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ASSOCIATIONS TO CONTEXTUAL STIMULI AS A DETERMINANT OF LONG-TERM HABITUATION

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ASSOCIATIONS TO CONTEXTUAL STIMULI AS A DETERMINANT OF LONG-TERM HABITUATION

by

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A dissertation submitted to the Graduate Faculty in Psychology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

ASSOCIATIONS TO CONTEXTUAL STIMULI AS A DETERMINANT OF LONG-TERM HABITUATION

by

Nancy A. Marlin

Advisor: Professor Ralph R. Miller

Wagner has presented a model for habituation in which an unconditioned stimulus (US) is differentially effective in eliciting an unconditioned response (UR) based upon whether the US is "surprising" or "expected". A surprising US is assumed to be more effective in eliciting a UR than is an expected US. The expectancy process hypothesized to underlie habituation is dependent upon whether or not the stimulus is prerepresented or "primed" in short-term memory (STM) at the time of its presentation. Priming may result either from a recent presentation of the stimulus or from retrieval cues that predict the occurrence of the stimulus. The two methods by which the stimulus may be primed involve different temporal aspects of habituation. Wagner hypothesizes that "short-term" habituation is a temporally-localized decrement attributable to priming by recent past stimulus presentations, while "long-term" habituation results from priming by the retrieval cues of the test situation. The contextual cues in long-term habituation are assumed to function as conditioned stimuli in a traditional Pavlovian paradigm.

The present research tests four predictions of Wagner's model of long-term habituation by examining the hypothesized association between the contextual cues and the habituated stimulus. Experiment 1 established parameters for long-term habituation of the rat's acoustic startle response. Experiment 2 attempted to overshadow associations to contextual cues by providing a more reliable predictor of the US occurrence; Experiment 3 investigated the effect upon long-term habituation of changes in contextual cues; Experiment 4 provided treatments designed to extinguish the associations between the contextual cues and the habituated stimulus; and Experiment 5 examined latent inhibition of habituation by giving prior exposure to the contextual cues. The results of these experiments uniformly failed to support Wagner's associative model of long-term habituation, but are consistent with a nonassociative memorial model concerned with habituation to the entire experimental situation rather than exclusively to the US.

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Habituation is typically defined as a decrease in responding to a stimulus which results from repeated presentations of the stimulus and cannot be accounted for solely in terms of sensory adaptation or motor fatigue. Because the term habituation is frequently used to refer both to the observed behavioral change as well as to the underlying process, the former usage will presently be termed a "response decrement" to avoid ambiguity. Although habituation represents a behavioral change due to specific experiential factors, it has been largely ignored by learning theorists other than those directly concerned with the neurophysiology of learning. This has been primarily due to a preoccupation of learning theorists with classical and instrumental conditioning paradigms (Rescorla & Holland, 1976). This preoccupation and the concommitant disinterest in habituation can be related to two assumptions about how classical and instrumental conditioning differ from habituation.

One assumption is that habituation has frequently been considered to be a short-lived phenomenon, lasting only seconds or minutes, and therefore of little consequence for long-term changes in behavior. However, this view has been demonstrated to be erroneous. As early as 1955 Sharpless and Jasper on the basis of their findings from recordings of arousal in human subjects, suggested that a distinction be made between "short-term" and "long-term" habituation. More recently, additional supportive evidence for the existence of long-term habituation has been obtained. Although there are no clear temporal parameters dividing short-term from long-term habituation, it has become overwhelmingly clear that some forms of habituation can last at least on the order of days (Carew, Pinsker & Kandel, 1972; Leaton, 1974; Logan & Beck, 1978), and Kandel has suggested that some of the physiological changes underlying long-term habituation may in fact be permanent (Castellucci & Kandel, 1976).

A second, more fundamental, issue that has excluded habituation from the study of learning is that habituation is considered to be nonassociative. Rachlin illustrates this point in his text: "many psychologists restrict the term 'learning' to processes requiring associations between stimuli and responses. Under this more restrictive definition habituation and sensitization would not be examples of learning" (Rachlin, 1976, p. 104). Throughout the history of psychology, learning in the broadest sense has been concerned with the formation of associations. Although it is agreed that both classical and instrumental conditioning reflect such associative processes, it is less certain what types of behavioral changes represent nonassociative learning. In some cases, such as the conditioned taste-aversion literature, the term "nonassociative" has been used somewhat synonymously with instinctual behavior (e.g., Mitchell, Scott, & Mitchell, 1977).

Referring to habituation, the term "nonassociative" implies that the observed response decrement is dependent solely upon the parameters of US presentaton. However, this statement must be qualified. It is possible that habituation represents associative learning in which the iterated stimulus is associated with the nonoccurrence of any biologically significant event. That is, a stimulus which initially elicits an orienting or arousal response may alert the animal to the possibility of some potentially important event, but with repeated presentations the subject could learn to ignore the stimulus. Thus the repeated stimulus would no longer elicit a response, as it would be associated with nothing of biological importance for the subject. Seemingly this process involves associative learning in the same way as does Mackintosh's mechanism of learned irrelevance (Mackintosh, 1973). It could also be argued that, because habituation necessitates that the subject have a memory of the prior presentations, this process must therefore involve some aspect of associative learning. The subject must minimally have associated the elements comprising the stimulus and, further, have associated the stimulus temporally as having occurred at specific times in the past. Accepting this assumption, of course, leads one to the conclusion that nearly everything involves associative learning.

On a more conventional level of analysis, there have been several interpretations of habituation as being an associative process within the traditional concept of associative learning. The most recent and the most explicitly stated of these theories has been postulated for long-term habituation by Allan Wagner (1976) as an extension of his more general theory of differential rehearsal. To summarize Wagner's orientation which is discussed in detail below: a stimulus is differentially effective in promoting memorial processing depending upon whether the stimulus is "surprising" or "expected." If it is surprising, the stimulus promotes memorial processing; whereas if it is expected, it does not. Stimuli are considered expected if their memorial representations are present in short-term memory (STM) at the time of their presentation. In the case of long-term habituation this memorial representation is assumed to be associated with the environmental or contextual stimuli in which the habituation procedure occurred. Thus the contextual cues will elicit the STM representation of the habituated stimulus, and, according to Wagner's interpretation of habituation, the response to an expected stimulus will be diminished relative to the response to an unexpected stimulus. Consequently, long-term habituation is assumed to be dependent upon the integrity of the association between the contextual cues and the potentially habituated stimulus.

Wagner's application of his differential rehearsal model to habituation is predicated largely upon his interpretation of the data from a dissertation by Michael Davis (1970a). Recording the percentage of startle responses to a 50-msec, 120-dB pure tone, Davis first matched subjects for responsiveness to the tone at random interstimulus intervals of 2, 4, 8, and 16 seconds. Following this "pre-habituation" treatment he exposed one group of rats to 1000 tones presented at a constant interstimulus interval of 2 seconds, and a second group to 1000 tones at a constant interstimulus interval of 16 seconds. Both groups were then tested again for their startle response to the tone at the original four interstimulus intervals, either one minute or one day after the habiutation training. The major finding was that within the habituation training session the 16-second group was more responsive than the 2-second group; however, this pattern was reversed when they were tested one minute or one day later. On both these tests, the 2-second group was more responsive at all four interstimulus intervals than was the 16-second group. Wagner attributes this effect to the fact that during habituation training greater associative processing of the contextual cues and the tone occurred in the 16-second group than in the 2-second group. There are two interrelated reasons within his theory why this would be predicted: 1) the tone for the 16-second group was more surprising and therefore evoked more processing than in the 2-second group in which the memorial representation of the tone at the time of each tone onset was greater due to the more recent prior presentation of the tone, and 2) there was a greater opportunity for memorial processing and consequent formation of associations between the contextual cues and the tones in the 16-second group owing to the greater temporal spacing between presentations. Thus, on the long-term tests using the four interstimulus intervals, the tone would be more expected in the 16-second group, which should therefore display the greater long-term habituation. To fully appreciate Wagner's interpretation of long-term habituation, it is necessary to view Davis' data within the scope of Wagner's more general theory of learning.

Wagner's Model of Differential Rehearsal

In recent years theories of animal learning have increasingly accepted the concept that the expectancy of an organism in a particular situation is a critical determinant of the organism's behavior in that situation. Although such concepts have a relatively long history in theories of learning (e.g., Tolman, 1932), recently there has been a resurgence of interest in such cognitive conceptions of animal behavior (e.g., Hulse, Fowler & Honig, 1978). One of the probable reasons underlying the previous reluctance of many learning theorists to utilize the animal's expectancy as an intervening variable was the lack of theoretical rigor of expectancy theories. Unlike the precisely defined mechanisms of some alternate approaches, analyses in terms of expectancies frequently did not extend beyond a descriptive account of the behavior. Despite the intuitive appeal of such descriptions, they were often seriously lacking as theoretical models of behavior. To further our understanding of learning processes, some basic questions need to be answered concerning expectancies. One of the few theories attempting to address such issues is the Rescorla-Wagner Model (1972), which incorporated concepts proposed earlier by Kamin.

Kamin (1968, 1969) had suggested that only surprising events are effective in promoting the formation of new associations. Fully predictable reinforcers were assumed not to facilitate conditioning. That is, to the extent the animal fully expects the unconditioned stimulus (US) based on the conditioned stimulus (CS), no subsequent conditioning would occur. The data supporting this interpretation were based primarily on blocking and overshadowing experiments involving compound stimuli in Pavlovian conditioning. Kamin's hypothesis has proven extremely influential in expectancy theories of animal learning. More recently, Allan Wagner and his colleagues (Wagner, Rudy & Whitlow, 1973; Wagner, 1976, 1978, 1979) have proposed a differential rehearsal model as the basis for the role of expectancy in learning theory. Wagner's differential rehearsal model represents an elaboration of Kamin's basic idea, including a theoretical mechanism by which such expectancies are formed and a statement as to how they influence behavior. The development of Wagner's theory and the empirical investigations of its predictions are particularly important in that they provide a more complete theoretical framework for expectancy theories.

In their monograph entitled "Rehearsal in Animal Conditioning," Wagner, Rudy and Whitlow (1973) first set forth the principle of how animals differentially process surprising and expected events. Over the several years since this influential publication, Wagner and his students have refined and extended the theory, but its essential aspects have remained unaltered. The differential rehearsal model places major emphasis upon the memorial processing of events. Toward this end, a variation of the memory models espoused by information-processing theorists (Atkinson & Shiffrin, 1968; Waugh & Norman, 1965) was adopted. This approach distinguishes between a short-term memory (STM) of limited capacity and a long-term memory (LTM) of seemingly unlimited capacity. Information is maintained in STM during active processing, typically termed rehearsal, that increases the probability that some representation of the information will be transferred to LTM. Such active processing does not appear to be required for maintenance of information in LTM. Although the use of the term rehearsal has conventionally been restricted to memory processes in human subjects, in the present context rehearsal will be used to refer to the post-trial processing the memorial representation of the stimulus undergoes. Borrowing these assumptions concerning the structure of memory, Wagner hypothesized that the amount of rehearsal given to incoming information will vary as a function of the expectancy of the organism. Information provided by expected events will provoke little or no rehearsal whereas surprising events will induce much rehearsal. While being rehearsed information is maintained in STM; hence, Wagner's theory predicts that the representation of surprising information will be retained in STM for a longer duration than will the representation of an expected event.

As the critical variable in this formulation is the expectancy of the organism, that is, the degree to which the event is expected or surprising, it is necessary to be able to operationally define this expectancy dimension. Rescorla and Wagner, (1972) in their attempts to specify this variable, have begun to come to terms with a common weakness of expectancy theories. Consistent with the Rescorla-Wagner model of conditioning, Wagner defines expectancy of an event "on the basis of the entire aggregation of cues which preceded it" (Wagner, Rudy & Whitlow, 1973, p. 422). Reinforcers that are highly predicted by preceding cues (in a Pavlovian paradigm these cues are typically the CSs) are expected and not rehearsed, whereas reinforcers (or USs) that are not predicted are surprising and elicit rehearsal. Rehearsal subsequently provides for a transfer of the event trace (CS-US association) into LTM. Furthermore, associations depend upon the duration of conjoint rehearsal of the stimuli composing the event (Terry & Wagner, 1975).

If the memorial representation of a stimulus is active in STM at the time the stimulus is presented less rehearsal will ensue. Wagner labels this prestimulus representational process _priming_. There are two different ways in which priming may occur; however, the behavioral influence of having the memorial representation in STM at the time the stimulus is presented is the same regardless of the method of priming. STM priming of a particular stimulus may be _self-generated_, resulting directly from a recent occurrence of the stimulus itself, or it may be _retrieval-generated_ (more recently termed associatively-generated, Wagner, 1979), by the internal retrieval of the memorial representation from LTM to STM due to the presentation of associated cues.

Wagner cites three different lines of research which are supportive of his conceptions concerning differential rehearsal of retrieval-generated priming (Wagner, 1976, 1978, 1979). Though it is acknowledged that each phenomenon itself may be subject to viable alternative explanations, Wagner's model has the theoretical power to integrate the results from these distinctly different areas as well as to make predictions concerning other behavioral phenomena including habituation as described above. Because of their importance, I will briefly review these three experiments involving retrieval-generated priming, as well as a fourth study demonstrating the effects of self-generated priming. In these experiments, all of which involve Pavlovian conditioning, the surprising or expected event is the US. However, Wagner's model is not limited to expectancies concerning the US, and similar analysis can be made about the processing of the CS in a Pavlovian situation (see Wagner, 1979).

The first series of experiments investigated the effects of blocking. Blocking refers to the observation that prior conditioning to stimulus A, which is later presented in compound with stimulus X, will reduce or "block" the associative strength that X acquires relative to the strength it would have acquired without the prior conditioning of stimulus A. A necessary factor for the blocking phenomenon is that the reinforcer remain the same; that is, if the US is changed when the compound AX is presented, "unblocking" will occur, such that on subsequent tests X will be shown to have acquired appreciable associative strength. Wagner's interpretation of these findings, consistent with Kamin's original proposal that an unexpected reinforcer would cause the subject to engage in "retrospective contemplation" of the CS, is that only a surprising US will promote the processing necessary for associative learning to occur.

Wagner (1976, 1978, 1979) reports two studies from his laboratory that support this interpretation. In both experiments eyelid conditioning in rabbits was recorded. In the first study, one group of subjects was highly trained to CSa, and a second group was weakly trained to CSb. The strength of the association was manipulated by the number of training trials given and was evident in the percentage of conditioned responses emitted at the end of acquisition. Subsequent training on a compound stimulus, CSax or CSbx respectively for the two groups, was then followed by nonreinforcement test trials in which only CSx was presented. As predicted, the magnitude of blocking was greater in the first group, the group that had received greater pretraining, than in the second group. In the second study, subjects were also either highly trained to CSa or weakly trained to CSb, and additionally, all were highly trained to CSx. Each subject then received nonreinforced presentations, half the subjects with compound CSax and the remaining half with compound CSbx. A faster rate of extinction was reported with CSax, in which the signal value was stronger due to the greater degree of training. The results were such that they could not be accounted for by ceiling or floor effects. Thus, both blocking and unblocking effects vary in magnitude as a function of the expectancy of the animal. Such effects, although consistent with Wagner's model, are not uniquely supportive of his differential rehearsal model to the exclusion of other interpretations, notably Mackintosh's theory of learned irrelevance (e.g., Mackintosh, 1973).

A second series of studies, first reported by Wagner, Rudy, and Whitlow (1973), tested the role of rehearsal in the formation of asociations more directly. It was reasoned that if rehearsal of surprising events must be protracted for entry into LTM, and if STM is a limited capacity store, then competing information presented shortly after a surprising event would disrupt rehearsal of the former and thus retard associative learning about that event. Moreover, the intefering material should be more effective in this capacity if it itself were unexpected, as surprising information would command a greater fraction of the limited capacity and consequently be max disruptive to processing of the initial target information. To test these hypotheses, the eyeblink of rabbits was conditioned. The animals were trained to discriminate between CSa which was reinforced and CSb which was nonreinforced. Following acquisition of this discrimination, all subjects were trained on a third stimulus in a different modality, CSc, which was consistently reinforced. Ten seconds after each CSc-US pairing, four groups of subjects were presented with a posttrial episode that was congruent with their initial training in that the occurrence of a US or $\overline{\text{US}}$ was predicted by the CS (CSa-US or CSb-$\overline{\text{US}}$) or a posttrial episode that was incongruent with their basic discrimination and would therefore be surprising to the animal (CSa-$\overline{\text{US}}$ or CSb-US). The two groups with the incongruent posttrial episode acquired the conditioned response to CSc at a significantly slower rate than did the groups with a congruent posttrial episode. Subsequent experiments in this series demonstrated that the performance of the groups presented with incongruent posttrial episodes was in fact depressed rather than learning in the congruent groups being facilitated, and that this depression was specific to the CSc trials preceding incongruent events. Moreover, in a further study using intervals of 3, 10, 60, or 300 seconds between CSc trials and potentially interfering trials, a significant effect of time on the acquisition of the response was obtained, with the best performance exhibited by the 300-second interval group and the poorest by the 3-second interval group. A similar finding using a conditoned emotional response (CER) procedure has been reported by Kremer (1979).

These studies are consistent with the premise that rehearsal is necessary for the formation of associations between a CS and US, and that surprising information will disrupt this rehearsal process by competing for STM processing capacity. However, one rather disturbing aspect of this effect is the continued effectiveness of the incongruent posttrial episode to function as surprising information. After some number of trials, each of which were always followed ten seconds later by the same posttrial episode, the question can be raised as to why this event continued to be surprising to the animal. Of course, despite the fact that the performance of the incongruent groups was always poorer than that of the congruent groups, acquisition did occur over trials in both groups. For the incongruent groups, this acquisition presumably reflects the summation of the ten seconds of rehearsal available on each trial prior to the posttrial episode. Alternatively, it could be that the incongruent posttrial episode is no longer surprising enough to compete for rehearsal time with the target information due to acquisition on earlier trials of information concerning the initially incongruent event. Wagner's data do not allow for a distinction to be made between these two explanations; however, this possibility could be tested by employing diverse surprising posttrial episodes rather than consistently repeating the identical one.

Another curious feature of this research is that in the last study in which the time between the trial and the interfering event was varied, acquisition continued to improve with increasing delays in the onset of the incongruent event up to and including the maximal interval used. Compared to studies of physiological intervention of posttrial processing (e.g., Chorover & Schiller, 1965; Marlin, Berk & Miller, 1979), 300 seconds appears to be a comparatively long duration over which essential rehearsal is assumed to be taking place. Although it is clearly dangerous to compare experiments with different parameters, tasks, and subjects, in many studies in which memorial processing was disrupted by such drastic treatments as electroconvulsive shock, performance was not seen to differ from control animals receiving no physiological intervention if only a few seconds elapse between training and the interfering treatment. As a control group not receiving any posttrial episodes was not included in Wagner, Rudy, and

Whitlow's (1973) study, it is difficult to assess when the performance was essentially asymptotic.

A third series of studies (Terry & Wagner, 1975) attempted to address the difficult but theoretically important issue of whether the memorial representation of a surprising event is in fact maintained in STM longer than the memorial representation of an expected event. This experiment necessitated a rather complicated procedure. Rabbits were required to learn that a particular stimulus, CSx, would be reinforced or nonreinforced depending upon the occurrence or nonoccurrence of the US some seconds *prior* to CSx. That is, CSx was followed by the US on a random half of the trials, and its occurrence was predictable by a prior delivery of US or $\overline{US}$. These "preparatory" USs, which functioned as discriminative cues, had been separately used as reinforcers in a Pavlovian paradigm in which CSa was reinforced and CSb was nonreinforced. Thus, analogous to the interference studies discussed above, the preparatory US could be viewed as surprising or expected as a function of its being preceded by CSb or CSa respectively. The basic finding was that when the preparatory US was surprising (i.e., the preparatory sequence was either CSa-$\overline{US}$ or CSb-US), subsequent responding to CSx was enhanced relative to when the preparatory US was expected based on its preceding CS. Given their control over responding, it appears that the representations of surprising USs are kept active in STM longer than the representations of expected USs, even when the subjects had been trained to utilize the US occurrence as a discriminative cue.

To summarize, each of these three different areas of research lends support to the hypothesis that surprising information is processed differently from expected information. The locus of this differential processing appears to be in the duration of processing that the memorial representation of the US receives. USs are considered surprising if they are not predicted by other cues, and therefore are not pre-represented or primed in STM at the time of their occurrence. If they are predicted by preceding stimuli, the associated cues will retrieve the representation of the US from LTM and thus it will be primed. Each of the three above studies involve this form of retrieval-generated priming.

Wagner's model also predicts that self-generated priming, resulting from the memorial pre-representation of the US occupying STM due to a recent presentation of the US, would also have the same disruptive influence on rehearsal processes. Evidence for such an occurrence is perhaps best exemplified by William Terry's dissertation (Terry, 1975). Again using eyelid conditioning in rabbits, Terry, employing both within- and between-group designs, compared responding by subjects exposed to CS-US pairings and US-CS-US sequences where the first US occurred four seconds prior to the CS-US pairing. Consistent with the predictions based on self-generated priming, conditioning in the latter group was significantly poorer both during acquisition and when tested for responding to the CS alone. Based solely on these results, several alternative explanations appear highly plausible. It may be that the priming US, being a highly salient stimulus, overshadows to some extent the CS as a predictor of the second US, thus diminishing the associative strength of the CS. It could also be reasonably argued that the initial US disrupts the CS-US association in a general nonspecific fashion. Terry (1975) presents rather convincing data against both of these alternatives. First, he has demonstrated that the effect is specific to the US. If the priming US differs from the second US, the effect is not obtained. Moreover, the imposition of a distracting stimulus during the interval between the priming US and the CS obliterates the effect. This is precisely the outcome predicted by Wagner, as the distractor should displace the US in STM, and is the exact opposite of the results that would be expected if the priming US functioned as a nonspecific disruptor. However, there is at least one additional viable explanation that cannot be totally dismissed by Terry's data. This hypothesis involves the role of associations to the situational or contextual cues, which, as discussed below, are able to function in a similar manner to a nominal CS as a predictor of the US. Assuming, as does the Rescorla-Wagner model (1972), that any US can maximally sustain a given amount of associative strength, some associative strength in Terry's preparation would have been absorbed by the context, as this was the best predictor of half the US occurrences. This explanation is also consistent with his finding that the effect is not obtained if a different US is used as the priming US. The use of a distractor following the priming US may have disrupted the associations between the context and the priming US; this possibility could be tested by having the distractor follow all US presentations.

A recent series of experiments (Dickinson & Mackintosh, 1979) has important theoretical implications for Wagner's model. As noted by Dickinson and Mackintosh, Wagner, as well as other researchers has used stimuli that are the same as the reinforcer to form surprising or expected events. For example, in Terry and Wagner's experiment (1975), the preparatory stimulus and the reinforcer were both electric shocks. Dickinson and Mackintosh attempted to examine the generality of these effects by providing surprising or expected information that was different from the reinforcer. Using an "unblocking" design, they measured the associative strength acquired by an added CS when surprising information was given. Their major finding was that surprising events enhanced conditioning to the second CS when the event was the same as the reinforcer (food-food or shock-shock), but _not_ when the surprising event was different from the reinforcer (food-shock or shock-water). These findings pose limitatons on the generality of Wagner's model, and Dickinson and Mackintosh suggest that a theory of learned relevance may be better able to accommodate such data.

Despite the foregoing reservations, both in terms of experiments involving retrieval-generated priming as well as self-generated priming, there is an impressive body of data utilizing Pavlovian conditioning that supports Wagner's hypothesis: surprising events receive more rehearsal than expected events.

Theories of Habituation

Most of the recent research on habituation has addressed the physiological mechanisms mediating habituation rather then behavioral phenomena. Although the research presently reported is not directly concerned with the physiology of habituation, it is appropriate to briefly describe current physiological theories of habituation, particularly as they directly bear on the critical question of whether habituation can be attributed to sensory impairment or motor fatigue.

Given the wide diversity of preparations that have been used to investigate the physiology of habituation, it is pleasing to note the similarities of findings, many of which are summarized in the nine behavioral characteristics of habituation described by Thompson and Spencer (1966). The overriding goal of most physiological studies of habituation is an understanding of the neural changes responsible for habituation and/or the localization of the neuroanatomical sites of such changes. Such research is analogous to the search for the "engram" in associative memory research to the extent that the physiological alterations underlying learned behavioral changes are sought. The recent surge of interest in habituation has stemmed partly from the hope that habituation, usually considered the simplest type of behavioral modification in response to external stimuli, might be more amenable to such an analysis than complex learning and thus might facilitate our understanding of the physiology of associative learning.

One of the most highly developed and well-documented physiological theories of habituation is the dual-process theory of Groves and Thompson (1970). This theory proposes that the observed decrease of a response following habituation training reflects the interaction of two separate processes: habituation, which results in a response decrement, and sensitization, which results in a response increment. Although these processes manifest themselves in a common behavioral response system, they are assumed to be independent processes mediated by different neural mechanisms. Habituation is thought to occur within the specific neural pathway of the particular response system involved; sensitization is postulated to be subserved by the overall "state" or general level of responsiveness of the organism at the time of stimulus presentation. One unique aspect of the dual-process theory is that dishabituation, the increase in responding due to extraneous stimulation, is encompassed entirely by the sensitization process; that is, Groves and Thompson state that dishabituation does not result from an attenuation of habituation, as its name implies, but rather from an increase in sensitization which, given constant reactivity, increases the probability of responding.

Empirical support for the independence of habituation and sensitization and for the equivalence of sensitization and dishabituation was first presented by Thompson and Spencer (1966). They hypothesized that if dishabituation resulted from a disruption of the actual habituation process, no decrease in responding following dishabituation would be predicted in the absence of further habituation training. Alternatively, if dishabituation is due to an increase in sensitization, a state of the organism that they assume would dissipate with time, a decrease in responding ought to be observed over time following dishabituation, and this decrease should be independent of any further habituation training.

To test this prediction Thompson and Spencer (1966) recorded the hindlimb flexion of the acute spinal cat. Their preparation, which measured contraction of the left tibialis anterior muscle in response to a cutaneous electric shock applied to the left hindlimb of an unanesthetized cat with a spinal transection at T-12, has been shown to demonstrate the characteristics of habituation, such as spontaneous recovery, generalization, and dishabituation, found in intact organisms. After producing a response decrement in the hindlimb flexion to the electric shock presented once every second, they obtained a response increment (dishabituation) by pinching the limb. No subsequent stimulation was presented to the hindlimb for one minute, at which time they began testing for responding to the original electric shock at one-minute intervals, a rate which does not maintain the response decrement. The observed response rapidly decreased to the habituated level following dishabituation and then gradually rose to the original prehabituation level. The observation of the decrease in responding following the dishabituating stimulus, even though the habituated stimulus was no longer being presented at a sufficient rate to produce a response decrement, indicates that dishabituation represents a separate facilitating process, sensitization, rather than a disruption of habituation.

The gradual decay of the response decrement with repeated testing suggests that the increase in responding following the dishabituating stimulus resulted from a dissipation of sensitization rather than a savings in habituation; however, this possibility cannot be totally dismissed in the present experiment. Groves and Thompson (1970) controlled for this in a later study in which the iterated stimulus, a shock every .5 seconds, was either continued or was omitted after presentation of a dishabituating stimulus. For one group the shocks were continued at the same rate following the response increment due to the dishabituating stimulus; the second group received only a test shock five seconds after the dishabituating stimulus. Both groups showed the same degree of response decrement to the shock that occurred five seconds after the dishabituating stimulus presentation. This again offers support for the view that dishabituation consists not of diminished habituation, but represents a transient response increment, that summates with habituation to produce the observed behavior. Furthermore, using single cell recording techniques, Groves and Thompson (1970) have found that the activity of certain classes of interneurons within the spinal cord of the cat appear to parallel the observed behavioral processes of habituation and sensitization. Despite the correlational nature of these data, their attempts to localize the physiological substrates of habituation are impressive. Groves and Thompson extended the generality of these findings by obtaining similar results from studies of habituation and sensitization in intact organisms. Additional evidence for the independence of habituation and sensitization processes is seen in the strong incremental effect that a dishabituation stimulus has on an unhabituated response. Dishabituation frequently increases responding above the initial prehabituation levels.

Despite the tremendous influence the dual-process theory has had upon the study of habituation, several recent experiments have pointed to possible inadequacies in the theory. In one such study Connolly and Frith (1978) conducted an experiment similar to that of Groves and Thompson (1970) with the intention of evaluating the independence of habituation and sensitization. A response incrementing stimulus, a tone, was applied immediately prior to a visual pattern presentation to which the orienting response of human subjects, as measured by skin conductance, was asymptotically habituated. Following this tone presentation, which itself produced a significant increase in the orienting response, various visual patterns continued to be presented at the same rate to the first group while for the second group several of the visual patterns were omitted following the tone. When these presentations resumed for the second group, orienting responses of the two groups to the visual pattern were compared. According to the findings of Groves and Thompson, these two groups should have been equal in performance due to the assumed independence of habituation and sensitization. However, Connolly and Frith report significantly greater responding by the group in which several of the visual patterns had been omitted. This observation, however, is difficult to interpret as the sensitizing stimulus did not produce a response increment to the visual stimulus in the group for which the visual stimuli continued to be presented following the tone. Thus it appears likely that the response increment obtained in the group in which the visual stimuli were omitted following the tone is attributable to the passage of time without visual stimulus presentations rather than sensitization due to the tone, a possibility for which Connoly and Frith did not control.

One suggestion Connolly and Frith (1978) offer to explain their apparent inconsistency with the dual-process theory is that their study utilitized variable stimuli - the visual block patterns varied in terms of their contour and information - while most studies of habituation, including those of Groves and Thompson, involve repeated presentations of the same stimulus. Although there are numerous additional methodological differences between the two sets of studies, if Connolly and Frith (1978) are correct in their presumption that "the laws governing habituation and sensitization ... may differ markedly between variable and static stimulus contents" (p. 513), this imposes a severe restriction on our current theoretical understanding of habituation in naturalistic contexts.

A more specific criticism of the theory of Groves and Thompson is that when response increments and decrements are independently varied, the results are not totally consistent with the dual-process theory (Davis, 1974; Wedeking & Carlton, 1979). Recording the startle response of rats to a 110-dB tone presented for 100 msec, Wedeking and Carlton investigated the effect of a flashing light upon responding. The flashing light, which did not itself elicit a startle response, increased the startle response to the tone. By comparing habituation to the tones between groups with and without the flashing light present, they attempted to factor out, assuming an algebraically additive relationship between habituation and sensitization, the sensitizing contribution of the light. After obtaining this function based on a difference in response amplitudes between the two groups, they tried to reproduce this sensitization function by exposing subjects to the light throughout the two-hour session and at eight times (ranging from 10 seconds to 2 hours) during the session measuring startle responses to probe trials of the tone. If sensitization is independent of habituation as postulated by the dual-process theory, the amplitude of the startle response at the different times during the session should correspond to the previously obtained sensitization function. The results did not support this hypothesis as no differences were found in response amplitude for any of the trials; the startle response did not differ as a function of the amount of prior exposure to the sensitizing stimulus. Moreover, Wedeking and Carlton report several sensitization functions that appear multiphasic. This is again inconsistent with the dual-process theory which predicts sensitization to initially increase and then to decrease, with the rate of decrease depending upon the particular stimulus used. A related finding was reported earlier by Davis (1974). Varying the duration of preexposure to an 80-dB background noise prior to presenting the habituating stimulus, a tone, he found startle responses to continuously increase to an apparent asymptote, but not to decrease as a function of the duration of the prior exposure, at least throughout the 75 min of his maximal pretraining session.

On a more general level, Gubernich and Wright (1979) criticize the dual-process theory for essentially ignoring parametric differences in habituation. They advocate obtaining measures of habituation from several response systems within the same species, claiming that these differences reflect important evolutionary influences, and that an appreciation of such influences is important for a theoretical understanding of habituation. Although obtained differences are difficult to interpret due to the problem of equating stimulus intensities in different modalities, their multi-response system approach represents a possible comparative aspect to the study of habituation, and presents a likely progression from the study of single response systems. The tendency to monitor a single response system holds, not only for experiments focusing on the dual-process theory, but for most studies of habituation. Although the concept of evolutionary forces acting upon behavior has come to greatly influence learning theories in general, the likely adaptive value of habituation has been virtually ignored (but see Glass, 1972).

For the purposes of the present investigation, one of the most important findings of the physiological studies of habituation is that they have established habituation and sensitization to be due to changes in the central nervous system rather than to temporary or permanent sensory debilitation or motor fatigue. Such studies are critical, as it is unclear how on a behavioral level one can conclusively demonstrate that response decrements reflect such central changes. Although groups controlling for sensory or motor impairments are often included in behavioral studies of habituation, such control procedures cannot totally eliminate interpretations based on changes in peripheral processes.

To logically demonstrate that a response decrement is not due to sensory or motor fatigue, some change in the pattern of stimulation must be made following habituation training to again evoke the response. One way this can be done is temporally, by simply not presenting the stimulus for some period of time and then, upon re-presentation, observing the response again at the prehabituation levels. However, this procedure allows for the real possibility that any sensory damage or motor fatigue present during habituation training may have recovered with time. An alternative method commonly used is to change the characteristics of the stimulus being presented. For example, Sokolov (1963) obtained renewed responding when the intensity of the tone was decreased, as did Whitlow (1975) when the frequency of the auditory stimulus was changed. Although these studies argue strongly against motor fatigue producing the observed response decrement, they cannot adequately address the problem of sensory deficits because altering the stimulus likely changes the sensory receptors being stimulated. However, based on our understanding of neural coding of auditory information this alternate argument is more compelling for changes in frequency than intensity. Furthermore, any change in the stimulus is also confounded by the fact that habituation shows, as do other behavioral phenomena, effects of stimulus generalization. Thus, based solely on a behavioral analysis, these control problems appear largely inextricable.

Fortunately questions concerning the locus of neural change underlying habituation can be illuminated by the physiological manipulations. Groves and his colleagues have performed such analyses upon the hindlimb flexion response of the acute spinal cat by directly recording afferent sensory activity to the stimulus and measuring the electrophysiological excitability of the motorneurons rather than muscular movements (Groves, Wilson & Miller, 1976). Changes in these two systems were not observed during habituation training; rather, the neural changes for the response decrement in this preparation appear to occur in spinal gray interneurons, with these changes directly corresponding to behavioral habituation. In an elegant series of studies that is particularly pertinent to the present report, Groves has elucidated the neural pathways mediating habituation of the acoustic startle response in the rat (Groves & Lynch, 1972; Groves, Wilson & Miller, 1976; Groves, Wilson & Boyle, 1974). Primarily through the use of lesioning techniques, Groves et al. (1976) conclude that short-term changes in neural activity responsible for increases and decreases occur largely in the parvicellular reticular formation. It is particularly intriguing that while they feel the pathways they have mapped reflect the short-term changes, Groves et al. (1976) speculate that long-term habituation may be modulated by a different system, particularly dependent upon cortical input. Support for this assumption includes the finding that rats with frontal or auditory cortex damage demonstrate short-term but not long-term startle response habituation (Groves, Wilson & Boyle, 1974).

The physiological analysis of habituation on the cellular level, which in many respects parallels that done on intact organisms, has been greatly advanced by the extraordinary research of Eric Kandel and his colleagues using the invertebrate marine mollusc _Aplysia californica_. Invertebrates such as _Aplysia_ have several major advantages for physiological research. They have fewer and larger neurons than do vertebrates, with axons up to 1 mm in diameter. More importantly, the cellular connections are invariant across animals, permitting precise replicable electroanatomical mapping of the response systems. This allows for intracellular recording from isolated ganglia as well as recordings from intact subjects in which the ganglia have been exposed. Both techniques have been used extensively by Kandel in investigating habituation of the gill and siphon withdrawal response in _Aplysia_. These responses are basically defensive reactions on the part of the organism that are reliably elicited by tactile stimulation. They decrease in strength with repeated stimulation, and intercellular stimulation and recordings have demonstrated that the response decrement is not attributable to motor or sensory fatigue (Byrne, Castellucci, & Kandel, 1974; Carew, Pinsker, Rubinson & Kandel, 1974).

Kandel and his coworkers have extensively investigated the cellular alterations responsible for the observed response decrement. The neural circuitry involved in these responses is relatively simple, consisting of only about forty cells, and is well understood owing to Kandel's research. Through physiological and biochemical manipulations, they have successfully identified the physiological change responsible for habituation of these responses in Aplysia as a depression or decrease in the amplitude of an excitatory postsynaptic potential on motor neuron L7 of the reflex circuit. This depression has been shown to result from a decrease in the amount of transmitter substance released from the neurons that synapse on L7 (Castellucci, Pinsker, Kupferman & Kandel, 1970). More recently, Castellucci, Carew and Kandel (1978) have demonstrated that these same physiological changes underlying short-term habituation also mediate long-term habituation in Aplysia. This represents the first attempt to isolate the physiological locus of long-term habituation, and is particularly impressive as these findings may generalize to other long-term behavioral changes, although they contrast with the differential mechanisms Groves et al. (1974) propose underlie short- and long-term habituation.

There is one finding of Kandel's research that is particularly noteworthy as it supports the observation of Davis (1970a). This observation is that improved retention of habituation is seen following spaced presentations of the stimulus as compared to massed presentations. Carew, Pinsker, and Kandel (1972) gave 40 presentations of tactile stimulation to Aplysia with an interstimulus interval of 30 seconds. For one group of subjects, all 40 presentations were given in one session, while for a second group of subjects 10 trials were administered on each of four consecutive days. Both groups were tested for retention of habituation one day and one week later. The spaced group showed significant retention relative to untrained controls at both retention intervals, but the massed group did not differ from the control group at either interval. Similar findings were obtained by Carew and Kandel (1973).

There are a number of other physiological theories of habituation, but none of these have been as systematically investigated or are supported by as many data as are the dual-process theory and Kandel's model. Many of these theoretical interpretations, nevertheless, have been influential in the formation of current behavioral theories of habituation. Larry Stein (1965), for instance, proposed that habituation is a specialized case of classical conditioning in which the conditioned response is the buildup of a central inhibitory process supressing responding. Stein hypothesized that presentation of a stimulus elicits excitatory as well as inhibitory neural mechanisms. The excitatory system is assumed to remain constant with repeated stimulus presentations while the inhibitory modulation becomes conditioned to the onset of the stimulus and thus increases in strength. Increases of this inhibitory influence will produce a weakening of the response until inhibition reaches maximal strength, at which point the response decrement will be asymptotic. Although there are no data to support his physiological model that could not be explained equally well by alternative theories, his attempt to incorporate habituation within the established paradigm of classical conditioning was an important theoretical approach to habituation. With regard to the model of habituation that is the major concern of the present studies, Wagner (1979) acknowledges how the models of Konorski (1967) and Sokolov (1963), each of which stresses memorial representation of the habituated stimulus, have influenced his own current theory. Although they use different terminology, both Konorski's and Sokolov's models stress the memorial representation of the stimulus. According to their models, a response decrement is produced when the incoming sensory input is matched by information active in memory.

Associations to Contextual Cues

One aspect of Allan Wagner's model of long-term habituation (Wagner, 1976) that fits particularly well within contemporary theorizing concerning memory processes is his emphasis on the associations formed to contextual or environmental cues. Both within the human cognitive literature (Block & Reed, 1978; Lubow, Rifkin & Alek, 1976; Smith, in press; Smith, Glenberg & Bjork, 1978) as well as within animal learning research (Bouton & Bolles, in press; Dweck & Wagner, 1970; Hennig, 1979; Kremer, 1974; Odling-Smee, 1978; Siegel, 1977), it is becoming increasingly recognized that contextual cues may acquire stimulus control over responding. Context may be very broadly defined; Spear, for example, considers contextual stimuli to be "those that are noticed by an individual during the acquisition of a memory, with the exclusion of stimuli such as conditioned or discriminative stimuli that are necessary to determine that the memory was acquired" (Spear, 1978, p. 56). His definition thus includes proprioceptive, temporal, and state-dependent as well as external environmental cues. However, the present discussion will concern only the apparatus cues as these are the stimuli assumed by Wagner to initiate the retrieval-generated priming of the US that he hypothesizes underlies long-term habituation.

Studies involving associations to contextual stimuli can be divided into two categories. The first encompasses situations in which the contextual cues serve as background stimuli for a more reliable predictor of the reinforcement contingencies. This category would include the role of apparatus cues in most studies of classical conditioning in which each US is preceded by a discrete CS, as well as instrumental paradigms in which responding is under the control o discrete discrimininative stimuli. In such cases contextual cues may gain associative strength, as evidenced by the fact that responding is greatly disrupted if the contextual cues are altered (e.g., Welker, Tomie, Davitt & Thomas, 1974), despite the fact that they are essentially redundant cues. Why less reliable predictors should acquire associative strength is unclear; perhaps these redundant cues serve as additional discriminative stimuli or perhaps, as Spear (1978) hypothesizes, they function as memorial attributes that can enhance retrieval processes. It is clear, however, that changes in context often influence behavior even when the context is not the most reliable predictor of reinforcement and the reinforcement contingencies remain the same. This finding is not limited to contextual cues; a similar observation arises in the case of compound CSs in which overshadowing is rarely complete. Acquisition of associations by contextual cues may even occur in circumstances where stimulus selection is known to be extremely strong, such as gustatory stimuli in the formation of conditioned taste aversions (Archer, Sjoden, Nilsson & Carter, 1979; Batson & Best, 1979).

The second category of studies concerning associations to contextual cues includes preparations in which the context itself serves as the most reliable predictor of reinforcement. Such preparations involve otherwise unsignaled US occurrences, thus including habituation, as well as instrumental situations lacking discriminative stimuli. The environmental stimuli in such circumstances do not provide precise temporal information concerning when the US will occur, unlike most traditional discrete CSs, but do convey information that the US will occur within that particular context. In such cases there is a perfect correlation over sessions between the contextual cues and the occurrence of the US. Even with only one session, subjects in certain circumstances may readily form specific associations to the context. For example, immediately following unsignaled shocks rats exhibit much greater fear, as indexed by freezing behavior, in the context in which the shocks were presented than when placed in a markedly different enclosure (Bolles & Collier, 1976). With appetitive reinforcement, Tomie (1976a, 1976b) has demonstrated that pigeons presented with unsignaled food form associations to the apparatus which will interfere with later acquisition of autoshaping. That such interference is due to contextual conditioning rather than nonassociative factors such as "learned laziness" (Engberg, Hansen, Welker & Thomas, 1972) is demonstrated by the alleviation of this effect when autoshaping takes place within a different context. As a result of the context constantly undergoing both acquisition and extinction in the above examples, it is likely that the degree of contextual conditioning will be a function of the US density distribution.

It must be acknowledged that although contextual conditioning appears to be a fairly robust phenomenon in the above studies, there are also reported failures to obtain any disruption of behavior following changes in context under circumstances in which contextual cues would have been expected to be the most reliable predictor of US occurrences (e.g., Leaton, 1974; Popik & Frey, 1978). Thus despite the many demonstrations that contextual stimuli can acquire associative strength in certain circumstances, this does not always appear to occur. The purpose of the present series of experiments is to investigate whether long-term habituation is mediated by associations to contextual cues as postulated by Wagner's model.

Experiment 1 -- Parameters for Long-Term Habituation

The response system chosen for this series of studies was the acoustic startle response of the rat. This preparation was selected because it is well understood behaviorally and physiologically (Groves, Wilson & Miller, 1976), and it is known to yield long-term habituation (Davis, 1970a). Furthermore, much of the empirical basis on which Wagner has formulated his model of long-term habituation was obtained from this preparation.

The purpose of Experiment 1 was to establish parameters that would produce long-term habituation of the startle response in our experimental setting. A within-subjects design was used in which subjects were exposed to repeated brief presentations of a loud acoustic stimulus in a stabilimeter apparatus (Session 1). Following a retention interval in their home cages, subjects were returned to the stabilimeters and again presented with the same series of tones (Session 2). Within each session the acoustic stimulus was presented quasi-randomly at 2-, 4-, 8-, or 16-sec interstimulus intervals (ISIs). These intervals were adopted from Davis (1970a). Variable ISIs, rather than a fixed duration ISI, were utilized to prevent temporal cues from competing with the contextual stimuli for associative strength. A one-hour retention interval was used between Sessions 1 and 2. Although much longer retention is possible with appropriate parameters, one hour was considered to exceed the duration necessary to eliminate the possibility of self-generated rather than retrieval-generated priming operating at the beginning of Session 2.

Method

Subjects. Twenty-four experimentally naive male Sprague-Dawley CD rats (Charles River Co, Wilmington, Mass.) weighing between 300 and 400 g served as subjects. All were individually housed in continuous light and maintained on ad lib. water and Purina Laboratory Chow. Subjects had previously been on a water deprivation schedule for approximately two weeks to maintain their body weights within the desired range, but were returned to ad lib. water at least two days prior to the experimental day.

Apparatus. The apparatuses were four Lafayette (Lafayette, Ind.) stabilimeters (No. 86010). Each subject was confined to the 30 X 30 cm Formica floor of the stabilimeters by a 30-cm high enclosure surrounding the platform. The ceilings, which were perforated for ventilation, and the front walls of these enclosures were constructed of Plexiglas; the remaining three walls were stainless steel. Each stabilimeter was positioned in a sound-attenuating chamber furnished with a ventilation fan, a 45-ohm speaker which continuously provided a 60-dB (re: 20 $\mu N/m^2$) white noise background, and was illuminated by a 7.5-watt light bulb positioned approximately 15 cm from the ceiling of the apparatus. The stabilimeter output was gated through a Lafayette Activity Monitor (No. 86010). The sensitivity of these activity monitors was calibrated to record a response approximately 50% of the time that a .5-gram weight was dropped from 5 cm above the platform.

The acoustic stimulus was a 90-dB (re: 20 $\mu N/m^2$, as measured on the A-scale of a Scott sound level meter with the microphone placed within the stabilimeter near the level of the rat's head) 50-msec broad-band noise, thereby minimizing spatial resonances. It had a characteristic frequency of approximately 2500 Hz, produced by a Mallory (Indianapolis, Indiana) Outdoor Horn, No. ROH185. Following Davis (1970a), a startle was defined as a stabilimeter response during the 50-msec interval of the tone presentation. Oscilloscopic monitoring confirmed that the recording interval occurred simultaneously with the presentation of the acoustic stimulus. The oscilloscopic recordings also demonstrated that both at the beginning and end of the habituation session the startle response, when it did occur, took place within 50 msec of the tone onset.

Procedure. All subjects were handled daily by the experimenter for four days immediately prior to the test day. Subjects were randomly divided into two groups of twelve animals each. Each subject in the first group (Experimental) was placed in a stabilimeter and, after a 15-min adaptation period (following Davis, 1970a), received 800 presentations of the acoustic stimulus. Two hundred of these occurred at each of the four ISIs, 2, 4, 8, or 16 sec, quasi-randomly mixed but counterbalanced for first-order sequential effects. Immediately following Session 1 subjects were returned to their home cages for the one-hour retention interval, and then returned to the same stabilimeter for Session 2 which was identical to Session 1 except that no adaptation period was given. The stabilimeters were not cleaned between Session 1 and Session 2.

Subjects in the second group (Activity Control) were treated identically to subjects in the Experimental Group but were never presented with the acoustic stimulus. Their responses were recorded during the same 50-msec intervals in which the tones had occurred for the Experimental Group.

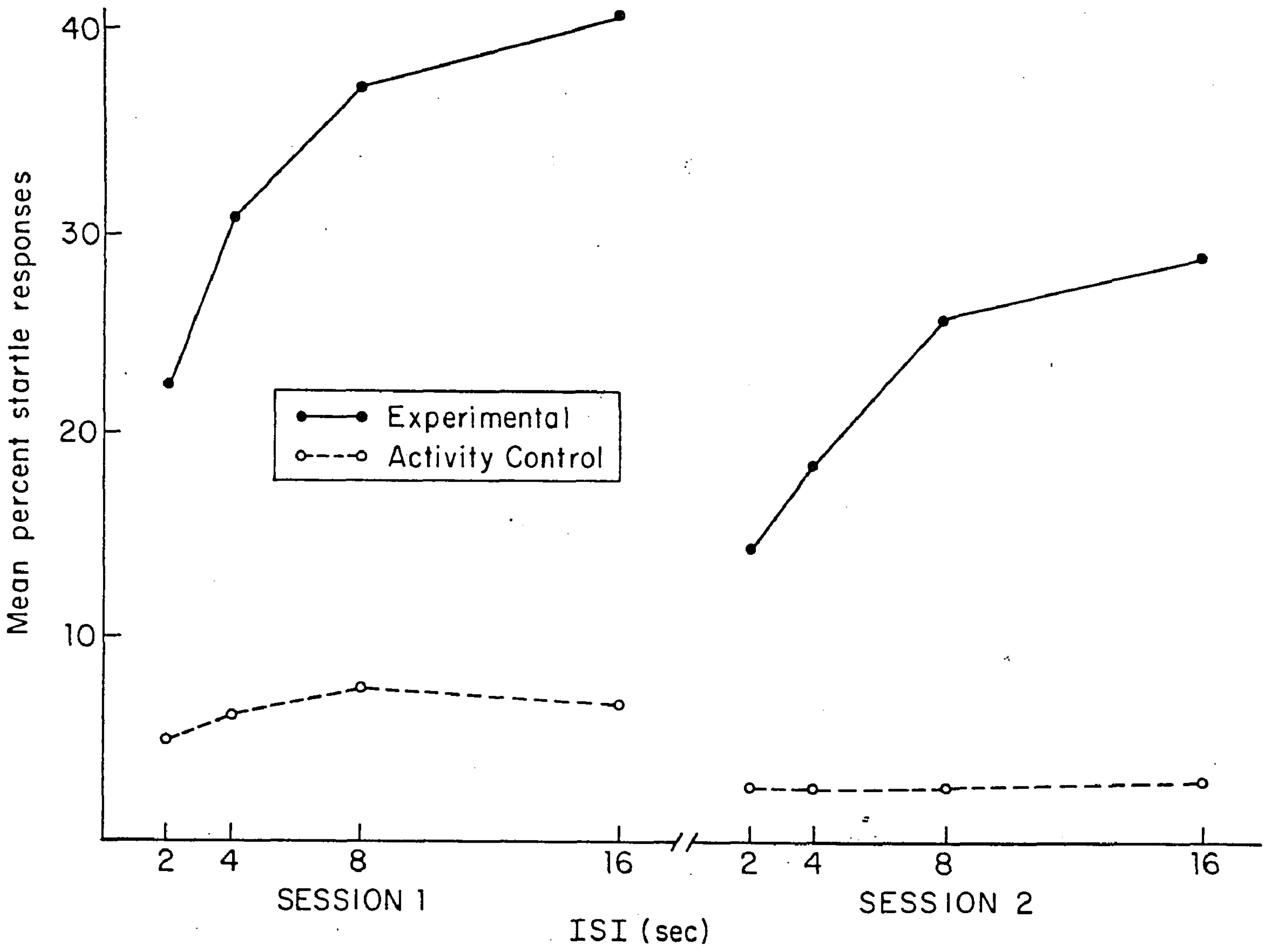
Experiment 1 was performed in three replications with experimental and control groups run alternately rather than simultaneously due to the intensity of the tone making it impractical to acoustically insulate half of the boxes.

Results

The mean percent of startle responses for each of the four ISIs in Sessions 1 and 2 is shown in Figure 1. Characteristic of within-session or short-term habituation, the percent of responses by subjects in the Experimental Group increased as a function of the time since the last stimulus presentation. This was a highly robust finding with the percent of responses at each ISI differing from the adjacent ISIs in both Sessions 1 and 2, all ts(11)>1.95, ps<.05.

Collapsing over ISIs, a Group X Session ANOVA revealed an overwhelmingly higher percentage of startle responses by

Figure 1. The mean percent of startle responses as a function of ISI for the experimental and control groups in Experiment 1.

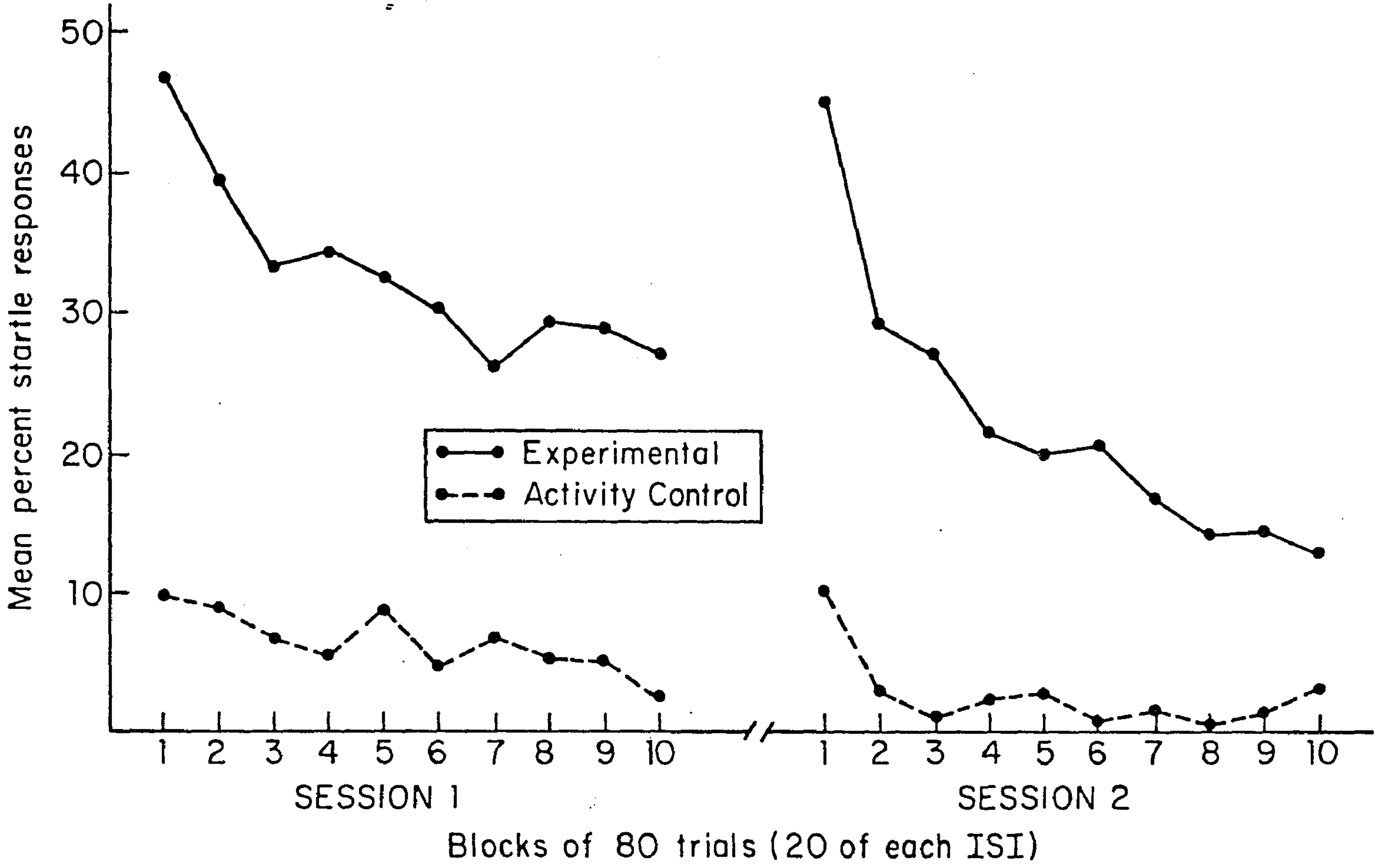

Mean percent startle responses
40
30
20
10
Experimental
Activity Control
2
4
8
16
SESSION 1
2
4
8
16
SESSION 2
ISI (sec)

the experimental subjects than the activity $F(1,22)=59.57$, $p<.001$. Long-term habituation was evident in the greater responding in Session 1 than in Session 2, $F(1, 22)=1,22)=27.17$, $p<.001$. For the Experimental subjects this retention of habituation across sessions was reliable at each of the four ISIs: $ts(11)=3.05$, 3.49, 4.80 and 3.52, all $ps<.05$, for the 2-, 4-, 8-, and 16-sec ISIs respectively. Additionally, a Group X Session Interaction was obtained with the Experimental Group showing a greater response decrement over sessions than the Activity Control Group, $F(1,22)=6.86$, $p<.025$.

To illustrate the response decrement over trials within each session, the mean percent of startle responses over ten blocks of 80 trials were obtained for each session. Every block consisted of 20 trials from each of the the four ISIs (see Figure 2). Comparisons of the first and last block of each session yielded significant response decrements within Sessions 1 and 2 in the Experimental Group, $ts(11)=4.14$ and 6.21 respectively, $ps<.01$, as well the Activity Control Group, $ts\ (11)=4.14$ and 3.20 respectively, $ps<.01$.

Despite the obtained response decrements in both groups, visual observations of the animals indicated that most subjects engaged in a great deal of exploration and remained fairly active throughout both sessions. In the experimental animals, the startle response appeared as an overall flinch, which was followed by freezing during the initial presentations of the acoustic stimulus. After

Figure 2. The mean percent of startle response over blocks of 80 trials in Sessions 1 and 2 for the experimental and control groups in Experiment 1.


50
40
30
20
10
Mean percent startle responses
Experimental
Activity Control
1
2
3
4
5
6
7
8
9
10
SESSION 1
1
2
3
4
5
6
7
8
9
10
SESSION 2
Blocks of 80 trials (20 of each ISI)

approximately 100 trials, freezing was virtually absent and the startle response was less pronounced behaviorally. The control animals' within-session response decrement arose from their decrease in exploratory activity, and their "startle" scores were initially far below those of the experimental subjects.

Discussion

The results of this experiment, especially the observation of retention between sessions, indicate that the present preparation is appropriate to investigate the contextual specificity of long-term habituation. It is particularly advantageous that the one-hour retention interval allows for partial recovery from the response decrement present at the end of Session 1 thereby eliminating the possibility that any differences between groups in the following studies would be obscurred by floor effects.

No evidence of intitial sensitization (Groves & Thompson, 1970), that is, a response increment preceding the response decrement, was observed in Experiment 1; nor was this trend seen when the data were examined in finer detail using blocks of 20 trials rather than of 80 trials. Sensitization may have been eliminated by the adaptation period, consistent with the absence of sensitization reported by Davis (1974) when the background white-noise level was 60 dB as in the present study.

Of critical importance for the demonstration of long-term habituation is the observed interaction over sessions between the Experimental and Activity Control Groups. If there had been no interaction, there would be no basis on which to attribute the response decrement over sessions to long-term habituation to the acoustic stimulus. That is, if both groups showed a proportional decrease in responding between Sessions 1 and 2, this could be interpreted as simply representing a decrease in general activity or exploration with no change over sessions in the Experimental animals' startle responses to the tone. This possibility is particularly important when applied to the long-term habituation study of Davis (1970a). The basic finding of his experiment, as described above, was that rats receiving 1000 tones at a constant 16-sec ISI were less responsive on a long-term habituation test (indicative of better retention) than were animals receiving the same 1000 tones at a fixed 2-sec ISI. Wagner's interpretation of this effect was that, due to the longer ISI, each presentation of the tone was more unexpected in the 16-sec ISI group (Wagner, 1976). Alternatively, the basic long-term habituation finding of Davis (1970a) might be due to the fact that the 16-sec ISI group spent eight times as long in the apparatus during training as compared to the 2-sec ISI group. As no activity control group was included, it is conceivable that Davis' results merely reflect a decrease in general activity rather than any associations to contextual cues - or even any short- or long-term habituation to the tone. A third possibility, assuming actual habituation to the tone both within and between sessions did take place, is that the greater response decrement of his 16-sec group on the long-term test could reflect a summation of habituation to the tone and the apparatus. Evidence against these latter two explanations has been offered by Davis (1970b). In that study, a 2-sec ISI group was exposed to 50-msec, 120-dB tones for the duration of the session length of the 16-sec ISI group; hence, they were given eight times the number of tones as was the 16-sec group. All subjects were subsequently tested for their mean percent of startle responding to interspersed 100-, 110-, and 120-dB tones of the same frequency as the training stimulus. Although the 2- and 16-sec ISI groups did not differ significantly at the first two intensities, the 16-sec group exhibited less startle responding to the 120-dB tone than did the 2-sec ISI group. These data, which by their intensity specificity at the same frequency again indicate that the decrease in startle re is not attributable to motor fatigue, would seem to refute the above suggestion that the results of Davis (1970a) did not reflect habituation to the acoustic stimulus. However, whether the results of a test utilitizing a variable intensity, fixed ISI acoustic stimulus can be generalized to his earlier experiment involving a test with a variable ISI, fixed intensity tone is uncertain.

Experiment 2 -- Overshadowing of Habituation

Numerous conditioning phenomena, particularly those involving compound stimuli, have provided strong support for the view that, given two equally salient stimuli, a US is most likely to be associated with the stimulus that best predicts the occurrence of the US (Kamin, 1969; Wagner, Logan, Haberlandt & Price, 1968). In habituation the contextual cues, even though they do not provide precise temporal information about US occurrences, ordinarily serve as the most reliable predictors of the US. If, however, a discriminative stimulus were presented immediately preceding each US event, more associative strength of the habituating stimulus should accrue to that stimulus, which would function as a typical Pavlovian CS, as compared to the contextual cues. The availability of a more reliable predictor of the US should "overshadow" the contextual cues. Such overshadowing ought to be apparent on a long-term test conducted in the presence of the same contextual cues but without the more reliable stimulus, through a comparison of the performance of this overshadowing group with that of a group which was not exposed to the more reliable cue during initial habituation training.

A second expectation, according to Wagner's associative model of long-term habituation, is that the response decrement during the initial habituation session should occur more quickly for the group receiving the more reliable cue than for the one with only apparatus cues present. This prediction follows from Wagner's basic assumption about performance in which he states that "the stimulus is less likely to provoke a response when it is primed in STM by associated retrieval cues" (Wagner, 1976, p. 119). Owing to its greater reliability, the cue immediately prior to each US should function as a stronger retrieval cue, thus producing greater retrieval-generated priming than the contextual stimuli do, amd hence less of a startle response.

Method

Subjects and Apparatus. Thirty-six rats, identical to those described in Experiment 1, served as subjects. The apparatus and recording procedures were also the same as in the first experiment, but to achieve balanced replications only three of the stabilimeters were used.

Procedure. Subjects were randomly divided into three groups of 12 animals each. All subjects received 800 presentations of the acoustic stimulus at ISIs of 2, 4, 8, and 16 sec in Sessions 1 and 2. These sessions were separated by a one-hour retention interval during which subjects remained in their home cages undisturbed.

During Session 1 the houselight in one group (Correlated) went off for 1 sec immediately preceding the onset of each acoustic stimulus and came back on simultaneously with the offset of the tone; thus the light-off duration on each tone presentation was 1050 msec. For the second experimental group (Uncorrelated) the houselight went off for 1050 msec on the average of every 7.5 sec (the mean ISI) throughout Session 1, but this was independent of the US. This group was included to assess any generalized effects that the brief periods of darkness might have upon activity levels. The houselight of animals in the third condition (No Cue) remained illuminated continuously throughout Session 1.

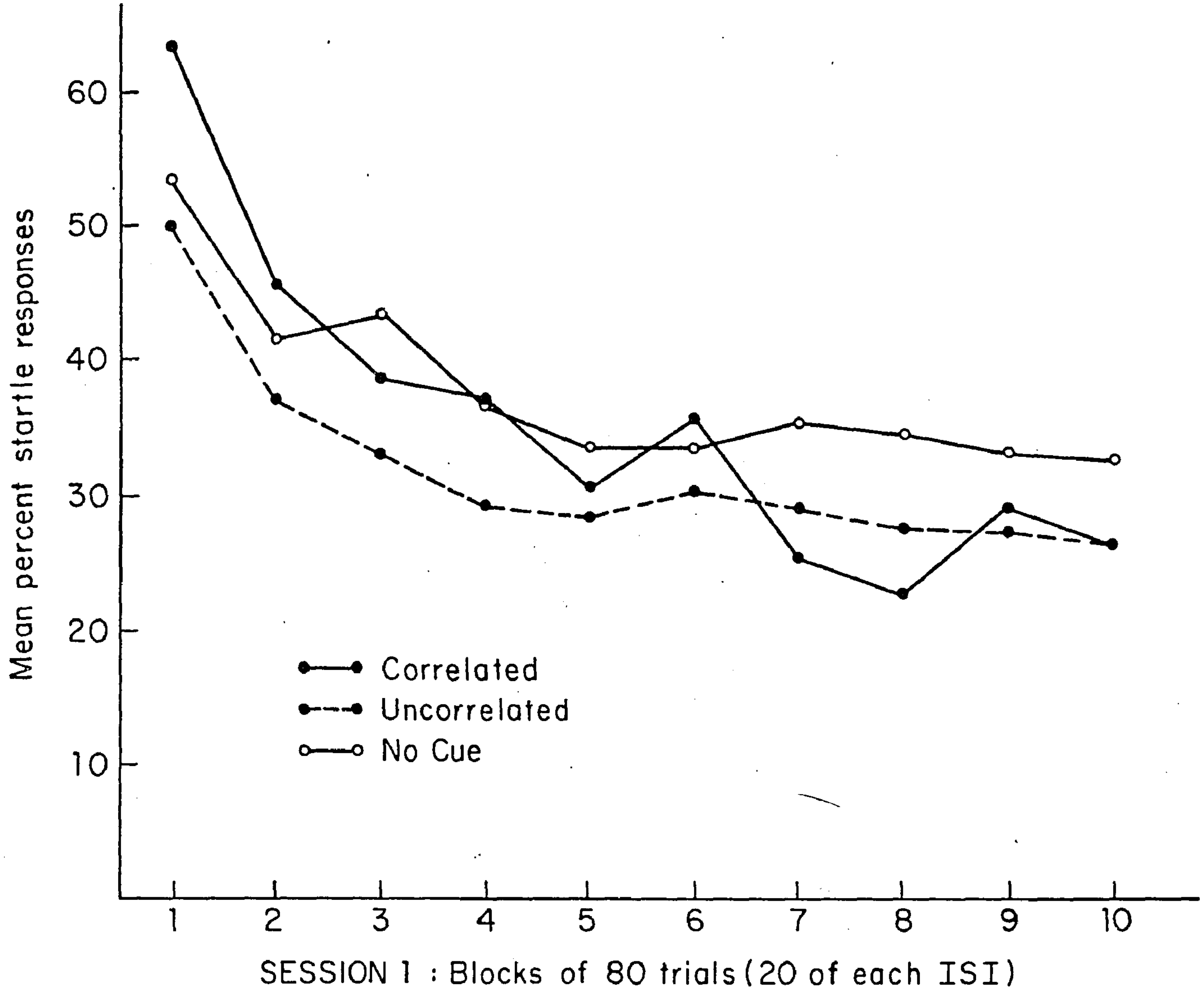
In Session 2 the houselights remained on continuously in all three conditions. This experiment was conducted in 12 balanced replications.

Results

The mean percent of startle responses by each group in Session 1, collapsed over ISIs to form blocks of 80 trials, is illustrated in Figure 3. Over the entire session, which was analyzed by a Treatment X Trials X ISI ANOVA with repeated measures on the last two factors, there were no significant differences among the three treatment groups, $\underline{F}(2,33)= .80$, $\underline{p}>.45$. A within-session response decrement was obtained, $\underline{F}(9,297)=45.57$, $\underline{p}<.001$.

Of primary interest for the evaluation of any overshadowing of associations to contextual cues is the Correlated Group's performance in Session 2 relative to the performance of the other two conditions. These data are shown in Figure 4. No difference in startle response among the three conditions was observed, $\underline{F}(2,33)=.49$, $\underline{p}>.50$. Again a reliable difference over ISIs with the shorter ISIs producing less responding, $\underline{F}(9,99)=31.04$, $\underline{p}<.001$, and a

Figure 3. The mean percent of startle responses over blocks of 80 trials during Session 1 for the Correlated, Uncorrelated, and No Cue Groups of Experiment 2.


Mean percent startle responses
60
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
SESSION 1 : Blocks of 80 trials (20 of each ISI)
Correlated
Uncorrelated
No Cue

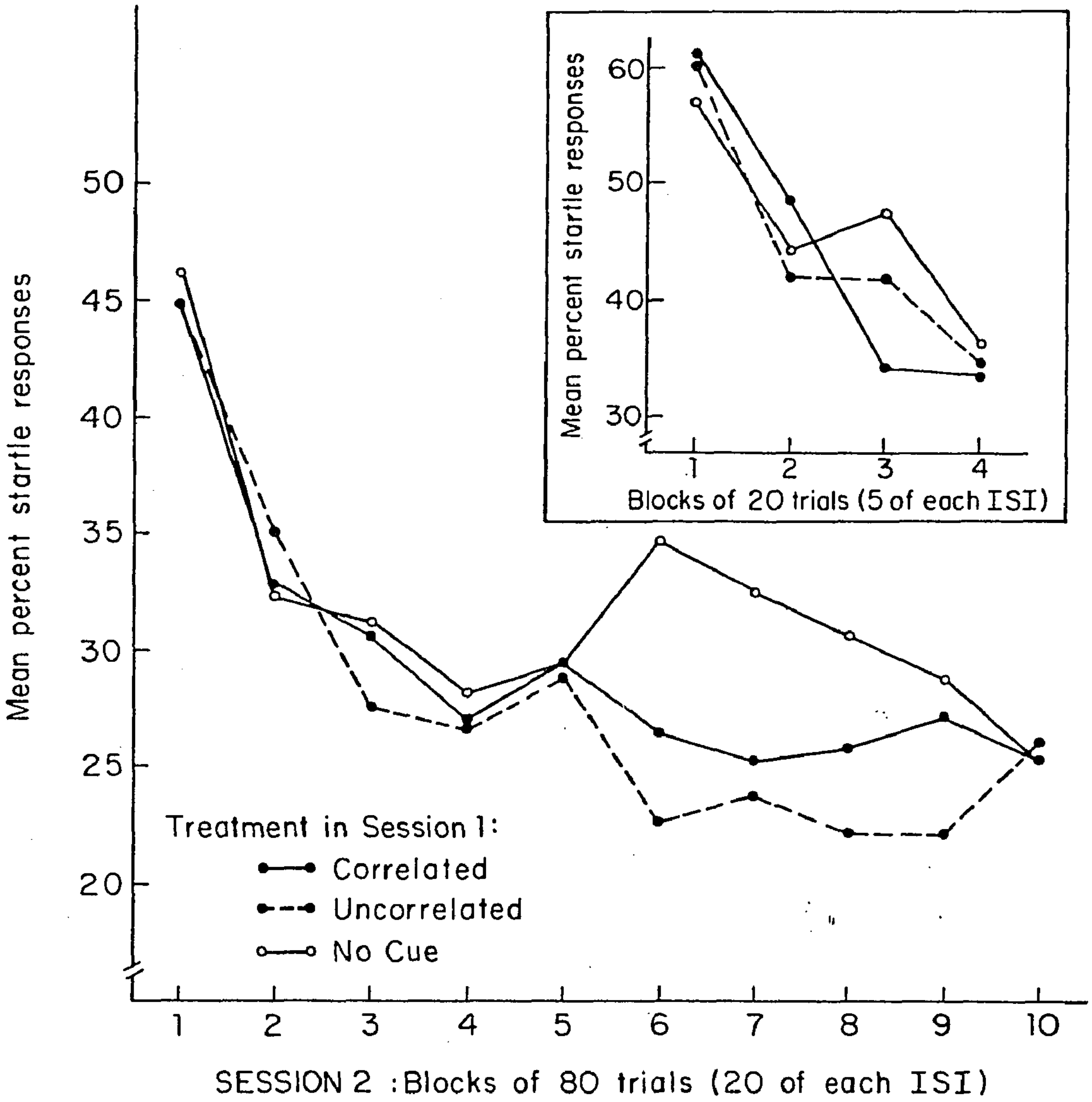
response decrement over trials were present, $F(9,297)=18.78$, $p<.001$.

If differences among the three groups were present in Session 2 as a consequence of the treatments during Session 1, they should be most pronounced on the initial trials of the second session. To ascertain that the present blocking procedure of blocking by 80 trials was not insensitive to such differences, the data comprising the first 80-trial block were reanalyzed by subblocks of 20 trials (5 trials of each ISI). This is illustrated in the inset of Figure 4. Even for the first subblock of 20 trials on Session 2, no differences among the three treatments were found, $F(2,33)=.03$, $p>.50$.

Discussion

According to Wagner's associative model of long-term habituation, the Correlated Group should have demonstrated impaired habituation on Session 2 relative to the No Cue and the Uncorrelated Groups due to the overshadowing of the contextual cues in Session 1 by the more reliable predictor of the US. No support for this prediction was obtained. The results of Experiment 2 are congruent with a nonassociative model of habituation in which the critical parameters concern only the US presentations themselves. As subjects in all three conditions were exposed to the same number of tones at the same times, a nonassociative model of habituation would call for similar response decrements both within and between sessions.

Figure 4. The mean percent of startle responses over blocks of 80 trials during Session 2 for the Correlated, Uncorrelated, and No Cue Groups of Experiment 2. The inset presents the responses for the first block of 80 trials broken into subblocks of 20 trials.


Mean percent startle responses
50
45
40
35
30
25
20
1
2
3
4
5
6
7
8
9
10
SESSION 2 : Blocks of 80 trials (20 of each ISI)
Treatment in Session 1:
Correlated
Uncorrelated
No Cue
Mean percent startle responses
60
50
40
30
1
2
3
4
Blocks of 20 trials (5 of each ISI)

The lack of differences in startle responses among the three conditions could be explained if one hypothesized that subjects in the Correlated Group did not associate the darkness with the tone either because of its lack of salience or its temporal characteristics. Although this could account for the present results, it seems unlikely that the long-term habituation observed between sessions is mediated by associations to the less reliable contextual cues if the animals lack the potential to form associations to the more reliable light stimulus.

Also contrary to the prediction that a more reliable cue would evoke greater priming of the US and subsequently less responding was the finding of no differences in the rate of habituation among the groups in Session 1. As an example of such an effect, Wagner (1976) cites the classical conditioning phenomenon of "conditi diminution of the unconditioned response (UR)" (Kimble & Ost, 1961; Kimmel, 1966; Kimmel & Burns, 1975). Conditioned diminution of the UR refers to the observation that the UR in a CS-US pairing is reduced relative to the UR to a US not preceded by the CS. Although it is not possible to entirely rule out factors such as fatigue due to an immediately preceding CR, this diminution of the UR does seem to be largely an associative effect with the inhibition specific to the previously paired US (see Kimmel & Burns, 1975).

If, however, the decrease in the UR results from the greater expectancy of the US following a reliable retrieval cue as postulated by Wagner, the same reasoning can be applied to the expectancy concerning the CS. Over trials the CS should likewise become more expected based on retrieval-generated priming from contextual conditioning due to conditioned contextual cues, and hence the CR should decrease. This, of course, is the exact opposite of most empirical acquisition functions in which the CR increases either in probability and/or amplitude with increasing numbers of trials, and also runs counter to predictions based on current analyses of classical conditioning (e.g., Rescorla & Wagner, 1972).

On a different level of analysis, such a counterintuitive prediction would not be derived from the theoretical interpretation that Kimmel and his colleagues have given to conditioned diminution of the UR. They view classical conditioning as an adaptive process through which the subject interacts with its environment and hypothesize that the CR might functionally serve to reduce the noxiousness of aversive events. Because of this adaptive value of the CR, the US might be perceived as being of decreased intensity, thus the UR is in turn decreased only when preceded by the CR. Even though no enhancement of the startle response due to overshadowing was obtained in the present experiment, this line of reasoning is particularly intriguing as it can be applied directly to habituation paradigms. That is, perhaps under certain circumstances the subject does associate the US with the context, but rather than this association resulting in a response decrement directly due to priming, the decrement may stem from an adaptive or "preparatory" response (Perkins, 1968) made by the subject with priming mediating the appropriate functional response. For example, in the present situation such a response might involve contracting the muscles of the inner ear when an loud noise is expected. In fact, the finding of no change in sensory input during habituation reported by the physiological investigations described above suggests that preparatory responses, if they occur for the acoustic startle response, are central rather than peripheral; however, the locus of the hypothesized preparatory response is irrelevant to the current analysis. What is intriguing to note is that the functional analysis put forth for classical conditioning may also be advanced for an associative model of habituation.

Experiment 3 -- Generalization of Habituation

In studies of habituation, as in most learning experiments, care must ordinarily be taken to present the entire environmental situation in an unchanging fashion over sessions to minimize any disruption of behavior that might arise due to stimulus generalization decrements. According to a nonassociative theory of habituation, the need for such stimulus control is evident for the iterated stimulus, but not for the background cues unless the overall stimulus input was increased to the degree that it would produce sensitization. However, if associations between the apparatus cues and the US mediate long-term habituation as postulated by Wagner (1976), retention should be disrupted by changes in the context between sessions.

For purposes somewhat unrelated to the present hypothesis, other experimenters have attempted to evaluate long-term habituation following changes in background cues. Peeke and Veno (1973) did so while studying habituation of aggressive behavior in sticklebacks. During the first session a decrease in the frequency of attacks by the resident stickleback on another male stickleback was seen. In the second session of their experiment, the test fish itself and/or the location of the test fish was manipulated factorially. A response decrement between sessions was observed in the control group in which the test fish and its location remained the same in both sessions. When only the context, i.e. the location, of the test fish changed between sessions, the increase in aggressive behavior between this group and the control group approached but did not achieve significance. Reliable differences from the control group were obtained only in the conditions in which the identity of the test fish itself was altered. Of the two groups in which the test fish itself was changed, a significantly greater increase in attack responses was seen in the condition where both the test fish and its location were altered between sessions, suggesting an interactive effect of these two factors.

Leaton (1974) also attempted to evaluate the contextual specificity of long-term habituation by modifying the context between sessions. His dependent variable was the duration for which a thirsty rat would interrupt licking when a 2-sec, 90-dB pure tone was presented. Habituation to the tone was observed as a total lack of supression. In this situation habituation occurs very rapidly and is retained for several weeks. No disruption of a long-term response decrement was found when the apparatus cues were changed between sessions. However, this lack of effect is somewhat difficult to interpret. Owing to the nature of Leaton's measure, any differences due to the contextual changes may have been obscured by floor effects as no suppression to the tone was evident in either group. Alternatively, these null results may be due to the fact that the contextual changes, which consisted of covering the grid floor of his apparatus with a solid floor and turning off a dim light, may not have been sufficiently salient to the subject. Differences in long-term habituation would be predicted by Wagner's associative model only if the contextual changes were highly discriminable to the subject.

The present study was designed to determine if generalization decrement occurs when contextual cues are modified between initial habituation and a test of long-term retention. As it is difficult to speculate which of the apparatus cues are most salient to the subject, gross qualitative changes in tactile, visual, and olfactory cues, rather than the more traditional quantitative changes along one dimension of stimulation, were imposed between Session 1 and Session 2 to maximize the probability that the change in context would be discriminable to the subjects.

Method

Subjects and Apparatus. Thirty-six rats, similar to those described in Experiment 1, served as subjects. Three sets of stabilimeter conditions, designated as Stabilimeters A, B, and C, were used. Stabilimeter A was the basic stabilimeter apparatus used in the previous studies, and consisted of a smooth Formica floor surrounded by an enclosure with three walls made of stainless steel and the remaining wall and ceiling constructed of clear Plexiglas. In this condition the houselight remained off throughout the session. Stabilimeter B was the same stabilimeter apparatus, but the houselight remained on continuously and the floor was tightly covered with a rough black cotton cloth. In Stabilimeter C the houselight was on, the floor was covered by a rough black cloth, all four walls of the enclosure were covered with 2.5-cm wide vertical black and white stripes, and an absorbent towel soaked with 2 cc of lemon extract was placed over the perforated ceiling of the enclosure.

Procedure. The subjects were randomly divided into two squads of 18 rats each. One squad received habituation training in Stabilimeter A while the other squad was trained in Stabilimeter C. The parameters and procedures for habituation training and testing, Sessions 1 and 2 respectively, were identical to those of Experiment 1. Following the one-hour retention interval, one third of the subjects from both these squads (Group Same) received Session 2 in the same apparatus as they had been trained in; one third (Group Similar) received Session 2 in Stabilimeter B; the remaining one third (Group Different) received Session 2 in a different apparatus, either Stabilimeter A or C, from their training apparatus in Session 1.

Results

The data for Session 1 were analyzed by the subject's scheduled test condition (Same, Similar, or Different) in Session 2. As is evident in Figure 5, there were no differences in startle responding on Session 1 among the three groups, $F(2,33)=.60$, $p>.50$, and a reliable within-session decrement in responding was obtained, $F(9,297)=15.86$, $p<.001$. As in previous studies, greater responding was observed following the longer ISIs in both Session 1 and Session 2, both $Fs(3,99)>13.59$, $p<.001$.

The critical data concerning long-term habituation as a function of the similarity of contextual cues between sessions are represented in Figure 6, which depicts the mean percent of startle responses elicited from each of the three treatment conditions groups by blocks of 80; the inset expands the first block of 80 trials into subblocks of 20 trials. Within Session 2 a response decrement across groups was seen over trials, $F(9,297)= 27.72$, $p<.001$, but, most

Figure 5. The mean percent of startle responses over blocks of 80 trials during Session 1 for Groups Same, Similar, and Different of Experiment 3.

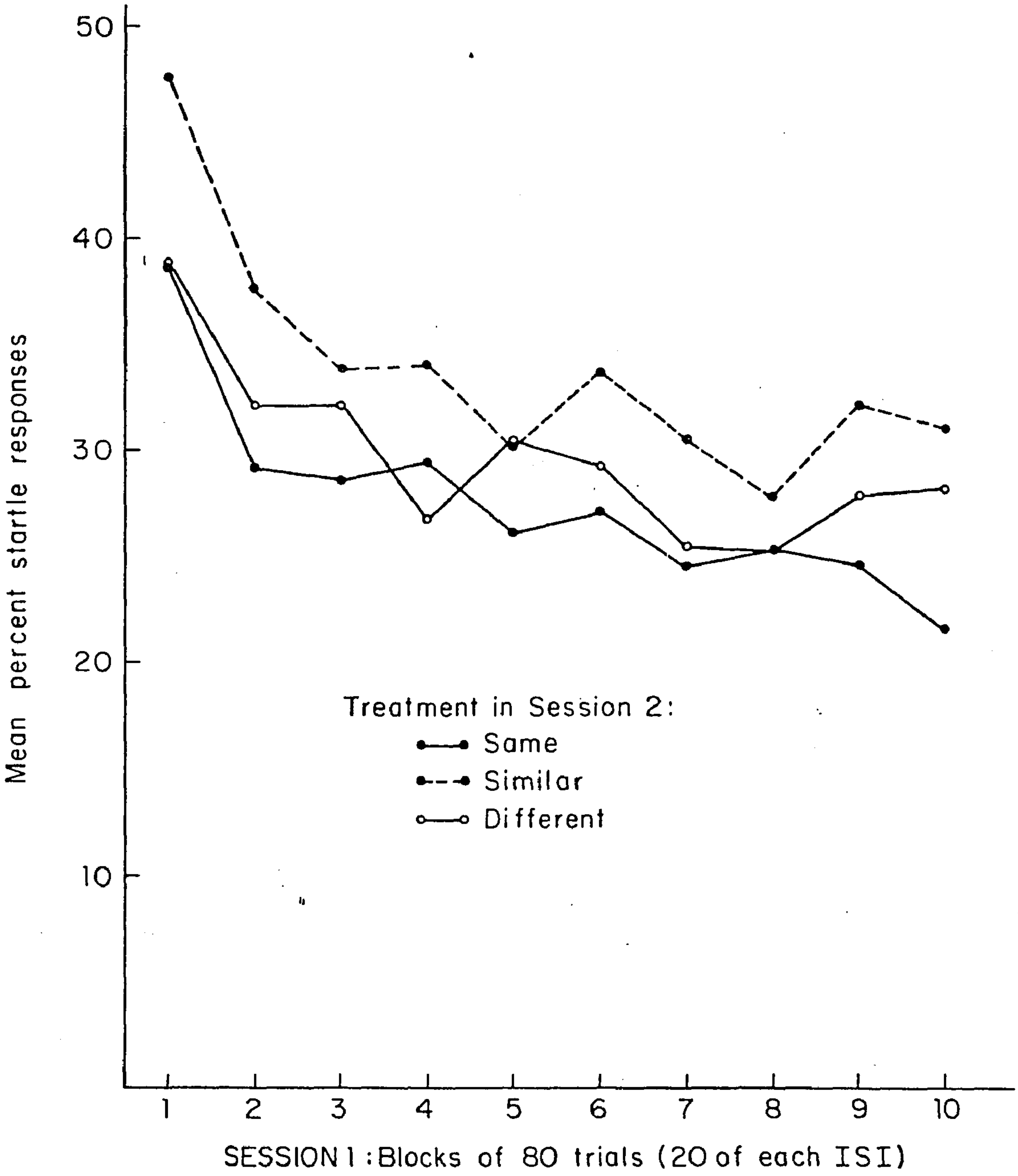
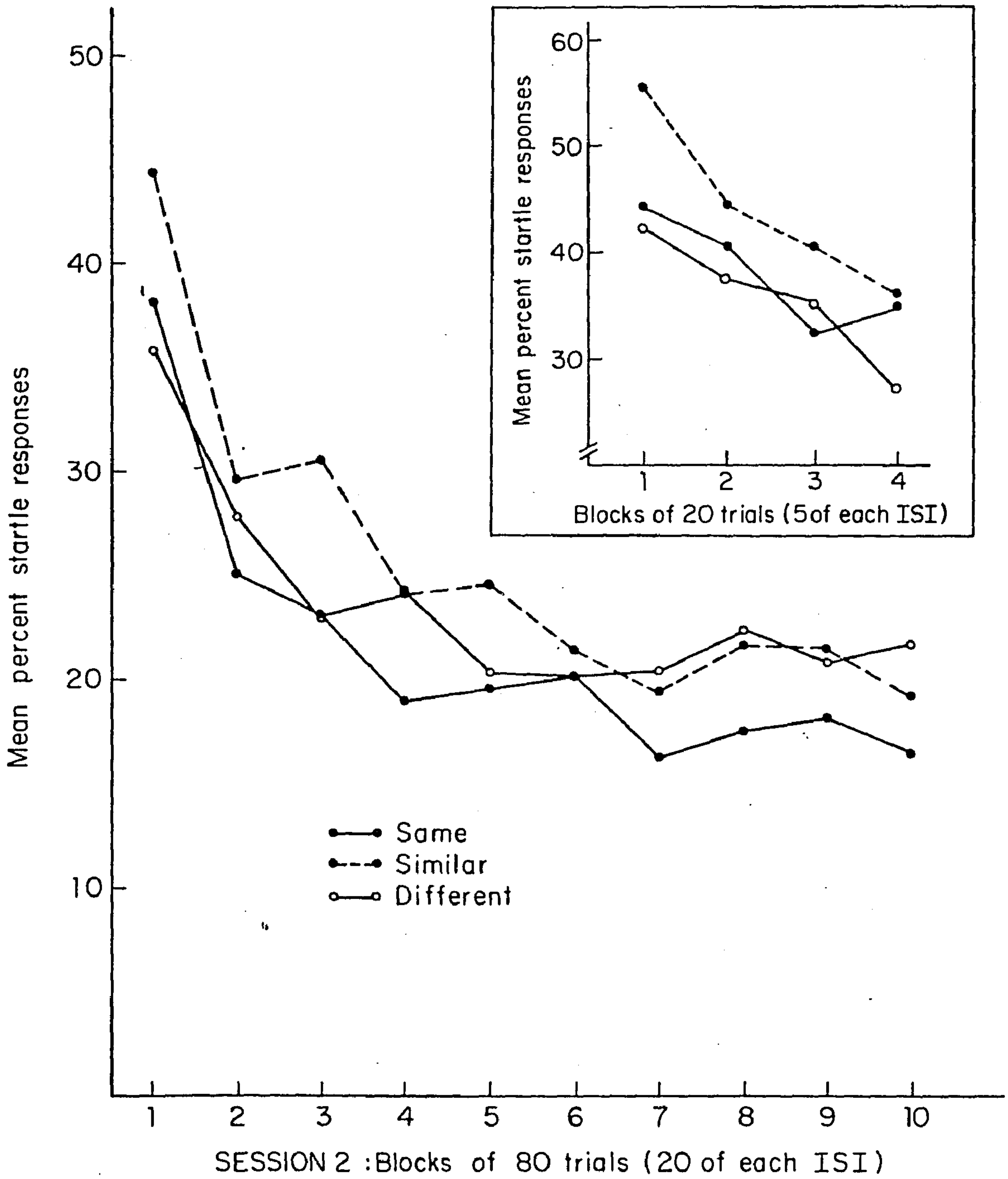

50
40
30
20
10
Mean percent startle responses
1
2
3
4
5
6
7
8
9
10
SESSION 1 : Blocks of 80 trials (20 of each ISI)
Treatment in Session 2:
Same
Similar
Different

Figure 6. The mean percent of startle responses over blocks of 80 trials during Session 2 for Groups Same, Similar and Different of Experiment 3. The inset presents the responses for the first block of 80 trials broken into subblocks of 20 trials.


Mean percent startle responses
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
SESSION 2 :Blocks of 80 trials (20 of each ISI)
Same
Similar
Different
Mean percent startle responses
60
50
40
30
1
2
3
4
Blocks of 20 trials (5of each ISI)

importantly, no differences were found among the three groups, *F*(2,33)=.25, *p*>.50. No difference was found in the first block of 80 trials, nor even in the initial subblock of 20 trials, *F*s(2,33)<.62, *p*s>.25

Discussion

Wagner's theory states that habituation is a consequence of the increasing degree to which the US is primed or expected at the time of its occurrence. In the case of long-term habituation, retrieval-generated priming is assumed to be mediated by the associative strength of the contextual stimuli. Following from these assumptions, a generalization decrement, as evidenced by a disruption of between-session retention of habituation, would be predicted when the contextual cues are altered between sessions. It was expected that in Session 2 a generalization gradient would be seen such that Group Same would be least responsive and Group Different most responsive to the startle stimulus, with Group Similar intermediate to the other two conditions. Such a gradient was not observed in Session 2 of the present study.

The present results are consistent with the findings of similar investigations described above. However, all of these null results are subject to the criticism that the lack of difference in responding may reflect a lack of discriminability between the background cues present in Sessions 1 and 2. Despite the attempt in the present study to maximize discriminability by radically changing aspects of the apparatus in several sensory modalities, it is possible that enough cues remained constant (e.g., the geometry of the enclosure) to evoke the necessary retrieval-generated priming. Given this possibility, it would be desirable to investigate the contextual specificity of long-term habituation in experiment in which the dissimilarity between the contextual cues would not be constrained by what stimuli can be varied within the stabilimeter apparatus itself. Experiments 4 and 5 were designed allow for such manipulations.

Experiment 4 -- Extinction of Habituation

As noted by Wagner (1976), one powerful prediction that can be derived from his associative model of long-term habituation concerns extinction of the association between the contextual cues and the habituated stimulus. If the contextual stimuli function as a the CS, then posthabituation exposure to the context in the absence of the US should be equivalent to the traditional extinction paradigm of presenting the CS alone and ought produce extinction of the association. Such extinction would be indexed on a long-term test by greater responding of a group given an extinction treatment following initial habituation training than a group not receiving any exposure to the context alone between initial habituation and retention testing.

Classical conditioning experiments which included groups receiving such treatment have yielded mixed results. In conditioned emotional response (CER) training, Dweck and Wagner (1970) reasoned that a greater number of unsignaled shocks would yield increased fear conditioning to the apparatus cues and that such fear would be diminished by additional exposure to the contextual cues independent of training. Accordingly, they trained off-baseline two groups of rats that were both food- and water-deprived: in one group the US was correlated with an auditory or visual CS; in the other group the CS and US occurrences were uncorrelated. Half the subjects within each group received prolonged exposure to the context alone preceding and following each CER training session. Consistent with their predictions, greatest fear to the apparatus cues, as evidenced by a longer latency to begin licking a sucrose solution on the day following the termination of CER training, was seen in the uncorrelated group that did not receive additional apparatus exposures. This uncorrelated group took significantly longer to emit its first lick as compared to each of the three other treatment groups which did not differ from one another in their latencies to commence licking. Thus the pre- and post-contextual exposures, by decreasing the overall correlation between the contextual cues and the US presentations, functioned to reduce the fear conditioned to the apparatus.

A related finding has been reported by Tomie (1976a). In pigeons, prior uncorrelated US and discrete CS presentations interfere with subsequent acquisition of autoshaping. Tomie found that this interference can be attenuated by extinguishing contextual cues. However, such an effect was not obtained by Popik and Frey (1978) in an eyeblink conditioning experiment. These researchers administered unsignaled shocks to rabbits in a conditioning chamber, followed by up to eight days of exposure to this chamber without any CS or US presentations. It was hypothesized that this exposure would extinguish the association between the contextual cues and the US. Extinction was assessed by the degree to which pre-exposure to the unsignaled shocks retarded acquisition of a tone-shock association. No acquisition differences were observed between the experimental groups that remained in the conditioning chamber and their respective control groups that spent the same retention interval in their home cages. The detrimental effect of the US pre-exposure was not alleviated by exposure to the conditioning chamber, suggesting that this pre-exposure decrement was not mediated by contextual associations blocking subsequent acquisition to the auditory CS. The basis of this difference from the above reports is not clear as there were numerous differences in procedures and parameters.

There are very few direct studies of long-term habituation that have attempted to extinguish associations to contextual stimuli; however, contradictory findings as to the effectiveness of such a manipulation also appear using this procedure. In an unpublished experiment (reported in Wagner, 1976), rabbits received sufficient presentations of a pure tone to produce decrement in startle response. During the intervening day between training and long-term testing, one group of animals remained in their home cages while the second group was placed in the experimental apparatus. Upon testing, greater responding, indicative of extinction of long-term habituation, was seen in the group that had received the exposure to the contextual cues during the retention interval.

Although the above study described by Wagner is apparently the only experiment to date explicitly designed to evaluate the effect of extinction of contextual associations upon long-term habituation, a number of long-term habituation investigations have incorporated for other reasons what can operationally be considered extinction procedures. For example, Leaton (1974) exposed rats to the training apparatus for five consecutive days between habituation training and a long-term test to reestablish stable baseline licking behavior. Despite this amount of exposure to the apparatus cues, no disruption of long-term habituation was reported, although, as mentioned earlier, this may be due to the floor effects inherent in Leaton's measure.

Experiment 4 was designed to investigate the effects of extinguishing any contextual associations to the US between Session 1 and Session 2. Given that explicitly unpaired presentations of the CS and US appear to be the most effective method of actually extinguishing an associative relationship between the two stimuli (Frey & Butler, 1977), the present experiment included this condition as well as the more conventional "CS only" extinction procedure. According to Wagner's associative model of habituation, startle responding during Session 2 should be greater in the groups receiving extinction treatments relative to the control group receiving no extinction treatment during the retention interval.

Method

Subjects and Apparatus. The subjects (N=48) were similar to those of Experiment 1; the stabilimeter apparatus were the same as those described in Experiment 1. Additionally, two step-through chambers, which were selected for being highly dissimilar to the stabilimeters, were used in the explicitly unpaired extinction conditions. Each step-through apparatus was divided into a white, lighted compartment 16 cm long, and black, dark compartment 44 cm in length. The two compartments were connected by an opening which had a 3.3-cm high hurdle in it. The floor of the apparatus, totalling 60 cm in length, was made of two parallel metal plates, each 2-cm wide, with a 1-cm longitudinal gap between them. The two side walls angled outward equally from the 5-cm wide floor to a maximum width of 20 cm at the 28-cm high Plexiglas ceiling. The two end walls of the apparatus were covered with 2.5-cm wide vertical black and white stripes, and 2 cc of lemon extract were uniformly spread on the bedding beneath the apparatus.

Procedure. The subjects were randomly divided into four groups of 12 rats each. Habituation training and testing procedures for all groups were the same as those used in Experiment 1. Four different extinction conditions were imposed during the one-hour retention interval between Sessions 1 and 2.

Subjects in the Explicitly Unpaired Condition received unpaired presentations of the stabilimeter contextual cues and the US during the retention interval. This was accomplished by alternately exposing these subjects in ten-minute blocks to the tone while they were in the novel step-through apparatus and not presenting the tone while they were in the stabilimeters. The tone was presented at the same intensity, duration and ISI as during training and testing. To control for any effect the exposure to the step-through apparatus would have upon subsequent startle responding during Session 2, an Explicitly Unpaired Apparatus Control Group was treated in the identical way as the Explicitly Unpaired Group, except that they received no US presentations either in the stabilimeter or step-through apparatus. The third condition, Contextual Cue Exposure, was effectively a "CS only" extinction procedure. This group remained in the stabilimeter throughout the one-hour retention interval. No tones were presented during this time. The fourth group of subjects (No Extinction) remained in their home cages during the retention interval and received no explicit extinction treatment. Subjects in the Contextual Cue Exposure and No Extinction Groups were handled every ten minutes during the retention interval to control for the necessary handling of the Explicitly Unpaired and Explicitly Unpaired Apparatus Control Groups.

Results

An analysis by blocks of 80 trials in Session 1 (see Figure 7) found no differences in startle responding among the four groups, $F(3,44)=.42$, $p>.50$, however, a within-session response decrement over trials, $F(9.396)=51.99$, $p<.001$ and a reliable effect of the ISI, $F(3,132)=50.84$, $p<.001$ were found.

Of primary interest is the relative responsiveness of the groups following the retention interval during which the extinction treatments were administered. These data for Session 2 are illustrated in Figure 8. Although no differences among the four groups were observed when the data were analyzed over the entire session, $F(3,44)=1.24$, $p>.30$, comparisons of the first subblock of 20 trials (see inset in Figure 8), where any differences present would be expected to be most pronounced, revealed a significantly <u>greater</u> percentage of startle responding in the No Extinction Group than in the Explicitly Unpaired Treatment condition, $t(22)=3.60$, $p<.05$. A similar difference between the No Extinction Group and the Explicitly Unpaired Apparatus Control Group approached significance, $t(22)=1.83$,

Figure 7. The mean percent of startle responses over blocks of 80 trials during Session 1 for the Contextual Cue Exposure, Explicitly Unpaired, Explicitly Unpaired Apparatus Control and No Extinction Groups of Experiment 4.

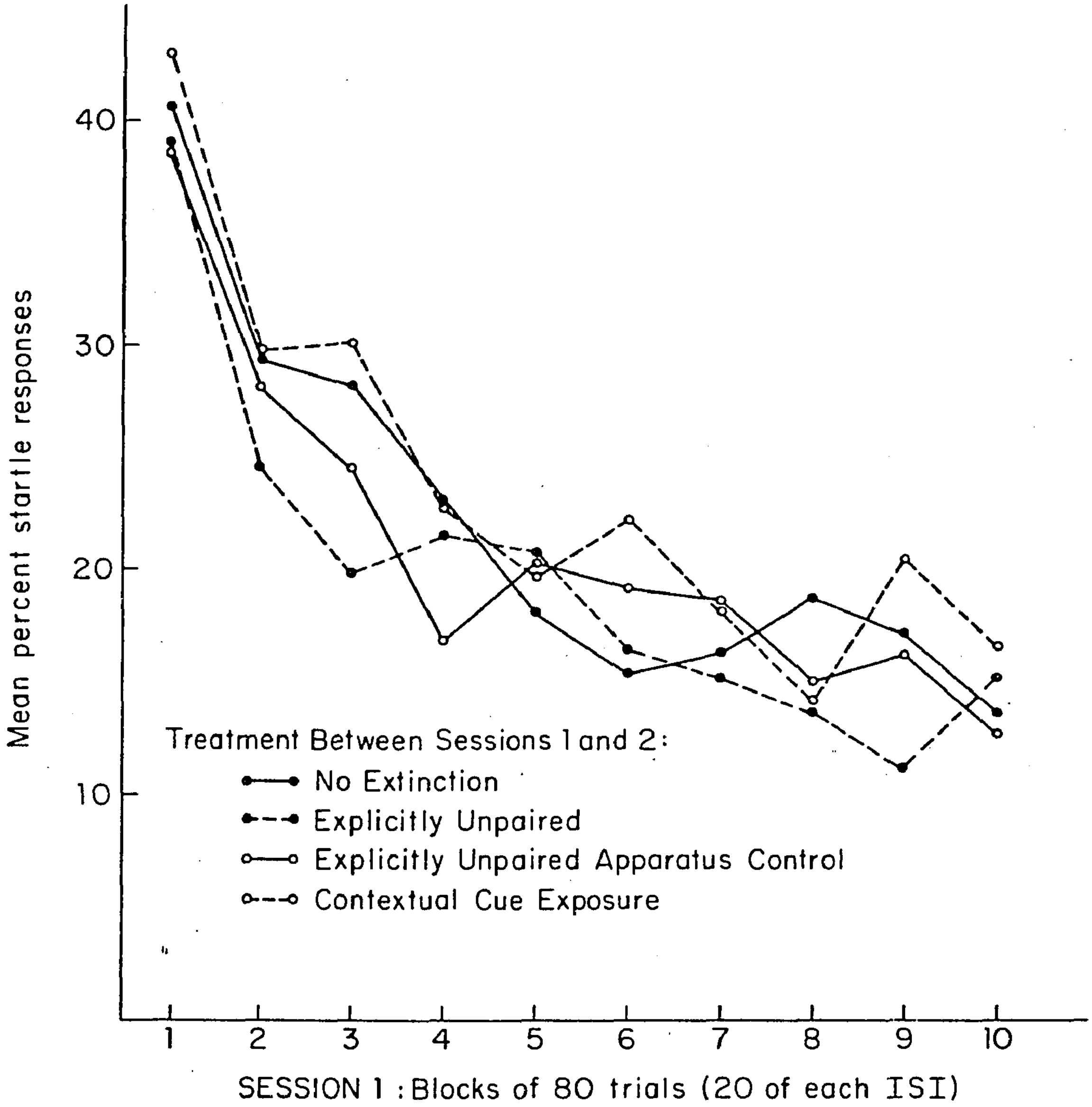
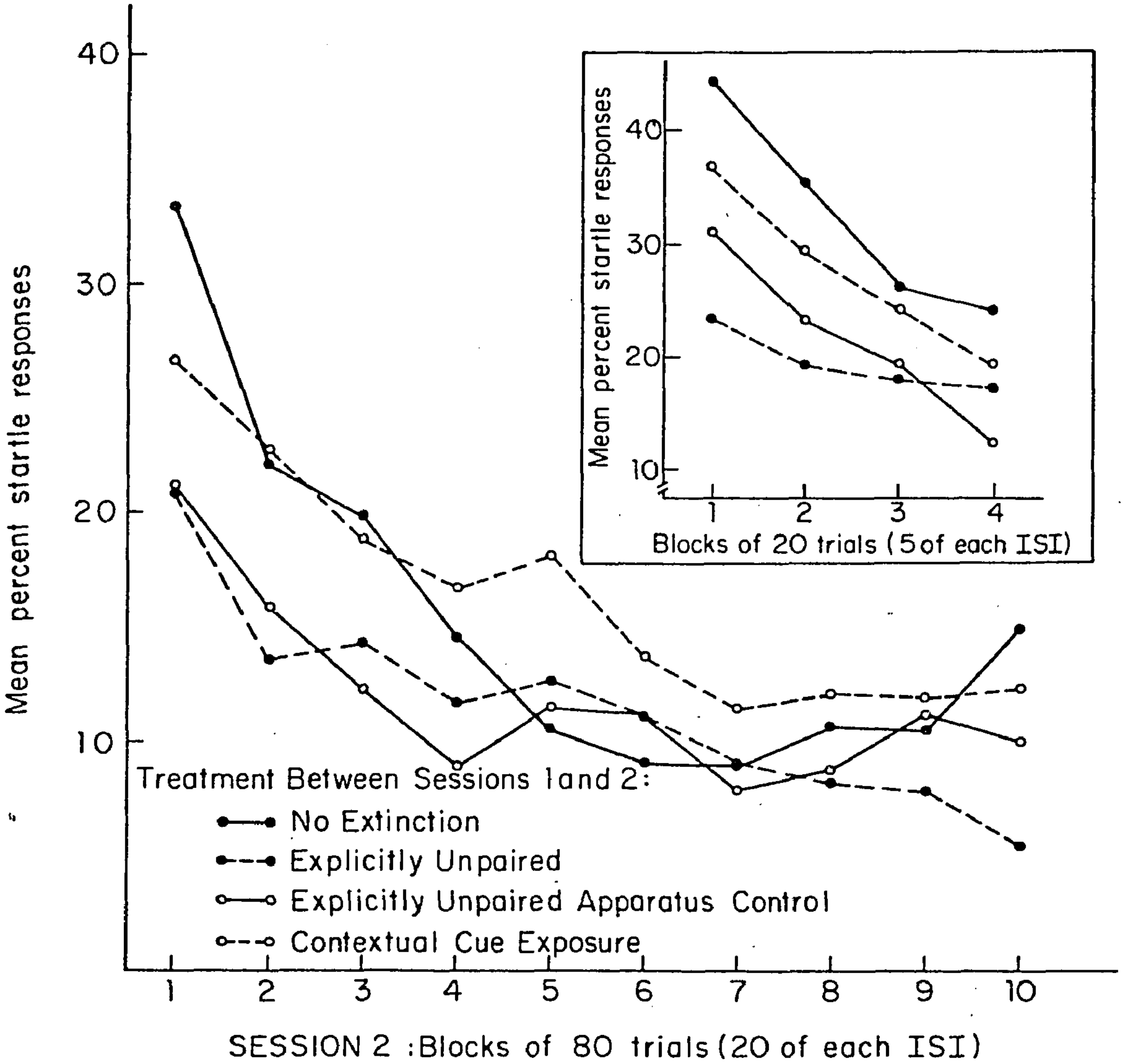

Mean percent startle responses
40
30
20
10
1
2
3
4
5
6
7
8
9
10
SESSION 1 : Blocks of 80 trials (20 of each ISI)
Treatment Between Sessions 1 and 2:
No Extinction
Explicitly Unpaired
Explicitly Unpaired Apparatus Control
Contextual Cue Exposure

Figure 8. The mean percent of startle responses over blocks of 80 trials during Session 2 for the Contextual Cue Exposure, Explicitly Unpaired, Explicitly Unpaired Apparatus Control and No Extinction Groups of Experiment 4. The inset presents the responses for the first block of 80 trials broken into subblocks of 20 trials.


Mean percent startle responses
40
30
20
10
Treatment Between Sessions 1 and 2:
No Extinction
Explicitly Unpaired
Explicitly Unpaired Apparatus Control
Contextual Cue Exposure
1
2
3
4
5
6
7
8
9
10
SESSION 2 : Blocks of 80 trials (20 of each ISI)
Mean percent startle responses
40
30
20
10
1
2
3
4
Blocks of 20 trials (5 of each ISI)

$p < .10$. On this first subblock of 20 trials the Explicitly Unpaired Group was also less responsive than the Contextual Cue Group, $t(22)=2.14$, $p < .05$. Over the entire session, a response decrement, $F(9,396)=24.31$, $p < .001$ and and ISI effect, $F(3,132)=50.05$, $p < .001$ were obtained.

Discussion

These data are essentially opposite the results that would be expected based on Wagner's model. According to his model of long-term habituation, the extinction treatments received by the Contextual Cue Exposure and Explicitly Unpaired Groups should have impaired the association between the contextual cues of the stabilimeter and the US. Therefore, upon testing, the contextual cues should not have produced the retrieval-generated priming needed for long-term habituation. In the present study no support for these predictions was obtained.

It is possible, however, to hypothesize various additional mechanisms that might interact with such an associative model of habituation to produce the present results. For example, it might be assumed that some limited amount of exposure to apparatus cues during a retention interval could serve to "remind" the subject of the US and thus strengthen the association (see Spear, 1976), while prolonged exposure would institute the extinction process. Such an admittedly *post-hoc* analysis could account for the ranking of the percentage of startle responses seen in the present study. The Explicitly Unpaired and Explicitly

Unpaired Apparatus Control Groups received half as much exposure to the stabilimeter apparatus during the retention interval as did the contextual Cue Exposure Group. This amount of exposure may have enhanced the association and thus maintained the greater response decrement seen in these groups. The greater apparatus exposure given to the Contextual Cue Exposure Group could have exceeded the amount which would function to reinstate and strengthen the association, and permitted extinction to begin in this group, thereby decreasing the degree of response decrement evident on testing. This post-hoc interpretation is compatible with the present data, but appears unlikely given the results of the other experiments in this series.

Except for the performance of the Explicitly Unpaired Apparatus Control Group, the results of Experiment 4 are perfectly consistent with a nonassociative model of habituation in which the critical determinant of the response decrement is the amount and pattern of US presentations. This is evident in the observation that the Explicitly Unpaired Group, which relative to the other conditions received a greater number of overall presentations of the tone more recently prior to the long-term test, exhibited less startle responding than any other group during Session 2. However, the behavior of the Explicitly Unpaired Apparatus Control Group, which did not hear the tone during the retention interval, should then also have been greater than the Explicitly Unpaired Group.

This was not found, suggesting that the tone exposure was not the sole factor controlling the difference in responsiveness among the treatment groups during Session 2.

A broader version of a nonassociative interpretation of long-term habituation could be fashioned by encompassing the total degree of exposure to the entire stimulus complex rather than simply to the US. That is to say, the greater the degree of exposure to all aspects of the training situation, the context as well as the US, the greater the response decrement would be expected. Nevertheless, by such an analysis the performance of the Explicitly Unpaired Apparatus Control Group relative to the Explicitly Unpaired Group would still be anomalous.

Experiment 5 -- Latent Inhibition of Habituation

One way to distinguish between the various associative and nonassociative explanations offered for the results of Experiment 4 would be to present the diverse treatments prior to habituation training. In this way associative alternatives based on reminder effects would be eliminated leaving clearer opposing predictions for nonassociative models and Wagner's associative hypothesis. Administering these treatments prior to training has the additional major advantage that the duration of the treatment would not be constrained by the length of the retention interval.

If long-term habituation is conceptualized as an associative process, prior exposure to the contextual cues in the absence of the probe stimulus would operationally correspond to the classical conditioning procedure of latent inhibition. In this paradigm, preconditioning exposure to the CS alone retards acquisition of the association when that CS is subsequently paired with a US (Lubow & Moore, 1959). According to Wagner's model, prehabituation exposure to the contextual cues ought to retard the formation of the association and thus produce a slower rate of habituation. However, if the parameters of US exposure are the only critical determinants of habituation, as stressed by most nonassociative models of habituation, no difference in the rate of habituation would be expected based on prior exposure to the contextual cues. Alternatively, a nonassociative model might relate startle responding to a summation of US and context novelty; thus a group receiving prior exposure to the contextual cues should yield a greater response decrement than a group that did not receive any such prior exposure.

Empirical support for this last hypothesis has been presented by Korn and Moyer (1966). They recorded startle responding in rats to the firing of a blank starting pistol. Subjects that received 30 min of daily apparatus exposure for seven consecutive days preceding training showed a significantly attenuated startle response to the initial gunshot relative to subjects receiving no prior apparatus exposure. Korn and Moyer attributed this effect to the reduced novelty of the situation, which produced a diminution of the initial startle response. As this effect was seen on the first trial, Wagner's model of habituation offers no explanation for these results.

Differential predictions of associative and nonassociative interpretations of habituation can also be made for a group receiving the Explicitly Unpaired Treatment of Experiment 4 prior to training. According to nonassociative models concerned either with the amount of exposure to the US or to the entire stimulus complex, a greater response decrement should be evident in this condition than a group that receives no prior treatment. Wagner's associative model of habituation would make the opposite prediction as the Explicitly Unpaired Condition represents a true inhibitory relationship between the contextual cues of the stabilimeter and the US which should subsequently interfere with their later excitatory association.

Method

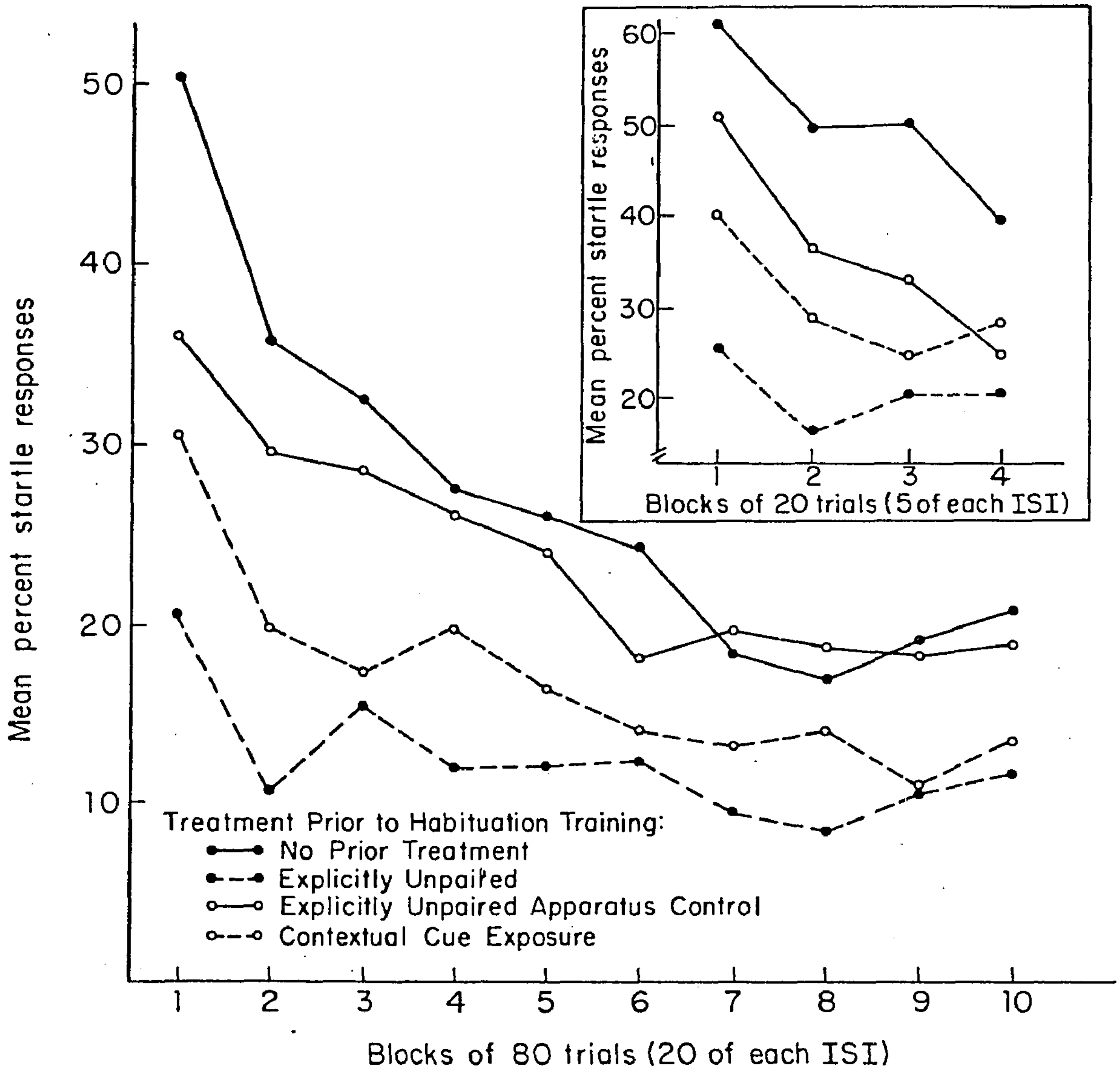
Subjects and Apparatus. The subjects (N=44) were similar to those of Experiment 1; the stabilimeters were identical to those used in Experiment 1, the step-through apparatus were the same as those described in Experiment 4.

Procedure. The subjects were randomly divided into four groups, Contextual Cue Exposure, Explicitly Unpaired, Explicitly Unpaired Apparatus Control, and No Prior Treatment, of 11 rats each. Except for the fact that these treatments were given prior to habituation training, the procedures for each group were identical to those of Experiment 4. For seven consecutive days preceding habituation training these treatments were administered daily for the same length as the training session (100 min). During this time the Contextual Cues Exposure Group was placed in the stabilimeters and handled every 10 min; the Explicitly Unpaired Group was alternated every 10 min between the stabilimeter and step-through apparatus in which the US was presented; the Explicitly Unpaired Apparatus Control Group also was switched between the stabilimeter and step-through apparatus, but no tones were presented in the step-through apparatus; and the No Prior Treatment Group remained in their home cages except for handling every 10 min. On the eighth day these these treatments were again given to the various groups, followed approximately 10 min later by initiation of the habituation training procedure described in Experiment 1. Experiment 5 was conducted in 11 balanced replications.

Results

The mean percents of startle responses for each condition, broken down into blocks of 80 trials, are illustrated in Figure 9. A significant difference among the treatments over the entire session was found, $F(3,40)=4.04$, $p<.02$. Analyses of the first subblock of 20 trials (see inset of Figure 9) yielded reliably greater startle responding in the No Prior Treatment Group as compared to the Contextual Cue Exposure Group, $t(20)=2.86$, $p<.01$, or to

Figure 9. The mean percent of startle responses over blocks of 80 trials for the Contextual Cue Exposure, Explicitly unpaired, Explicitly Unpaired Apparatus Control and No Prior Treatment Groups of Experiment 5. The inset presents the responses for the first block of 80 trials broken into subblocks of 20 trials.


Mean percent startle responses
50
40
30
20
10
1
2
3
4
5
6
7
8
9
10
Blocks of 80 trials (20 of each ISI)
Treatment Prior to Habituation Training:
No Prior Treatment
Explicitly Unpaired
Explicitly Unpaired Apparatus Control
Contextual Cue Exposure
Mean percent startle responses
60
50
40
30
20
1
2
3
4
Blocks of 20 trials (5 of each ISI)

the Explicitly Unpaired Group, *t*(20)=2.07, $p<.05$. Responding in the Explcitly Unpaired Apparatus Control Group was greater than in the Explicitly Unpaired Group, *t*(20)=2.49, $p<.05$. No differences in responding on this first block were observed between the Explicitly Unpaired Apparatus Control and the Contextual Cue Exposure Groups, *t*(20)=1.20, $p>.10$, or between the Explicitly Unpaired Apparatus Control and the No Prior Treatment Group, *t*(20)=2.07, $p>.05$.

During the habituation training session a decrement over blocks of trials, *F*(9,360)=35.37, $p<.001$, and an ISI effect, *F*(3,120)=72.31, $p<.001$ were found.

Discussion

The results of Experiment 5 appear highly consistent with Korn and Moyer's (1966) nonassociative interpretation of habituation. Assuming, as they do, that exposure to any aspect of the entire stimulus complex will contribute to the observed response decrement, the greatest decrement would be expected in the Explicitly Unpaired Group, as these subjects received prior exposure to both the US and the stabilimeter. The Explicitly Unpaired Apparatus Control and the Contextual Exposure Groups would, according to this interpretation, be more responsive than the Explicitly Unpaired Group but less so than the No Prior Treatment Group as they had been exposed only to the stabilimeter apparatus. The No Prior Treatment Group, which was not exposed to either the stabilimeter or the US prior to training, would be predicted to be most responsive. The present results clearly conform to these predictions and are in the opposite direction of the outcome that would be expected based on Wagner's associative model of habituation. As this study did not include groups that were pretreated but not presented with the tone to control for general activity, it is not possible to clearly factor out the proportion of responding due to the novel environment. However, on the basis of the Activity Control Group in Experiment 1, it is expected that this activity baseline would be rather low.

The nonassociative interpretation of the present findings contrasts with the results of Experiment 3 in which no stimulus generalization gradient was observed when the contextual cues were altered between Sessions 1 and 2. This apparent inconsistency may be a result of the degree of environmental change in the apparatuses between sessions. Despite the attempt to modify the stabilimeter apparatus following Session 1 of Experiment 3, at the onset of Session 2 subjects had, nevertheless, prior exposure to many aspects of the stabilimeter, whereas in the present experiment the stabilimeter was a totally novel enclosure.

These results also call into question the distinction between the mechanisms responsible for short-term and long-term habituation. Wagner postulates that short-term or within-session habituation is primarily due to self-generated priming produced by the recent presentation of the US while long-term or between-session habituation reflects retrieval-generated priming. These two methods of priming cannot logically be totally independent, as during habituation training the model calls for some association being formed between the contextual cues and the US if this association is manifest on a long-term test. Similarly, after the first stimulus presentation of the habituation retention test session, there would necessarily be a self-generated component present.

The present data also indicate that factors other than self-generated and retrieval-generated priming influence the degree of response decrement. In Experiment 5 the Contextual Cue Exposure Group exhibited a significantly smaller percentage of startle responses than the No Prior Treatment Group. As both these groups heard the US for the first time during habituation training, this difference cannot be accounted for by differences in priming of the US. These findings may be interpreted as being contrary, not only to Wagner's model, but also to learning theories focusing on attentional factors (e.g., Mackintosh, 1973). If stimuli are competing for access to a limited-capacity attentional system, the tone ought receive greater attention in the Contextual Exposure Group, in which the tone is the only novel stimulus, than in the No Prior Treatment Group, in which the entire experimental situation is novel to the subject.

General Discussion

The present series of experiments was designed to investigate the hypothesis that associations between contextual cues and the iterated stimulus mediate long-term habituation (Wagner, 1976, 1979). Measuring the acoustic startle response of the rat, the contextual specificity of long-term habituation was evaluated through the processes of overshadowing, generalization, extinction, and latent inhibition (Experiments 2 through 5 respectively). The results of these studies were inconsistent with the predictions of Wagner's associative model of long-term habituation.

It is important to emphasize that the obtained long-term habituation cannot be accounted for by a sensory deficit. As noted in studies described above (e.g., Groves, Wilson & Miller, 1976), physiological recordings from sensory pathways during startle habituation training procedures revealed no auditory damage, permanent or temporary, even with the use of auditory stimuli more intense than that used in the present experiments. Moreover, the present data do not lend themselves to an explanation based on sensory debilitation. For example, in Experiment 4 a significantly greater percentage of startle responding was observed in the first subblock of 20 trials in Session 2 by the No Extinction Group than by the Explicitly Unpaired Apparatus Control Group. As both these groups received identical exposure to the tone during

Session 1 and neither heard the tone during the retention interval, an explanation of long-term habituation based on auditory damage cannot account for differences such as these.

Given that none of the present experiments provide support for Wagner's associative model of long-term habituation, it appears appropriate to consider alternative explanations of the empirical underpinnings of his model. Wagner's interpretation is based primarily on Davis' (1970a) finding that a longer ISI during habituation training produces a greater long-term response decrement than does a shorter ISI . This seems to be a reliable phenomenon that has been reported in several independent laboratories using highly dissimilar preparations (e.g., Carew, Pinsker & Kandel, 1972; File, 1973).

One alternate hypothesis, discussed in Experiment 1, is that the greater amount of exposure to the apparatus cues in the longer ISI condition leads to the increased long-term response decrement. This interpretation becomes more plausible in light of the findings of Korn and Moyer (1966) and the results of Experiment 5, both of which suggest that familiarity with the habituation training environment produces decreased responding during habituation training.

A second complementary explanation can be put forth based on the fact that Davis' finding parallels the long-standing observation that spaced practice produces a higher level of performance than massed practice given an equal amount of exposure time in both conditions. The most commonly advanced theoretical explanation of this spacing effect - one that can be related directly to Wagner's model - is that spaced presentations of a stimulus allow for prolonged rehearsal. (See Hintzman, 1974, for a review of various alternate theoretical interpretations of the spacing effect in human memory research.) If greater rehearsal time produces a stronger association-free memorial representation of the US, then a greater response decrement might be expected on a long-term retention test. Relying upon the degree of rehearsal, it is therefore possible to reinterpret Davis' experiment within a nonassociative framework. (As mentioned earlier, the present use of the term nonassociative can be considered to be associative in the sense that the iterated stimulus is "associated" with no other events. Regardless of whether one wishes to consider this as associative or nonassociative, such a process clearly does not involve contextual specificity.)

There are several other aspects of Wagner's theory of habituation that warrant further consideration. One is his assumption that self-generated priming primarily determines within-session habituation while retrieval-generated priming is responsible for between-session habituation. Based on Wagner's model these two methods of priming would both have to be involved in the two types of habituation tests. As indicated above, the association between contextual cues and the US, i.e. retrieval-generated priming, would have to be established during Session 1 if it is to be present in Session 2. Moreover, if retrieval-generated priming were not involved in within-session habituation such that within-session habituation resulted solely from self-generated priming, a response increment rather than a response decrement would be expected. This prediction follows from two of Wagner's assumptions. First, Wagner has presented data indicating that surprising events are processed or rehearsed for a longer duration than expected events (Terry & Wagner, 1975). Second, a greater response decrement is observed when the representation of the event is primed in STM at the time of its occurrence, that is, "when the stimulus is prerepresented it will less likely evoke the response" (Wagner, 1976, p. 108). Therefore, the initial presentations of the US ought to be most surprising and thus have a higher probability of being primed at the time of the next US presentation. If the duration for which the US is maintained in STM decreases with increasing number of trials, and it appears reasonable that after several hundred presentations the stimulus itself would would be less surprising to the animal, then the US is less likely to be primed and thus would be more likely to produce the response.

This possibility raises questions about the performance rules of Wagner's theory. Wagner maintains the same performance rule in habituation as he does in his more general theory of classical conditioning. The fact that behavior in clasical conditioning and habituation paradigms moves in opposite directions during training invites speculation as to how performance in both situations can be governed by this same rule. In the case of classical conditioning, the CS is assumed to prime the representation of the US; hence, the CR is produced as a result of the representation of the US in STM. If, however, this analysis is extended to long-term habituation, the contextual cues should evoke the response through the same mechanism of retrieval-generated priming. This leads to the rather unlikely prediction that in the present experiments the animals ought to have emitted startle responses after habituation training simply upon being placed in the stabilimeters. Although responding in the present experiments was electronically recorded only during US presentations, observation of the animals when they were returned to the apparatus did not provide any support for this prediction (recorded startle responses were evident to the visual observer at the beginning of the session) nor have any supportive findings been reported in other habituation research.

In summary, although Wagner's associative model appears inapplicable to long-term habituation, the general approach of his theory has been influential and constructive. Wagner's analyses have served to firmly reestablish cognitive concepts within animal learning, and it is likely that the theory wll continue to be refined and more precisely delineated (e.g., Dickinson & Mackintosh, 1979) in describing how animals differentially process surprising and expected information. However, the present series of experiments suggest that the extrapolation of Wagner's model to long-term habituation, at least in regard to the acoustic startle response, is probably incorrect. Of course, it is possible that not all types of long-term habituation will ultimately be explained by the same theoretical mechanism, and that Wagner's interpretation might be found to be appropriate in preparations other than those involving startle responses.

The present findings indicate that, although contextual cues do not function as a CS in long-term habituation, there is a need to broaden nonassociative conceptions of habituation to include other elements of the experimental situation in addition to the US as critical determinants of responding. The degree of startle responding in the present series appears to reflect a summation of the novelty of the entire stimulus complex. Perhaps the novelty of the environmental situation produces sensitization which augments the startle response. By extinguishing any unconditioned responses elicited by the context, prolonged preexposure would serve to reduce this sensitization, thus yielding a decrease in startle responding to the tone.

Previous habituation research has stressed the importance upon responding of background stimuli within the same modality as the US (e.g., Davis, 1974). The present results extend this analysis to include stimuli in other modalities by suggesting that habituation is a nonassociative process in which the prior experience of the subject with the total stimulus complex is a critical factor. This was most evident in the results of Experiment 5 in which significantly less startle responding during initial habituation training was seen in animals that had received preexposure to the apparatus, largely a nonauditory experience, than in subjects that had not received this preexposure. congruent with the concept that habituation occurs within the central nervous system. Although the input channels of the various sensory modalities are relatively independent, integration of the incoming sensory information is performed centrally. The response is apparently determined not solely the the particular modality of the iterated stimulus, but by the integrated information provided by the entire experimental situation.

References

Archer, T., Sjoden, P. Nillson, L. & Carter, N. Role of exteroceptive background context in taste-aversion conditioning and extinction. Animal Learning and Behavior, 1979, 7, 17-22.

Atkinson, R. C. & Shiffrin, R. M. Human memory: A proposed system and its control processes. In K. W. Spence and J. T. Spence (Eds.), The Psychology of Learning and Motivation, New York: Academic Press, 1968.

Batson, J. D. & Best, P. J. Drug-preexposure effects in flavor-aversion learning: Associative interference by conditioned environmental stimuli. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5, 273-283.

Block, R. A. & Reed, M. A. Remembered duration: Evidence for a contextual-change hypothesis. Journal of Experimental Psychology: Human Learning and Memory, 1978, 4, 656-665.

Bolles, R. C. & Collier, A. C. The effect of predictive cues on freezing in rats. Animal Learning and Behavior, 1976, 4, 6-8.

Bouton, M. E. & Bolles, R. C. Role of contextual stimuli in the reinstatement of extinguished fear. Journal of Experimental Psychology: Animal Behavior Processes, in press.

Byrne, J., Castellucci, V., Kandel, e. r. Receptive fields and response properties of mechnoreceptor neurons innvervating siphon skin and mantle shelf in Aplysia. Journal of Neurophysiology, 1974, 37, 1041-1064.

Carew, T. J. & Kandel, E. R. A cellular analysis of acquisition and retention of long-term habituation in Aplysia. Science, 1973, 182, 1158-1160.

Carew, T. J., Pinsker, H. M. & Kandel, E. R. Long-term habituation of a defensive withdrawal reflex in Aplysia. Science, 1972, 175, 451-454.

Carew, T. J., Pinsker, H., Rubinson, K., Kandel, E. R. Physiological and biochemical properties of neuromuscular transmission between identified motorneurons and gill muscle in Aplysia. Journal of Neurophysiology, 1974, 37, 1020-1040.

Castellucci, V. F., Carew, T. J. & Kandel, E. R. Cellular analysis of long-term habituation of the gill-withdrawal reflex of Aplysia californica. Science, 1978, 202, 1306-1308.

Castellucci, V. & Kandel, E. R. An invertebrate system for the cellular study of habituation and sensitization. In T. J. Tighe and R. N. Leaton (eds.), Habituation. Perspectives from child development, animal behavior, and neurophysiology. Hillsdale, New Jersey: Erlbaum Associates, 1976.

Castellucci, V., Pinsker, H., Kupferman, I. & Kandel, E. R. Neuronal mechanisms of habituation and dishabituation of the gill-withdrawal reflex in Aplysia. Science, 1970, 167, 1745-1748.

Chorover, S. L. & Schiller, P. S. Short-term retrograde amnesia in rats. Journal of Comparative and Physiological Psychology, 1965, 59, 73-78.

Connolly, J. R. & Frith, C. D. Effects of a varying stimulus context on habituation and sensitization of the OR. Physiology and Behavior, 1978, 21, 511-514.

Davis, M. Interstimulus interval and startle response habituation with a "control" for total time during training. Psychonomic Science, 1970b, 20, 39-41.

Davis, M. Effects of interstimulus interval length and variability of startle-response habituation in the rat. Journal of Comparative and Physiological Psychology, 1970a, 72, 177-192.

Davis, M. Sensitization of the rat startle response by noise. Journal of Comparative and Physiological Psychology, 1974a, 87, 571-581.

Davis, M. Signal-to-noise ratio as a predictor of startle amplitude and habituation in the rat. Journal of Comparative and Physiological Psychology, 1974b, 86, 812-825.

Dickinson, A. & Mackintosh, N. J. Reinforcer specificity in the enhancement of conditioning by posttrial surprise. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5, 162-177.

Dweck, C. S. & Wagner, A. R. Situational cues and correlation between CS and US as determinants of the conditioned emotional response. Psychonomic Science, 1970, 18, 145-147.

Engberg, L. A., Hansen, G., Welker, R. L. & Thomas, D. R. Acquisition of key-pecking via autoshaping as a function of prior experience: "Learned laziness"?, *Science*, 1972, *178*, 1002-1004.

File, S. E. Inter-stimulus interval and the rate of behavioral habituation. *Quarterly Journal of Experimental Psychology*, 1973, *25*, 360-367.

Frey, P. W. & Butler, C. S. Extinction after aversive conditioning: An associative or nonassociative process? *Learning and Motivation*, 1977, *8*, 1-17.

Glass, D. C. & Singer, J. F. *Urban Stress*. New York: Academic Press, 1972.

Groves, P. M. & Lynch, G. S. Mechanisms of habituation in the brain stem. *Psychological Review*, 1972, *79*, 237-244.

Groves, P. M. & Thompson, R. F. Habituation: A dual-process theory. *Psychological Review*, 1970, *77*, 419-450.

Groves, P. M., Wilson, C. J. & Boyle, R. D. Brain stem pathways, cortical modulaion, and habituation of the acoustic startle response. *Behavioral Biology*, 1974, *10*, 391-418.

Groves, P. M., Wilson, C. J., & Miller, S. W. Habituation of the acoustic startle response: A neural systems analysis of habituation in the intact animal. In A. H. Hiesen & R. F. Thompson (Eds.), *Advances in* psychobiology, Volume three, New York: John Wiley & Sons, 1976.

Gubernick, D. J. & Wright, J. W. Habituation of two response systems in the lizard Anolis carolinenis. Animal Learning and Behavior, 1979, 7, 125-132.

Hennig, C. W. The effects of physical environment, time in captivity, and defensive distance on tonic immobility. Freezing, and Flight behaviors in Anolis carolinensis. Animal Learning and Behavior, 1979, 7, 106-110.

Hintzman, D. L. Theoretical implications of the spacing effect. In R. L. Solso (Ed.), Theories in cognitive psychology: The Loyola Symposium. Potomac, Maryland: Erlbaum Associates, 1974.

Hulse, S. H., Fowler, H. & Honig, W. G. (Eds.) Cognitive processes in animal behavior. Hillsdale, New Jersey: Erlbaum Associates, 1978.

Kamin, L. J. 'Attention-like' processes in classical conditioning. In M. R. Jones (Ed.), Miami symposium on the prediction of behavior: Aversive stimulation. Miami: University of Miami Press, 1968.

Kamin, L. J. Predictability, surprise, attention and conditioning. In B. A. Campbell and R. M. Church (Eds.), Punishment and aversive behavior. New York, Appleton-Century-Crofts, 1969.

Kimble, G. A. & Ost, J. W. P. A conditioned inhibitory process in eyelid conditioning. Journal of Experimental Psychology, 1961, 61, 150-156.

Kimmel, H. D. Inhibition of the unconditioned response in classical conditioning. Psychological Review, 1966, 73, 232-240.

Kimmel, H. D. & Burns, R. A. Adaptational aspects of condtioning. In W. K. Estes (Ed.), Handbook of learning and cognitive processes, Vol. 2. Hillsdale, New Jersey: Erlbaum Associates, 1975.

Konorski, J. Integrative activity of the brain. Chicago: University of Chicago Press, 1967.

Korn, J. H. & Moyer, K. E. Habituation of the startle response and of heart rate in the rat. Canadian Journal of Psychology, 1966, 20, 183-190.

Kremer, E. F. Effect of posttrial episodes on conditioning in compound conditioned stimuli. Journal of Experimental Psychology: Animal Behavior Processes, 1979, 5, 130-141.

Kremer, E. F. The truly random control procedure: Conditioning to the static cues. Journal of Comparative and Physiological Psychology, 1974, 86, 700-707.

Leaton, R. N. Long-term retention of the habituation of lick suppression in rats. Journal of Comparative and Physiological Psychology, 1974, 87, 1157-1164.

Logan, C. A. & Beck, H. P. Long-term retention of habituation in the sea anemone (Anthopleura elegantissima). Journal of Comparative and Physiological Psychology, 1978, 92, 928-936.

Lubow, R. E. & Moore, A. U. Latent inhibition: The effect of nonreinforced preexposure to the conditioned stimulus. Journal of Comparative and Physiological Psychology, 1959, 52, 415-419.

Lubow, R. E., Rifkin, B., & Alek, M. The context effect: The relationship between stimulus pre-exposure and environment pre-exposure determines subsequent learning. Journal of Experimental Psychology: Animal Behavior Processes, 1976, 1, 38-47.

Mackintosh, N. J. Stimulus selection: Learning to ignore stimuli that predict no change in reinforcement. In R. A. Hinde and J. Stevenson-Hinde (Eds.), Constraints on learning. London: Academic Press, 1973.

Marlin, N. A., Berk, A. M. & Miller, R. R. Vulnerability of memory to electroconvulsive shock in relation to onset and offset of reinforcement. Physiology and Behavior, 1979, 22, 217-221.

Mitchell, D., Scott, D. W. & Mitchell, L. K. Attenuated and enhanced neophobia in the taste aversion "delay of reinforcement" effect. Animal Learning and Behavior, 1977, 5, 99-102.

Odling-Smee, F. J. The overshadowing of background stimuli by an informative CS in aversive Pavlovian conditioning with rats. Animal Learning and Behavior, 1978, 6, 43-51.

Peeke, H. V. S. & Veno, G. Stimulus specificity of habituated aggression in three-spined sticklebacks

(Gasterosteus aculeatus). *Behavioral Biology*, 1973, *8*, 427-432.

Perkins, C. C., Jr. An analysis of the concept of reinforcement. *Psychological Review*, 1968, *75*, 155-172.

Popik, R. S. & Frey, P. W. Retarding effect of unsignalled shock presentations: Potential mediation by background stimuli. Paper presented at the Midwestern Psychological Association, Chicago, May 1978.

Rachlin, H. *Behavior and learning*. San Francisco: W. H. Freeman and Company, 1976.

Rescorla,R. A. & Holland, P. C. Some behavioral approaches to the study of learning. In M. R. Rosenweig and E. L. Bennett (Eds.), *Neural Mechanisms of learning and memory*. Cambridge, Massachusetts: M I T Press, 1976.

Rescorla, R. A. & Wagner, A. R. A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black and W. F. Prokasy (Eds.), *Classical conditioning II: Current research and theory*. New York: Appleton-Century-Crofts, 1972.

Sharpless, S. K. & Jasper, H. Habituation of the arousal reaction. *Brain*, *1956*, 79, *655-680*.

Siegel, S. Morphine tolerance acquisition as an associative process. *Journal of Experimental Psychology: Animal Behavior Processes*, 1977, *3*, 1-13.

Smith, S. M. Remembering in and out of context. *Journal of*

Experimental Psychology: Human Learning and Memory, in press.

Smith, S. M., Glenberg, A. & Bjork, R. A. Environmental context and human memory. Memory and Cognition, 1978, 6, 342-353.

Sokolov, E. N. Perception and the conditioned reflex. (S. W. Waydenfeld, translation) Oxford: Pergamon, 1963.

Spear, N. E. Retrieval of memories: A psychobiological approach. In W. K. Estes (Ed.), Handbook of learning and cognitive processes, Vol. 4, Hillsdale, New Jersey: Erlbaum Associates, 1976.

Spear, N. E. The processing of memories: forgetting and retention. Hillsdale, New Jersey: Erlbaum Associates, 1978.

Stein, L. Habituation and stimulus novelty: A model based upon classical conditioning. Psychological Review, 1966, 73, 352-356.

Terry, W. S. Effects of priming unconditioned stimulus representation in short-term memory on Pavlovian conditioning. Journal of Experimental Psychollogy: Animal Behavior Processes, 1976, 2, 354-369.

Terry, W. S. & Wagner, A. R. Short-term memory for "surprising" vs. "expected" unconditioned stimuli in Pavlovian conditioning. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 1, 122-133.

Thompson, R. F. & Spencer, W. A. Habituation: A model phenomenon for the study of neuronal substrates of behavior. *Psychological Review*, 1966, *173*, 16-43.

Tolman, E. C. *Purposive behavior in animals and men*. New York: Century, 1932.

Tomie, A. Inteference with autoshaping by prior context conditioning. *Journal of Experimental Psychology: Animal Behavior Processes*, 1976a, *2*, 323-334.

Tomie, A. Retardation of autoshaping: Control by contextual stimuli. *Science*, 1976b, *192*, 1244-1246.

Wagner, A. R. Priming in STM: An information-processing mechanism for self-generated or retrieval-generated depression in performance. In *Habituation. Perspectives from child development, animal behavior, and neurophysiology*. T. J. Tighe and R. N. Leaton (Eds.), Hillsdale, New Jersey: Erlbaum Associates, 1976.

Wagner, A. R. Expectancies and the priming of STM. In *Cognitive processes in animal behavior*. S. H. Hulse, H. Fowler & W. K. Honig (Eds.), Hillsdale, New Jersey: Erlbaum Associates, 1978.

Wagner, A. R. Habituation and memory. In *Mechanisms of learning and motivation*, A. Dickinson and R. A. Boakes (Eds.), Hillsdale, New Jersey: Erlbaum Associates, 1979.

Wagner, A. R., Logan, R. A., Haberlandt, K. & Price, T. Stimulus selection in animal discrimination learning. *Journal of Experimental Psychology*, 1968, *76*, 171-180.

Wagner, A. R., Rudy, J. W. & Whitlow, J. W. Rehearsal in animal conditioning. Journal of Experimental Psychology Monograph, 1973, 97, 407-426.

Waugh, N. C. & Norman, D. A. Primary memory. Psychological Review, 1965, 72, 89-104.

Wedeking, P. & Carlton, P. L. Habituation and sensitization in the modulation of reflex amplitude. Physiology and Behavior, 1979, 22, 57-62.

Welker, R. L., Tomie, A., Davitt, G. A. & Thomas, D. R. Contextual stimulus control over operant responding in pigeons. Journal of Comparative and Physiological Psychology, 1974, 86, 549-562.

Whitlow, J. W., Jr. Short-term memory in habituation and dishabituation. Journal of Experimental Psychology: Animal Behavior Processes, 1975, 104, 189-206.

Wilson, C. J. & Groves, P. M. Refractory period and habituation of acoustic startle response in rats. Journal of Comparative and Physiological Psychology, 1973, 83, 492-498.