$, $p > .05$, tests of simple effects confirmed that the difference between the Light and Light-Tone groups was significant on the subsequent blocks of trials [Block 2, $F(1,31)=5.30$, $p < .05$; Block 3, $F(1,31)=13.10$, $p < .01$; Block 4, $F(1,31)=12.96$, $p < .01$]. The differential effect of treatment over blocks is not attributable to between-group differences in the baseline rate of licking; a two-way analysis of variance (treatment x block) on the number of licks during the Pre-CS period confirmed that the

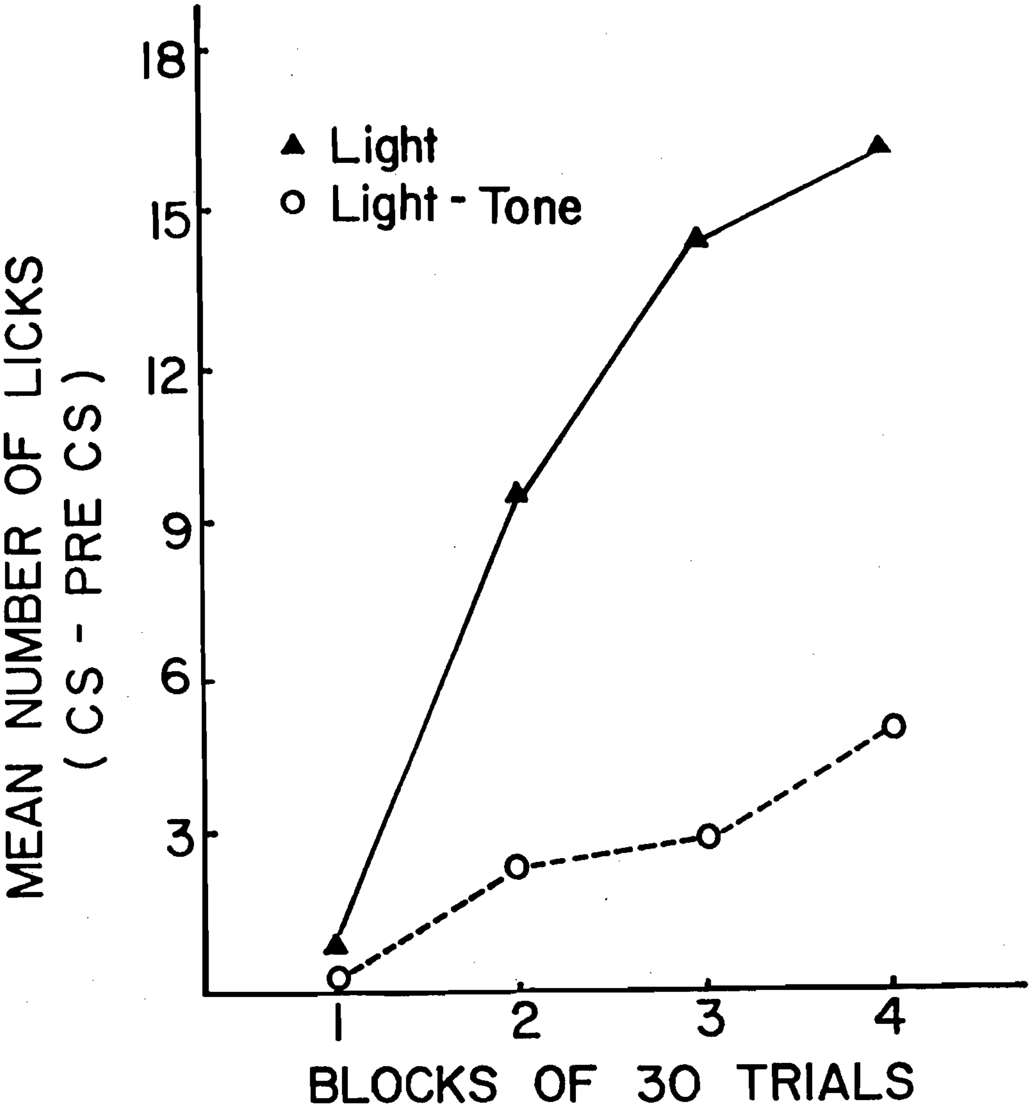

Figure 8. Mean conditioned licking scores of the Light and Light-Tone groups in Phase 1 of Experiment 5.

TABLE 12

Two-way analysis of variance comparing the effects of treatment condition and block on conditioned licking to a light CS

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	122179.70	1	122179.70	8.60 **
S(T)	255843.90	18	14213.55	
Block (B)	127447.80	3(1)	42482.61	25.22 **
TB	30365.85	3(1)	10121.95	6.01 *
BS(T)	90951.45	54(18)	1684.29	

* $p < .05$

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

main effect of treatment, $F(1,18)=0.02$, and the interaction between treatment and block, $F(1,18)=1.60$, were not statistically reliable, both p's $> .05$. Baseline licking did, however, vary according to blocks, $F(1,18)=5.89$, $p < .05$. (See Appendix I.)

More pertinent to the question of inhibition of delay is the latency to contact the water spout following light onset. The mean latency to the first lick during the CS was 7.47 and 5.87 sec for the Light-Tone and Light groups, respectively. A two-way analysis of variance (treatment x block), presented in Table 13, confirmed that this difference was significant, $F(1,18)=10.90$, $p < .01$. The treatment effect did not vary with blocks, $F(1,18)= 1.52$, $p > .05$, although a reliable main effect of block was obtained, $F(1,18)=27.97$, $p < .01$. Thus, the finding of less anticipatory conditioned licking and longer response latencies when the onset of water is indicated by a superimposed, synchronous stimulus extends to a light CS.

Phase 2. Differences in the development of conditioned licking to the clicker CS by the Light, Light-Tone and Original Learning groups were assessed using a two-way analysis of variance (treatment x block). This analysis, which is presented in Table 14, revealed a statistically reliable effect of block, $F(1,27)=34.32$, $p < .01$, as well as a reliable interaction between treatment and block, $F(1,27)=6.89$, $p < .05$. Analysis of the rate of licking during the 10-sec period immediately preceding clicker onset yielded no statistically reliable effects (all p's $> .05$; see Appendix J).

TABLE 13

Analysis of variance comparing the effects of treatment and block on the latency to the first lick upon light onset

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	50.88	1	50.88	10.90 **
S(T)	84.00	18	4.67	
Block (B)	55.27	3(1)	18.42	27.97 **
TB	3.01	3(1)	1.00	1.52
BS(T)	35.57	54(18)	0.66	

**$p < .01$

[a] conservative degrees of freedom are given in parentheses

TABLE 14

Two-way analysis of variance comparing the effects of treatment and block on conditioned licking during a clicker CS

Source of Variation	Sum of Squares	df^a	Mean Square	F
Treatment (T)	154280.60	2	77140.27	2.02
S(T)	1033069.00	27	38261.82	
Block (B)	211618.10	2(1)	105809.10	34.32 **
TB	84934.39	4(2)	21233.59	6.89 **
BS(T)	166506.50	54(27)	3083.45	

** $p<.01$

[a] conservative degrees of freedom are given in parentheses

The reliable treatment x block interaction is attributable to group differences in conditioned licking on Block 1 only, $\underline{F}(2,35)=5.08$, $\underline{p} < .05$; the mean difference scores on this block of trials of the Light-Tone, Light and Original Learning groups were, in order, 14.8, 21.1 and 3.9 licks. The two groups previously trained with the light did not show differential responding to the clicker, $\underline{Q}(2,35)=1.64$, $\underline{p} > .05$. However, both groups showed strong positive transfer from Phase 1 to Phase 2; the conditioned responding of the Original Learning group was reliably less than that of the Light, $\underline{Q}(3,35)=4.46$, $\underline{p} < .01$, and Light-Tone, $\underline{Q}(2,35)=3.83$, $\underline{p} < .05$, groups. Comparable levels of responding were observed, however, on Block 2, $\underline{F}(2,35)=2.45$ and Block 3, $\underline{F}(2,35)=0.55$, both $\underline{p}$'s $> .05$. The mean difference scores for the Light, Light-Tone and Original Learning groups on the last block of trials were 27.1, 21.8 and 26.1 licks, respectively.

A similar pattern of results obtained for the latency to lick upon clicker onset. A two-way analysis of variance (treatment x block) on these data, as shown in Table 15, yielded a reliable main effect of block, $\underline{F}(1,27)=25.27$ and an interaction between treatment and block, $\underline{F}(2,27)=9.83$, both $\underline{p}$'s $< .01$. The effect of treatment at each block of trials was analyzed using tests of simple effects. Reliable differences in response latency were observed on Block 1, $\underline{F}(2,38)=6.97$, $\underline{p} < .05$, but not on Block 2, $\underline{F}(2,38)=0.61$ or Block 3, $\underline{F}(2,38)=0.21$, both $\underline{p}$'s $> .05$. On the first block of trials, the mean latency to respond was 3.15, 3.42 and 5.16 sec for the Light, Light-Tone and Original Learning groups, respectively. The latter group took longer to contact the water

TABLE 15

Two-way analysis of variance on the effects of treatment and block on the latency to the first lick upon clicker onset

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	9.72	2	4.86	1.14
S(T)	115.06	27	4.26	
Block (B)	21.74	2(1)	10.87	25.27 **
TB	16.91	4(2)	4.23	9.83 **
BS(T)	23.23	54(27)	0.43	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

spout following CS onset on Block 1 than did the Light, *Q*(3,38)=7.36, and Light-Tone, *Q*(2,38)=4.21, groups, both *p*'s $< .01$. The difference between the Light and Light-Tone groups was not significant, *Q*(2,38)=0.65, $p > .05$. The mean latency to lick on Blocks 2 and 3 was 3.03 and 2.76 sec, respectively.

Light test. Differential responding to the light CS by the Light and Light-Tone groups was still evidenced following training with the clicker in Phase 2. A one-tailed *t* test confirmed that the Light group showed more conditioned responding than did the Light-Tone group (18.7 versus 10.0 licks), *t*(18)=1.95, $p < .05$. The mean latency to lick upon light onset was 6.11 and 4.45 sec for the Light-Tone and Light groups, respectively. This difference was also statistically significant, *t*(18)=2.45, $p < .05$. The Original Learning group did not show substantial responding to the light on this day; the mean difference score for this group was not significantly greater than zero, *t*(9)=1.20, $p > .05$.

Phase 3. For each subject, mean difference scores and latency to respond on the reinforced clicker and nonreinforced clicker-light trials were calculated for the four consecutive, 10-trial (2-day) blocks. A three-way analysis of variance (treatment x block x stimulus) was performed on each measure. Table 16 summarizes the results of this analysis on the mean conditioned licking difference scores. A reliable main effect of stimulus, *F*(1,27)=101.94, and a stimulus x block interaction, *F*(1,27)=18.18, were obtained, both *p*'s $< .01$; no other main effect or interaction was reliable (all *p*'s $> .05$). A two-way analysis of variance (treatment x block) on licking during the Pre-CS period yielded no statistically reliable effects (all *p*'s $> .05$; see Appendix K).

TABLE 16

Three-way analysis of variance comparing the effects of treatment, block, and stimulus on conditioned licking

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	2011.52	2	1005.76	1.03
S(T)	26316.75	27	974.69	
Stimulus (C)	12596.16	1	12596.16	101.94 **
TC	163.05	2	81.53	0.66
CS(T)	3336.17	27	123.56	
Block (B)	426.70	3(1)	142.23	3.43
TB	196.75	6(2)	32.79	0.79
BS(T)	3354.49	81(27)	41.41	
CB	2027.43	3(1)	675.81	18.18 **
TCB	494.28	6(2)	82.38	2.22
CBS(T)	3010.50	81(27)	37.17	

** $p<.01$

[a] conservative degrees of freedom are given in parentheses

The stimulus x block interaction is shown in the left panel of Figure 9. All subjects showed less conditioned licking on nonreinforced clicker-light (CS-) trials than on reinforced clicker (CS+) trials. This difference was statistically significant even on the first block of trials, $\underline{t}(76)=3.50$, $\underline{p} < .01$. And whereas anticipatory licking to the CS+ continued to increase with further training, responding on CS- trials steadily declined. Tests of orthogonal trend comparisons, using the method proposed by Scheffé (Winer, 1962), confirmed a strong linear component in responding to the clicker over days, $\underline{F}(1,161)=22.35$, $\underline{p} < .01$. Similarly, the linear comparison of the responding to the nonreinforced compound CS over days was significant, $\underline{F}(1,161)=29.30$, $\underline{p} < .01$.

The three-way analysis of variance (treatment x stimulus x block) on the mean latency to lick upon CS onset is presented in Table 17. This analysis yielded a reliable main effect of stimulus, $\underline{F}(1,27)=160.84$, $\underline{p} < .01$. Moreover, the effect of stimulus varied with treatment, $\underline{F}(2,27)=7.66$ and block, $\underline{F}(1,27)=14.15$, both $\underline{p}$'s $< .01$.

The mean latency to respond on CS+ and CS- trials as a function of blocks is shown in the right panel of Figure 9. The pattern of results obtained for this measure is consistent with that obtained with the conditioned licking scores. A strong linear trend was found in the latency to respond on CS+, $\underline{F}(1,158)=13.13$, $\underline{p} < .05$, and CS-, $\underline{F}(1,158)=23.16$, $\underline{p} < .01$, trials over blocks.

The reliable treatment x stimulus interaction, illustrated in Figure 10, was analyzed using tests of simple effects. Latency to respond to the clicker did not differ across groups, $\underline{F}(2,35)=1.06$,

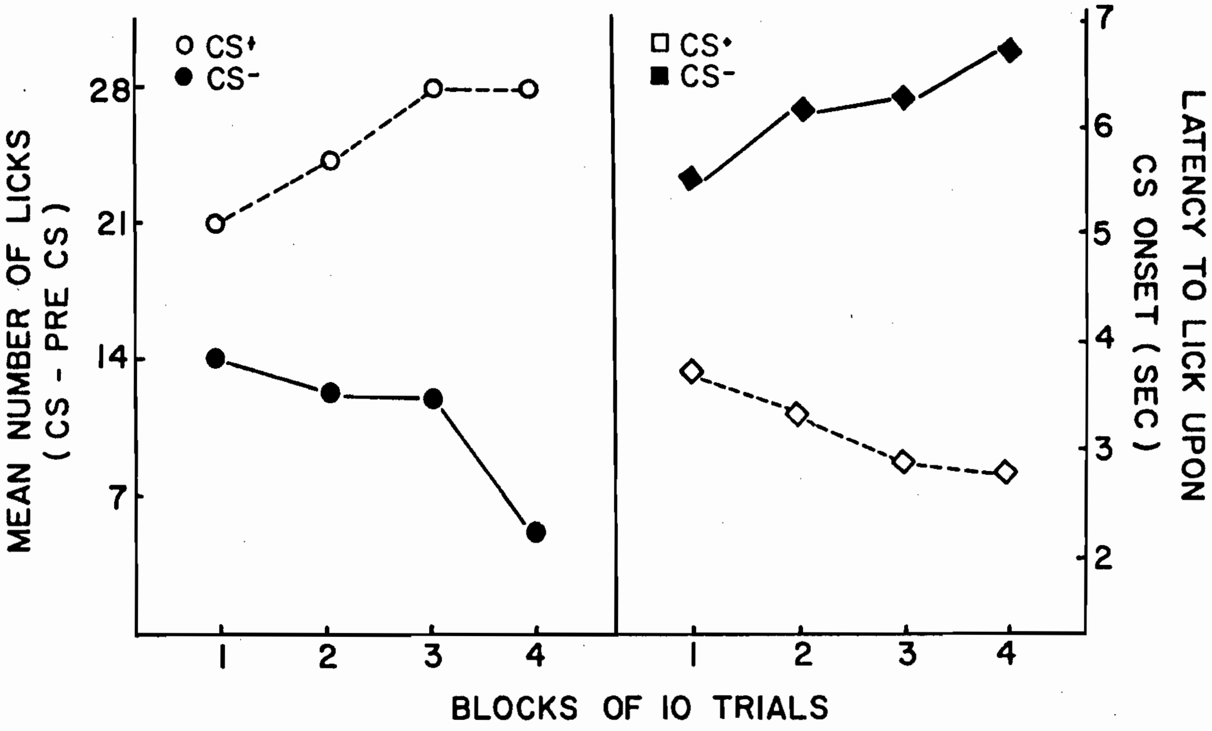

Figure 9. Differences in conditioned licking (left panel) and latency to the first lick following CS onset (right panel) on reinforced clicker and nonreinforced clicker-light trials in Phase 3 of Experiment 5.

TABLE 17

Three-way analysis of variance comparing the effects of treatment, block, and stimulus on the latency to the first lick upon CS onset

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	113.97	2	56.98	3.21
S(T)	479.28	27	17.75	
Stimulus (C)	489.63	1	489.63	160.84 **
TC	46.62	2	23.31	7.66 **
CS(T)	82.19	27	3.04	
Block (B)	2.81	3(1)	0.94	0.70
TB	11.04	6(2)	1.84	1.38
BS(T)	107.94	81(27)	1.33	
CB	42.14	3(1)	14.05	14.15 **
TCB	13.40	6(2)	2.23	2.25
CBS(T)	80.38	81(27)	0.99	

** $p<.01$

[a] conservative degrees of freedom are given in parentheses

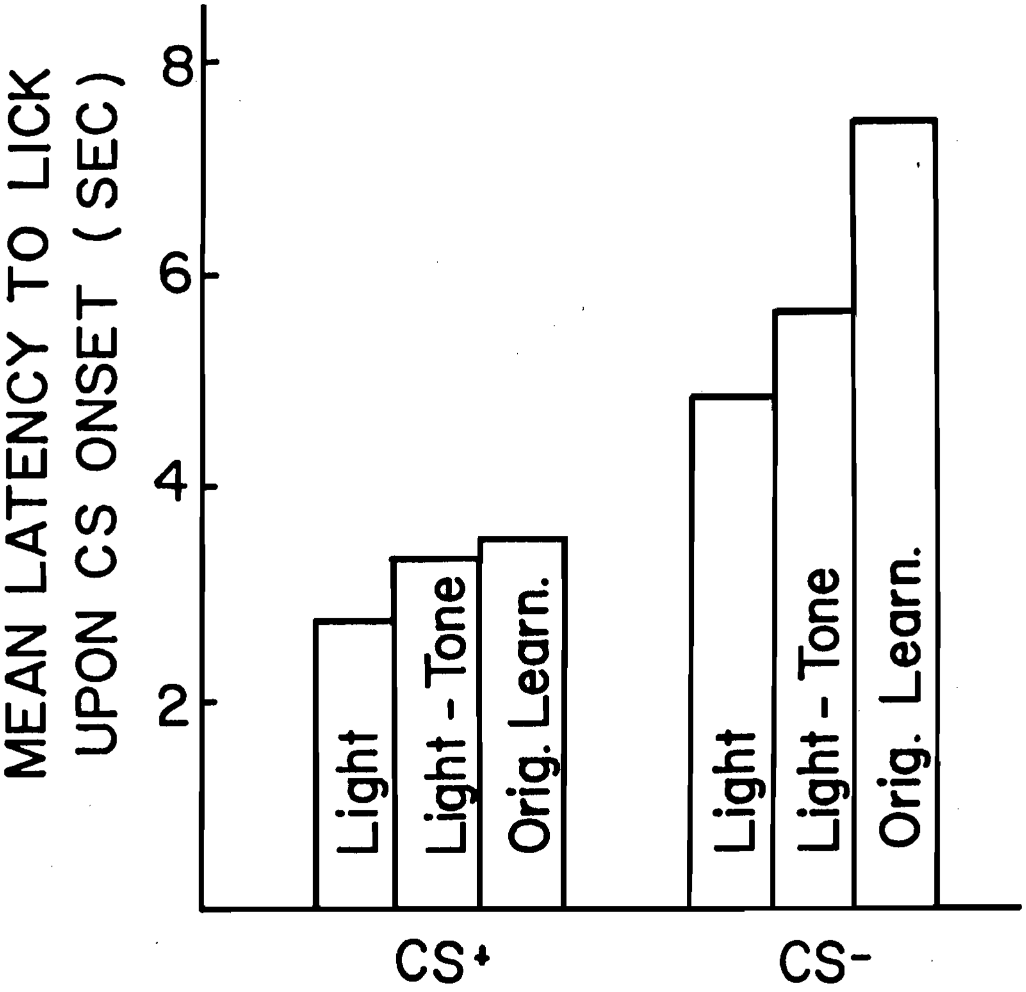

Figure 10. Differences between the Light, Light-Tone and Original Learning groups in the latency to lick upon clicker (CS+) and clicker-light (CS-) trials.

$p > .05$; responding to the clicker-light compound, however, was differentially affected by prior conditioning with the light, $F(2,35)=7.19$, $p < .01$. Subjects in the Original Learning group, who had not been pretrained with the light, took reliably longer to contact the spout than subjects exposed to the Light, $Q(3,35)=5.22$, $p < .01$, or Light-Tone, $Q(2,35)=3.69$, $p < .05$, procedures in Phase 1. Although these latter groups had previously shown differential response latencies to the light, no differences were found when the light was presented in compound with the clicker in this phase, $Q(2,35)=1.53$, $p > .05$.

Discussion

The results of Phase 1 provide strong support for the generality of the finding that marking the onset of water presentations with a synchronous event drastically alters the strength and time course of anticipatory conditioned licking. The reduction in anticipatory licking and the longer response latencies to a light CS observed when a brief tone is synchronous with water onset parallel the findings of Experiment 2 using the Tone-Light procedure. The present experiment also indicates that this effect is specific to the training stimulus since the Light and Light-Tone groups did not differ in the acquisition or asymptotic level of conditioned responding to the clicker in Phase 2; moreover, the subsequent training with the clicker, which was paired with water in a standard delay conditioning procedure, did not disrupt the differential responding to the light that had been established in Phase 1.

The main purpose of this experiment was to determine whether the reduction in anticipatory conditioned responding in the experimental group was attributable to the development of inhibition of delay to the CS. This question was examined in Phase 3 of this experiment. If the early portion of the light had become inhibitory, the acquisition of conditioned inhibition to the light should have been facilitated in the Light-Tone group, leading to less total responding and longer response latencies to the clicker-light compound CS. No evidence for such facilitation was found. The extinction of conditioned licking to the nonreinforced compound CS was comparable in all groups. An effect of treatment was found, however, in the mean latency to contact the spout on CS-, but not CS+, trials. But this effect is due to the longer response latencies of the subjects in the Original Learning group. Although the Light and Light-Tone groups showed significantly different response latencies to the light on the test day, this difference was not maintained when the light was presented in compound with the clicker. The failure to observe longer latencies to the compound CS in the Light-Tone group indicates that the early portion of the light was not inhibitory. The results of this experiment, therefore, provide no support for the hypothesis that the experimental treatment makes the CS somewhat inhibitory.

THE INFORMATION HYPOTHESIS

The effects of marking the onset of UCS presentations with a synchronous stimulus on anticipatory conditioned responding are compatible with an account of classical conditioning which provides an informational role for conditioned stimuli. According to this view, the organism is sensitive to the information provided by various stimuli in the conditioning situation about the likelihood and time of occurrence of some UCS; anticipatory responding is guided by this information in ways which best prepare the animal for UCS presentation while minimizing effort. It is thus understandable that anticipatory licking at a dry spout is reduced when a salient event, such as a light flash, marks the time of water presentation following the onset of a tone CS. In this conditioning procedure, the tone-water interval is always 10 sec so that tone onset can be said to provide accurate information about the time of water delivery; however, the synchronicity of the light and water onset may make the light even more informative than either the onset or duration aspects of the tone because of the immediacy of water delivery. The experiments described in this section examine anticipatory conditioned licking to a tone CS following experimental manipulations presumed to affect the informational value of the light.

Experiment 6

The synchronicity of the light and water onset was demonstrated in Experiment 4 to be important in the reduction of anticipatory licking to the tone CS. According to the information hypothesis, when the light reliably coincides with water onset, the light becomes a more informative signal for water delivery relative to tone onset. In the previous experiments, the informational significance of the light was inferred from the weaker conditioned responding to the tone when the light was present during conditioning trials and was synchronous with the onset of water delivery. The informational value of the light may be directly assessed by measuring the rate of licking following the occurrence of the light on nonreinforced test trials. Alternatively, if a light that had been synchronous with water onset is subsequently presented prior to water delivery, say 5 sec following tone onset, then an increase in licking during the portion of the tone following, but not preceding, light presentations should be observed. Evidence for such selective enhancement of anticipatory conditioned licking when the time of light presentations is changed in this way was sought in Experiment 6.

Method

Subjects and apparatus. The rats in the Tone and Tone-Light control groups of Experiment 4 served as subjects in this experiment. The apparatus was the same as that used previously.

Procedure. Following completion of Experiment 4 (Phase 1 of the present experiment), all subjects received 10 additional conditioning trials on each of 3 consecutive days. In Phase 2, the temporal relation between the tone and water presentations was identical to that described in Experiment 4; on all conditioning trials, water was delivered during the last 20 sec of the 30-sec tone. In the Tone-Light treatment, the light and onset of water delivery were synchronous in Phase 1; in Phase 2 the light presentation preceded water delivery by 5 sec. Subjects in the Tone group served as controls and received the same treatment in both phases of the experiment.

For all subjects, the number of licks during the two consecutive 5-sec periods of the tone prior to water delivery was recorded during both phases of the experiment.

Results

Changes in the distribution of anticipatory conditioned licking to the tone were assessed using a three-way analysis of variance (treatment x period x phase) which compared the mean number of licks during the two consecutive 5-sec periods following tone onset on the last day of Phase 1 and 2. This analysis is shown in Table 18. With the exception of the treatment x period interaction, all other interactions and main effects were reliable (all p's $< .05$). A two-way analysis of variance (treatment x phase) on the rate of licking during the Pre-CS period yielded no statistically reliable effects (see Appendix L).

As can be seen in Figure 11, the reliable three-way interaction is attributable to the differential effects of the time of light presentation in Phase 1 and Phase 2 on anticipatory responding of the Tone-Light group. As hypothesized, the subjects in this group showed increased licking following, but not preceding, light presentations in Phase 2. Two-tailed t tests confirmed that responding during the first 5-sec period following tone onset was not affected by the change in the time of light occurrence, $t(11) = 1.81$, $p > .05$, but that licking during the second 5-sec period was

TABLE 18

Three-way analysis of variance (Treatment x CS Period x Phase) on the mean conditioned licking scores from Experiment 6

Source of Variation	Sum of Squares	df	Mean Square	F
Treatment (T)	742.04	1	742.04	4.70 *
S(T)	3474.81	22	157.95	
CS Period (C)	1380.93	1	1380.93	53.52 **
TC	6.67	1	6.67	0.26
CS(T)	567.66	22	25.80	
Phase (P)	108.59	1	108.59	11.69 **
TP	84.19	1	84.19	9.06 **
PS(T)	204.44	22	9.29	
TCP	36.88	1	36.88	10.72 **
CPS(T)	75.68	22	3.44	

* $p < .05$

** $p < .01$

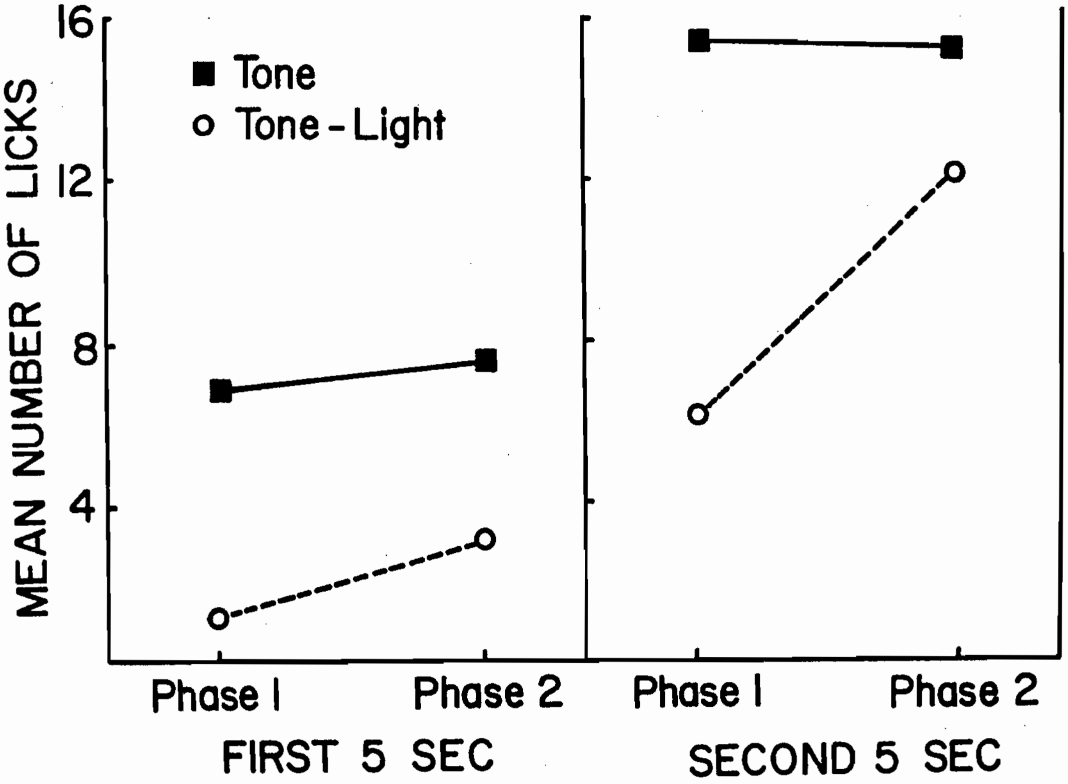

Figure 11. Total number of licks during the first and second 5-sec periods of the tone prior to water presentation in Phase 1 and 2 of Experiment 6.

enhanced in Phase 2, _t_(11)=5.73, $p < .01$. As expected, the Tone group did not show any change in responding from Phase 1 to Phase 2 during either the first, _t_(11)=0.62, or second, _t_(11)=-0.14, half of the tone, both _p_'s > .05.

Discussion

The results of this experiment support the contention that the experimental treatment reduces conditioned responding to the tone because the light synchronous with water onset may serve as a better indicator of the time of UCS occurrence. The change in the time of light presentations during conditioning trials in Phase 2 did not result in any general increase in conditioned responding to the tone; rather, increased anticipatory licking was observed only during that portion of the tone that immediately followed light presentations. Thus even when the light is no longer synchronous with water onset, but is presented 5 sec prior to water delivery, it may be regarded as a better indicator of the time of water presentations because of its closer temporal proximity to the UCS.

Experiment 7

According to the information hypothesis, the synchronous light reduces anticipatory conditioned licking during the tone because the rat uses the light as an indicator of the time of water delivery _following tone onset_. This raises the possibility that the informational value of the light is conditional upon the temporal priority of the tone.

It may be that the strength and distribution of anticipatory conditioned licking established in the Tone-Light condition is a consequence of "configural" conditioning (Razran, 1939). That is, the particular temporal arrangement between the tone and light may introduce a source of variation in conditioned responding which cannot be accounted for by the combined effects of conditioning to the tone and to the light based upon the temporal relation that each stimulus alone has with water deliveries. The presence of configural conditioning could be detected by holding the tone-water relation fixed, but reducing the correlation between the light and water in such a way that the informational significance of the light *when it is presented in compound with the tone* is maintained. One way in which this can be accomplished is to modify the Tone-Light procedure by the presentation of nonreinforced 0.5-sec lights during the ITI. Although this treatment degrades the correlation between the light and water, the information that the tone-light configuration provides about the exact time of water delivery is unaffected; little anticipatory licking during the tone would be expected since the time of water delivery during the conditioning trial would be reliably indicated by a synchronous light.

In order to control for the effects of the reduced light-water correlation, a second group of rats was trained with a light synchronous with the onset of water on only 50% of the conditioning trials with the tone CS. This group should show strong conditioned licking to the tone because the time of water presentation following tone onset is not reliably indicated by the presentation of a light. The development of anticipatory conditioned licking by rats administered these treatments was compared with that of control subjects trained with either the Tone or Tone-Light procedure.

Method

Subjects and apparatus. 48 male Sprague-Dawley rats served as subjects. This experiment was conducted concurrently with Experiment 3 and accordingly, the 24 animals assigned to the Tone and Tone-Light groups served as control subjects for both experiments. Housing conditions and apparatus were as previously described in Experiment 3.

Procedure. Conditioning began on the day following a session in which 10 unsignalled water presentations occurred so as to habituate the animals to the experimental apparatus and to insure that all subjects licked at the water spout. Twelve subjects were assigned to each of 4 treatment conditions. The treatments administered to subjects in the Tone (T) and Tone-Light (TL) groups have already been described in Experiment 3. The TL+ L- treatment consisted of conditioning to the tone-light compound CS as in the TL procedure but in addition, a single nonreinforced 0.5-sec light was presented at unpredictable times during each intertrial interval. For a fourth group of animals (T+ TL+), one-half of the 10 daily conditioning trials were reinforced presentations of the tone-light compound while on the remaining 5 trials the light was omitted and water was delivered during the last 20 sec of the 30-sec tone; the sequence of tone and tone-light trials was random.

For all subjects, the number of licks during the CS and Pre-CS period was recorded during each of the 15 consecutive conditioning sessions, each lasting approximately 35 min.

Results

The mean difference scores (licks during the CS minus licks during the Pre-CS period) for the 5 consecutive 30-trial blocks were calculated for each subject. The group means for each block of trials are shown in Figure 12. The effects of treatment on the development of conditioned responding to the tone were assessed using a two-way analysis of variance (treatment x block). As shown in Table 19, this analysis yielded reliable main effects of treatment, $F(3,44)=5.26$ and block, $F(1,44)=52.80$, both p's $< .01$, as well as a reliable interaction, $F(3,44)=3.16$, $p < .05$. Analysis of the Pre-CS licking yielded a reliable block effect only, $F(1,44)=11.92$, $p < .01$ (see Appendix M).

No effect of treatment on conditioned responding was observed on Block 1, $F(3,75)=0.14$, $p > .05$. However, tests of simple effects computed on the remaining blocks of trials indicated a strong treatment effect on each block [Block 2, $F(3,75)=3.23$, $p < .05$; Block 3, $F(3,75)=6.14$, $p < .01$; Block 4, $F(3,75)=7.50$, $p < .01$; Block 5, $F(3,75)=6.68$, $p < .01$]. The results of Newman-Keuls tests, comparing group means on each of these blocks, are shown in Table 20. On Blocks 3-5 the subjects in the Tone treatment showed greater anticipatory conditioned responding than any other group (all p's $< .01$); the responding of the TL, TL+ L- and T+ TL+ groups was not different on any block of trials (all p's $> .05$).

There was no evidence that the nonreinforced presentation of lights in the TL+ L- condition had any effect on licking during the ITI. The mean number of licks in the 10-sec period immediately following the nonreinforced light presentations was compared to licking during the preceding 10-sec period. The mean difference scores were -0.80, -0.20, 0.00, -0.40 and -1.10 for Blocks 1-5, respectively.

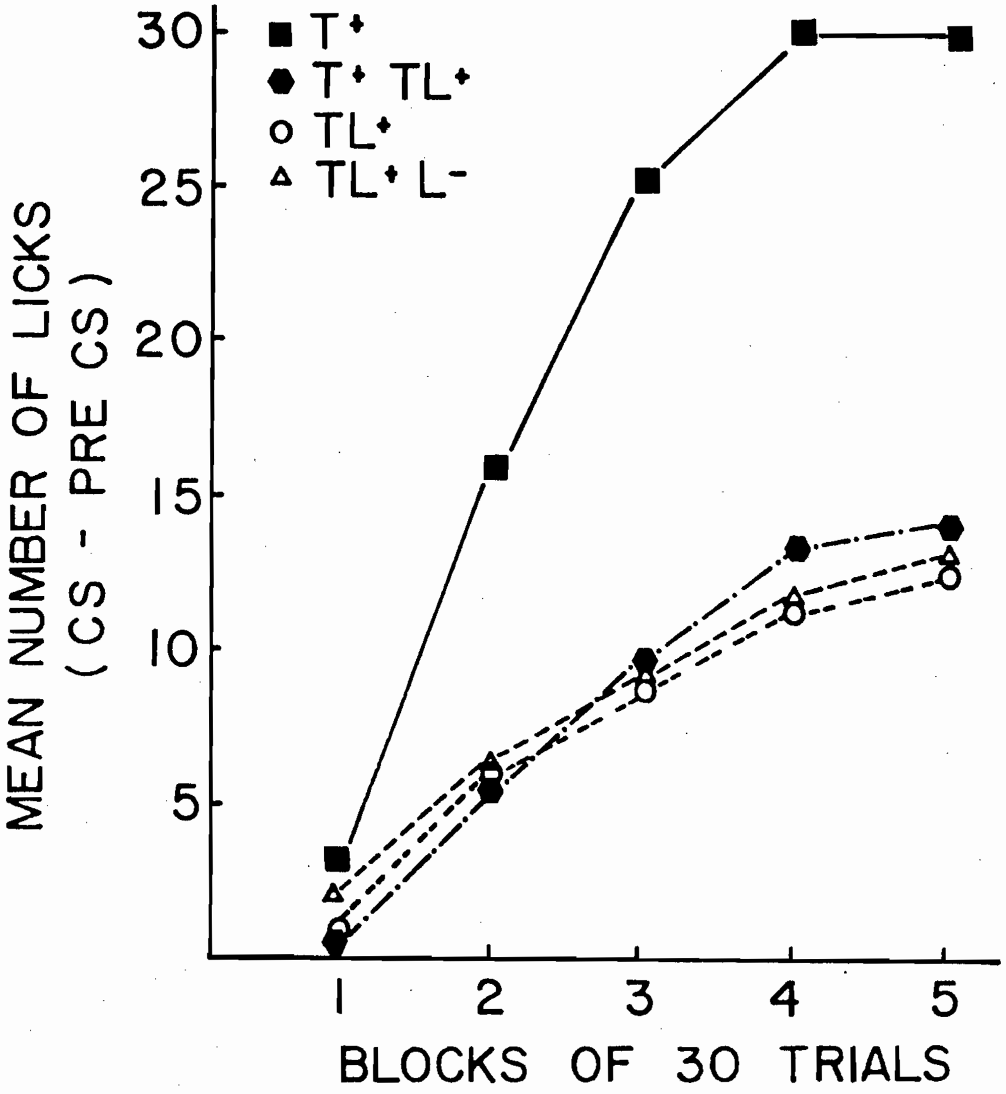

Figure 12. Mean conditioned licking scores of the T+, TL+, TL+ L-, and T+ TL+ groups in Experiment 7.

TABLE 19

Two-way analysis of variance to assess the effects of treatment and block on conditioned licking to the tone

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	785732.5	3	261910.80	5.26 **
S(T)	2192020.0	44	49818.65	
Block (B)	868985.0	4(1)	217246.30	52.80 **
TB	156162.4	12(3)	13013.53	3.16 *
BS(T)	724204.0	176(44)	4114.79	

* $p<.05$

** $p<.01$

[a] conservative degrees of freedom are given in parentheses

TABLE 20

Newman-Keuls tests comparing the effect of treatment at each block of trials
(I: TL+ L-; II: T+ TL+; III: TL+; IV: T+)

Block 2

	III	I	IV
II	0.08	0.25	3.70
III		0.17	3.62
I			3.45

Block 3

	I	II	IV
III	0.26	0.30	5.13**
I		0.04	4.88**
II			4.83**

Block 4

	III	II	IV
I	0.09	0.59	5.68**
III		0.50	5.59**
II			5.09**

Block 5

	I	II	IV
III	0.45	0.50	5.46**
I		0.05	5.02**
II			4.97**

** $p<.01$

$df_{error}=75$

Discussion

As hypothesized, the nonreinforced presentations of lights during the ITI had no measurable effect on anticipatory conditioned responding during the tone-light compound CS; the responding of the TL+ L- group was not different from that of the TL group on any block of trials, but throughout training both groups showed reliably less conditioned licking than did the T group. This result is consistent with the claim that the light can be informative about the time of UCS presentation given the temporal priority of the tone CS even when the conditional probability of water delivery given the occurrence of the light is reduced.

The finding of depressed anticipatory conditioned licking when the light is present on only 50% of the tone conditioning trials is less compatible with an informational account, for in this procedure the onset of water delivery following tone onset is not always marked by the presentation of a light. A similar result was obtained in Experiment 3 when light presentations were temporally contiguous, but not always synchronous, with the onset of water delivery. It may be that the effectiveness of the light to attenuate conditioned responding to the tone depends upon the <u>consistency</u> (or percentage of conditioning trials in which it occurs) as well as the <u>immediacy</u> of water delivery given its occurrence. It is possible that a light synchronous with water onset on one-half of the conditioning trials is sufficient to cause the rat to withhold anticipatory responding following tone onset until a time which closely approximates that of UCS presentation. This may be because the occasional synchronous light somehow emphasizes the temporal delay between the onset of the tone and the onset of the water presentation.

GENERAL DISCUSSION

In general terms, the experiments reported here explored the possibility that the occurrence and strength of anticipatory conditioned responding may be attributable to the animal's uncertainty about the time of UCS presentations. The finding of less anticipatory conditioned licking when the time of water delivery during conditioning trials is marked by a salient synchronous stimulus provides support for this hypothesis. The explanation of this main result, as well as a number of related details, may be sought in several different theoretical models; a few of these will be examined here.

Associative Models

Associative models of conditioning, although unable to specify the precise function which relates the strength of conditioned responding to the strength of association, assume that the relationship is monotonic. Within this framework, the weaker conditioned responding observed in the experimental condition would be attributed to a reduction in the effective excitatory associative strength of the CS when the onset of the UCS is marked by a salient stimulus. This reduction in the excitatory strength of the CS could result from (i) the general interference with conditioning to the CS by the marker stimulus; (ii) the overshadowing of conditioning to the CS by the marker stimulus; (iii) a reduction in the CS-UCS correlation due to a change in the stimulus sampling rate; or (iv) the development of inhibition to the CS. Each of these possibilities will be discussed.

Interference

According to the interference hypothesis, the intratrial presentation of a salient stimulus disrupts excitatory conditioning to the CS. If the salient stimulus acts merely as a general distractor, then its ability to attenuate conditioning to the CS should be independent of its temporal relation with the UCS. However, no attenuation of anticipatory conditioned licking was observed in Experiment 4 when the time of light presentations during conditioning trials with a tone CS had no consistent relation with the onset of water deliveries. A reduction in anticipatory responding was, however, observed in Experiment 3 when the light was proximal to, but not always coincidental with, water onset. These findings show that interference with conditioning to the CS, if present, requires that the putative distractor be temporally proximal to the onset of UCS presentation.

Overshadowing

The weaker associative strength of the CS could also be a consequence of the *overshadowing* of conditioning to the CS by the synchronous stimulus. As originally used by Pavlov (1927), overshadowing referred to the failure of the less intense, or less salient, component of a compound CS to elicit conditioned responding when presented alone on test trials even though this relatively weak stimulus could support reliable conditioned responding if it had been trained in isolation. One account of the phenomenon of overshadowing is provided by Rescorla and Wagner (1972).

They assume that the total associative strength supportable by any given UCS is bounded and must be distributed among the stimuli present in the conditioning situation and further, that the rate at which the available associative strength is engaged by any particular stimulus is governed by its relative salience. These assumptions necessarily imply that, even with identical reinforcement histories, the associative strengths of the components of a compound CS will be inversely related, with the more salient component gaining greater associative strength.

In the present experimental condition, the temporally prior CS and the marker stimulus can be considered as components of a compound CS. The associative strength of the temporally prior CS could be weak if the marker stimulus controlled a greater proportion of the available associative strength. Less anticipatory conditioned responding would thus be explained in terms of the overshadowing of conditioning to the CS by the relatively more salient marker stimulus.

It is unlikely, however, that the synchronous stimulus was relatively more salient either because of its intensity or modality. In the present study, the reduction of conditioned licking to the CS was observed using a number of different marker events including the removal of a stimulus (as in the Nonoverlap and Gap procedures of Experiment 1), as well as the presentation of a stimulus of a different modality than the CS (as in Experiments 2 and 5). It is possible that the very brief duration of the synchronous stimulus makes it startling, and thus more salient than the CS. If this is so, stronger conditioned responding to the CS should be observed if the marker stimulus is made less startling, perhaps by increasing its duration so that it is coextensive with the entire water presentation. In the event that conditioned responding to the temporally prior CS is unaffected by this manipulation, the overshadowing interpretation would have to postulate that temporal proximity to the UCS may make a stimulus more salient. There is no provision for such a postulate within the Rescorla-Wagner model as stated since the salience of a stimulus is assumed to be a function of its physical properties only. The possibility that CS salience is affected by the temporal relation between the CS and UCS could, however, be accommodated within the selective attention theory of Mackintosh (1975).

Unlike Rescorla and Wagner, Mackintosh assumes that the salience of a stimulus (represented as α_i) may be enhanced or diminished according to the schedule of reinforcement associated with that stimulus relative to that of other stimuli in the conditioning situation. Recently it has been suggested that the relative favourableness of the CS-UCS temporal relation may similarly influence stimulus salience (Dickinson & Mackintosh, 1978). Whether the greater salience of component A of the compound CS AB arises from its physical properties, its relation with the UCS, or a combination of both factors, the overshadowing of conditioning to B is explained as follows. Since the value of α_i will be greater for A than B early in training, $(\lambda - V_A)$ will always be larger than $(\lambda - V_B)$. Under these conditions, α_A should increase whereas α_B should decrease. Over trials then, the associative strength of A will approach λ but little conditioning of B should occur.

According to this account of overshadowing, the weaker associative strength of the CS in the experimental treatment would be accompanied by a decrease in the salience of the CS from its initial value. Such a reduction would have been indicated if, in Phase 3 of Experiment 5, the acquisition of conditioned inhibition to the light CS was _slower_ following the Light-Tone, than Light, pretreatment. This was not observed to be the case: the extinction of conditioned licking to the clicker-light compound CS was not different for these groups. However, the failure to observe a difference in this phase of the experiment may be due to the combined effect of differences in both the salience _and_ excitatory strength of the light following completion of Phase 1. Thus the rate at which inhibitory control over responding was acquired by the relatively less salient light with weak excitatory strength following the Light-Tone treatment may have been the same as that of the more salient, but strongly excitatory, CS established with the Light procedure. Whether the experimental treatment does, in fact, reduce the salience of the CS remains an open question for further investigation.

Degradation of the CS-UCS Correlation

Another way in which the experimental treatment could result in the weaker associative strength of the CS is suggested by Rescorla and Wagner's account of the effects of the CS-UCS correlation on conditioning. They imply that the duration of the CS may serve as a standard which is used to partition the intertrial interval (ITI) into discrete, but unmarked, trials. The frequency of reinforcement and nonreinforcement during these trials provides a means by which conditioning to the static background cues might be accomplished. Such an analysis could be applied to the present experimental situation. If the animal in the experimental treatment uses the duration of the synchronous stimulus, rather than the duration of the CS, as the standard, then the CS as well as the ITI might be partitioned into a series of unmarked trials. This would result in a significant number of trials of 0.5 sec duration in which the CS was present but not reinforced, thereby attenuating the associative strength of the CS. It cannot be that the duration of the briefest discrete stimulus present in the conditioning situation is always used as a standard. If this were so, the rate of conditioned responding to the CS of the Tone-Light and Tone-Light Variable groups in Experiment 4 should have been similar since these procedures result in an equivalent number of reinforced and nonreinforced 0.5-sec trials in which the CS is present. Thus, if the animal selects one stimulus from the many present in the conditioning situation to serve as a standard, this selection must, in part, be based on the relative temporal proximity to the UCS. Experimental manipulation of the duration of the marker stimulus may enable further evaluation of this correlational interpretation of the present experimental findings.

Inhibitory Conditioning

The longer response latencies to the CS and the scalloped distribution of licking during the CS found in Experiment 2 are consistent with the possibility that the experimental treatment makes the CS somewhat inhibitory. However, no support for this hypothesis was found in Experiment 5: the conversion of the light CS into a conditioned inhibitor of responding was not facilitated by pretraining with the experimental, as opposed to control, procedure. It is possible that a more sensitive testing procedure would have demonstrated that the initial portion of the CS was inhibitory. The development of inhibition of delay to the CS would be indicated if, for example, the presentation of a novel stimulus soon after CS onset results in the "disinhibition" of the licking response.

Informational Models

Although an explanation for the attenuation of anticipatory conditioned licking observed when a salient stimulus marks the onset of water presentations may be sought in terms of the limited or differentiated associative strength of the CS, an alternative approach is to examine the functional significance of the marker stimulus in terms of the informational role of conditioned stimuli in the experimental situation. In this context, conditioned responding is not viewed exclusively as a consequence of the momentary strength of associative connections activated by the current environmental stimuli, but rather as an outcome of the animal's knowledge of the interrelations among the main stimuli in the conditioning situation. Conceptually, this description of the experimental situation is similar to the Tolmanian approach to learning (Tolman, 1932, 1937; Tolman & Brunswik, 1935). Whereas Tolman emphasized the animal's sophisticated knowledge of the spatial relations within its environment, this discussion will focus on the knowledge that the organism acquires about the temporal relations between stimuli in the conditioning situation. Although the analysis of conditioning and conditioned responding in terms of the informational role of situational stimuli is less well articulated than the Rescorla-Wagner or selective attention models, nevertheless two general assumptions can be formulated which characterize this approach.

Informational Significance and Temporal Uncertainty

First, according to the informational interpretation of classical conditioning, the organism acquires knowledge about predictive relations between various situational stimuli, both conditioned and unconditioned, present in its environment. Stimuli which reduce the animal's uncertainty because their occurrence enables the animal to better predict when the next UCS is likely to be presented can be said to be informative. The informational value of the temporally prior, contiguous CS is obvious and attributable to the imminence of UCS presentation following CS onset. However, the apparatus cues, in the presence of which all paired presentations of the CS and UCS occur, can also be considered informative. Despite the rather imprecise quality of the information provided by such cues when compared to that of the discrete CS, the static stimulus aspects of the experimental chamber can nevertheless take on considerable importance when viewed in the larger context of the daily routine of the laboratory animal. This is particularly so when the UCS has always and only been experienced in the conditioning situation (as with the administration of shock in aversive conditioning procedures). On the other hand, the presence of intratrial cues which mark the passage of time during the conditioning trial may enable the animal to predict with even greater precision when the UCS will be presented following trial onset, thereby making the CS alone relatively less informative.

This description of the conditioning situation implies that the knowledge acquired by the organism in the conditioning situation involves multiple associations between stimuli. Further, this knowledge may be hierarchically organized according to the absolute temporal relations that these stimuli have with the UCS but the informational significance of any given stimulus may depend upon its relative temporal relation with the UCS, as Bindra (1976) has suggested. It follows that the more informative stimuli will be those that are most proximal to the time of UCS occurrence.

Informational Significance and Conditioned Responding

The second general assumption implicit in the informational approach to classical conditioning is that the acquisition of knowledge about predictive relations in the conditioning situation somehow enables the animal to respond selectively to stimuli in ways which favour behavioural adaptation. Responding in advance of the UCS often serves an adaptive function in that the animal may be better prepared for the UCS at the time of its presentation (e.g., salivation in advance of food ingestion). As such, preparatory responses established with classical conditioning procedures include those that insure the consumption of appetitive UCSs (e.g., approach to the site of food or water delivery) or minimize the deleterious effects of aversive UCSs (e.g., closure of the eyelid in response to forthcoming shock to the orbital region of the eye). This tendency to engage in conditioned responding anticipatory to the UCS may, however, be opposed by a tendency to avoid unnecessary work or energy expenditure. Accordingly, optimal behaviour in the conditioning situation would be the initiation of responding at times which most closely approximate the onset of UCS presentation. Clearly the animal's sensitivity to the differential informational value of stimuli in the conditioning situation can operate so that a balance between these opposing tendencies may be achieved, resulting in behavioural modification that is both preparatory and efficient.

This analysis of classical conditioning is consistent with the suggestion that the animal engages in anticipatory conditioned responding to the extent that it is uncertain about the exact time of UCS presentations. As such, the strength of conditioned responding must be considered a poor, if not misleading, index of the efficacy of various conditioning procedures. It may be argued that a better appreciation of the animal's sensitivity to and knowledge of the temporal relations in the conditioning situation may be obtained by examining <u>when</u> conditioned responding occurs during the experimental session. Indeed the distribution of conditioned responding anticipatory to UCS presentation can be shown to reflect the relative informational value of the sequence of stimuli in the conditioning situation.

In the event that apparatus cues best indicate the time of UCS presentation, anticipatory conditioned responding is temporally undifferentiated and is evidenced as a constant, if not low, response rate which is maintained throughout the experimental session (LaBarbera & Church, 1974; Seligman, 1968). When UCS presentations are programmed to occur at fixed intervals during the experimental session, the animal may use temporal cues to predict when the next UCS presentation is likely to occur; accordingly, anticipatory responding is inversely related to the time remaining until the next scheduled UCS (LaBarbera & Church, 1974; Pavlov, 1927). This temporal gradient of responding can be sharpened if the passage of time between UCS occurrences is marked by successive stimulus presentations (Hendry, Yarczower & Switalski, 1969). The occurrence of anticipatory responding is further restricted when UCS presentations are shortly and reliably preceded by some exteroceptive stimulus as in forward conditioning procedures; the animal now engages in anticipatory responding only or primarily in the presence of this stimulus.

The procedural differences across these experiments may be viewed as systematic variations along a continuum defined by the temporal specificity of the predictive relations found in the conditioning situation. The present experimental methodology thus represents a logical extension of this characterization of conditioning procedures. Further, the behavioural outcome of the experimental conditioning procedure used in the series of experiments reported here is what would be expected given the additional and more precise information that is available to the rat about the time of UCS presentations. When the onset of water deliveries is marked by a salient, synchronous stimulus, anticipatory licking is no longer uniform throughout the CS but is temporally differentiated with peak responding occurring at the time of water onset.

The general conclusion which may be drawn from these experiments is that there is a strong correspondence between the hierarchically ordered interrelations between stimuli in the conditioning situation as previously described and the temporal differentiation of anticipatory conditioned responding during the experimental session. In all experiments, the rate of anticipatory responding was found to be maximal in the presence of stimuli which most precisely (i.e., with the shortest delay) predicted the presentation of the UCS. The mechanism by which the relative informational significance of stimuli gets translated into the selective responding to particular stimuli needs to be specified. This empirical relation may be accounted for within the expectancy (e.g., Bolles, 1972) and incentive-motivational (e.g., Bindra, 1974; 1976) models of learning. According to these theoretical formulations, the arrangement of predictive relations between initially neutral stimuli in the conditioning situation and the UCS results in the establishment of expectancies or central motive states (cms) appropriate to the UCS. Further, it is assumed that the primary determinant of the likelihood of responding in ways appropriate to that UCS is the momentary strength of the expectancy or cms generated by the present environmental stimuli. It may be that the informational significance of conditioned stimuli, as conceptualized above, acts to modulate the strength of the expectancy or cms over time, resulting in the selective responding to stimuli in ways which are behaviourally adaptive.

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APPENDIX A

A two-way analysis of variance comparing licking during the Pre-CS period

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	8.57	2	4.29	3.02
S(T)	29.90	21	1.42	
Block (B)	6.24	3(1)	2.08	1.05
TB	11.16	6(2)	1.86	0.94
BS(T)	125.04	63(21)	1.98	

[a] conservative degrees of freedom are given in parentheses

APPENDIX B

Summary table of Newman-Keuls tests comparing the probability of licking during the CS presentation on the 4 30-trial blocks (I: Block 1; II: Block 2; III: Block 3; IV: Block 4)

	II	III	IV
I	13.07 **	15.56 **	15.86 **
II		2.48	2.77
III			0.29

** $\underline{p} < .01$

$df_{error}=63$

APPENDIX C

Two-way analysis of variance (treatment x block) on the time spent in the water alcove during Pre-CS Period

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	2.63	2	1.32	1.08
S(T)	25.64	21	1.22	
Block (B)	1.17	3(1)	0.39	0.47
TB	3.90	6(2)	0.65	0.78
BS(T)	52.27	63(21)	0.83	

[a] conservative degrees of freedom are given in parentheses

APPENDIX D

Two-way analysis of variance on the baseline rate of licking during the Pre-CS period by subjects in the Tone and Tone-Light groups

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	375.25	1	375.25	0.75
S(T)	11037.50	22	501.70	
Block (B)	2617.75	3(1)	872.58	5.73 *
TB	183.03	3(1)	61.01	0.40
BS(T)	10052.97	66(22)	152.32	

* $p < .05$

[a] conservative degrees of freedom are given in parentheses

APPENDIX E

Newman-Keuls tests comparing the mean rate of licking during the Pre-CS period on the four blocks of trials (I: Block 4; II: Block 3; III: Block 2; IV: Block 1)

	II	III	IV
I	0.35	0.47	5.05 **
II		0.12	4.69 **
III			4.57 **

** $\underline{p} < .01$

$df_{error}=66$

APPENDIX F

Two-way analysis of variance on the percentage of trials in which at least 1 lick occurred as a function of treatment condition and block

Source of Variation	Sum of Squares	df^a	Mean Square	F
Treatment (T)	0.6851	1	0.6851	4.99 *
S(T)	3.0205	22	0.1373	
Block (B)	1.1548	3(1)	0.3849	36.69 **
TB	0.0095	3(1)	0.0032	0.30
BS(T)	0.6925	66(22)	0.0105	

* $p < .05$
** $p < .01$

[a] conservative degrees of freedom are given in parentheses

APPENDIX G

Analysis of the baseline rate of licking during the pre-CS period

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	2034.51	2	1017.26	2.45
S(T)	13724.45	33	415.89	
Block (B)	5073.08	4(1)	1268.27	8.55 **
TB	1666.71	8(2)	208.34	1.40
BS(T)	19590.38	132(33)	148.41	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

APPENDIX H

Analysis of variance on the total number of licks during the pre-CS period

Source of Variation	Sum of Squares	df^a	Mean Square	F
Treatment (T)	452.60	2	226.30	0.69
S(T)	10769.56	33	326.35	
Block (B)	4577.06	3(1)	1525.69	8.69 **
TB	981.13	6(2)	163.52	0.93
BS(T)	17389.41	99(33)	175.65	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses

APPENDIX I

Analysis of variance comparing the effects of treatment and block on licking during the pre-CS period during Phase 1 of Experiment 5

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	2.21	1	2.21	0.02
S(T)	2199.00	18	122.17	
Block (B)	1151.43	3(1)	383.81	5.89 *
TB	312.14	3(1)	104.05	1.60
BS(T)	3521.18	54(18)	65.21	

* $\underline{p} < .05$

[a] conservative degrees of freedom are given in parentheses

APPENDIX J

Analysis of variance on the pre-CS licking in Phase 2 of Experiment 5

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	1319.78	2	659.89	1.51
S(T)	11783.39	27	436.42	
Block (B)	730.56	2(1)	365.28	1.60
TB	620.99	4(2)	155.25	0.68
BS(T)	12298.20	54(27)	227.74	

[a] conservative degrees of freedom are given in parentheses

APPENDIX K

Two-way analysis of variance on licking during the Pre-CS period in Phase 3 of Experiment 5

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	38.97	2	19.48	2.20
S(T)	239.45	27	8.87	
Block (B)	4.24	3(1)	1.41	1.03
TB	8.55	6(2)	1.43	1.04
BS(T)	110.57	81(27)	1.37	

[a] conservative degrees of freedom are given in parentheses

APPENDIX L

Two-way analysis of variance on licking during the Pre-CS period in Experiment 6

Source of Variation	Sum of Squares	df	Mean Square	F
Treatment (T)	38.03	1	38.03	0.43
S(T)	1607.25	18	89.29	
Block (B)	4.23	1	4.23	0.05
TB	65.03	1	65.03	0.83
BS(T)	1409.25	18	78.29	

APPENDIX M

Two-way analysis of variance on licking during the Pre-CS period in Experiment 7

Source of Variation	Sum of Squares	df[a]	Mean Square	F
Treatment (T)	2861.12	3	953.71	2.51
S(T)	16685.67	44	379.22	
Block (B)	8107.29	4(1)	2026.82	11.92 **
TB	1321.55	12(3)	110.13	0.65
BS(T)	29922.02	176(44)	170.01	

** $p < .01$

[a] conservative degrees of freedom are given in parentheses