INFLUENCES ON CONDITIONED TASTE AVERSIONS TESTED AT DIFFERENT RETENTION INTERVALS: DOES LATENT INHIBITION DEVELOP DURING LONG INTER-STIMULUS INTERVALS?

by

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DEDICATION

I dedicate this work to my loving and supportive family.

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ABSTRACT

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Latent inhibition (LI) may develop during the conditioned stimulus (CS)—unconditioned stimulus (US) interval in long delay learning. In addition, LI may represent the creation of a CS-no consequence association that transiently interferes with CS-US retrieval (Kraemer and Roberts, 1984). Experiment 1 determined that the specific CS used had little effect on this retention interval effect. Experiment 2 tested 1, 2, 5, or 10 days after conditioning. Avoidance achieved its maximal level at 5 days post-conditioning. Batsell and Best (1994) argued that this attenuation of conditioned responding 1 day post-conditioning may be sufficiently explained as a retrieval deficit caused by a surprising toxicosis experience. Experiment 3 investigated the relative contributions of LI and a surprising toxicosis experience on responding at 1 and 10 days post-conditioning. This experiment failed to find Batsell and Best's US preexposure effect, therefore Experiment 4 attempted to replicate this effect following a procedure as identical to Batsell and Best's as possible. Experiment 4 also failed to find their effect.

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1. INTRODUCTION

Two stimuli will tend to become associated when their presentations occur in succession. However, the strength of the association between the stimuli varies with the temporal interval (the inter-stimulus interval, or ISI) separating them (Pavlov, 1927)—so crucially that often ISIs of even a second can significantly impede learning (Gormezano & Kehoe, 1981; Pavlov, 1927).

Conditioned taste aversion (CTA) is a type of conditioning in which ISI constraints seem less restrictive. A substantial body of evidence reveals that animals can associate a taste with later illness even when hours separate them (e.g., Garcia, Ervin, & Koelling, 1966; Misanin, Greider, & Hinderliter, 1988; Revusky & Garcia, 1970). Smith and Roll (1967) provided a particularly dramatic example of the ability of rats to associate a taste with illness over an extraordinarily long delay. They observed that an aversion to saccharin could be conditioned by X-irradiation over a 12-h ISI.

The ability of an animal to acquire CTA over long ISIs has made it the topic of much investigation. Early on, an effort was made to reconcile CTA with other types of learning which require much shorter ISIs. One such effort proposed that perhaps the long delay between the CS and US is not functionally long at all. As Rozin and Kalat (1971) noted, the functional ISIs in taste aversion conditioning might be quite short if the toxicosis causes animals to regurgitate and re-taste the solution as illness progresses of if the aftertaste of the flavor simply persists over the ISI. Either possibility could conceivably allow the taste of the CS to occur in close temporal proximity to the US. However, Rozin and Kalat (1971) noted that neither of these ideas withstand closer scrutiny. Rats cannot vomit and thus cannot regurgitate the contents of their stomachs. Moreover, any regurgitation would have mixed

with the rats' stomach juices and thus would be of a different concentration than the original flavor in a fluid. If the rats were using regurgitated tastes as a cue, then one would expect the rats to show avoidance to stronger or weaker flavors (i.e., to the regurgitated concentration), not the concentration originally presented at conditioning. Rats can be conditioned to a specific concentration of saccharin (Gilley & Franchina, 1985; Rozin, 1969) and casein (Rozin, 1969) solutions. In addition, rats can be conditioned to a concentration of HCl lower than the normal gastric HCl concentration (Garcia, Green, & McGowan, 1972). Again, any regurgitated flavors in the experiment should be of a different concentration than the original solution and conditioned avoidance should be stronger to fluids with taste intensities that match the regurgitated fluid more than the one that was originally ingested during the conditioning episode. Rozin (1969) was able to condition a discriminated aversion between a strong and a weak concentration of a flavored fluid when one concentration, but not the other, was followed 30 min later by an injection of apomorphine. It is unlikely that aftertastes would allow a discrimination between two concentrations of the same fluid after so long an interval. Finally, after presenting a solution of HCl to rats, Garcia, McGowan, and Green (1972) applied litmus paper to the rats' tongues two minutes after they had finished drinking and found no measurable amount of HCl remained on the tongues even this soon after stimulus presentation; aftertastes do not seem to endure the hours necessary to explain the long ISI.

Other evidence also indicates that aftertastes are also an unlikely source of information in forming taste aversion after long delays. The temperature of an aftertaste of a fluid consumed earlier should become similar to of the rat's body. Therefore, if rats used aftertastes to associate the taste with illness, then the association would be to a fluid whose temperature approached that of the rat. Thus, evidence that rats can be conditioned to water

of a specific temperature different than the rat's body temperature (Nachman, 1970) also refutes the aftertaste explanation.

Other explanations also sought to reconcile long delay learning in taste conditioning with other forms of conditioning. Revusky (1971) proposed an ingenious explanation for the differences in the length of effective ISIs in different paradigms called the concurrent interference hypothesis. He claimed that events can be held in "associative memory" (a faculty which holds event representations so that they may become associated with each other) for long periods of time. This differs from traditional views, which argue that events are associable for only brief periods after their presentation. According to Revusky, since event representations can occupy the associative memory for a long time, a larger temporal gap may separate them without preventing an association from forming. The reason that even functionally short delays between events impede conditioning is that intervening events interfere with the association of the CS and US. In other words, it is not the time between the two target events per se that lowers their ability to be associated, but the occurrences of other events that fill this time that interfere with conditioning. Revusky called this interference "concurrent interference" which, as the term implies, is different from proactive or retroactive interference in that it comes from events that co-occur with the targeted CS in associative memory. Revusky argued that concurrent interference prevents conditioning by allowing the interfering events to form associations with the two target events (i.e., with the CS and US) and that these other associations prevent the target association (i.e., between the CS and US) from forming.

Revusky argued that differences in the opportunity for concurrent interference to reduce conditioning to a CS account for the differences between CTA and other forms of conditioning in their sensitivities to ISI effects. He noted that not all stimuli are equally associable with all other stimuli (Garcia & Koelling, 1966; Seligman, 1970). Specifically,

illness is associated readily with flavor cues but is not easily associated with exteroceptive (e.g., visual or auditory) stimuli whereas USs applied in standard conditioning procedures (shocks, air puffs, noise, etc.) are more readily associated with exteroceptive stimuli than with tastes. Revusky argued that typical experimental procedures are more effective in minimizing extraneous gustatory stimuli than exteroceptive cues. Thus, tastes can be associated with subsequent illness even when hours separate the taste and illness because there are few other tastes during those hours to cause concurrent interference that would prevent interference the taste-illness association. On the other hand, when conditioning is conducted with exteroceptive CSs and USs, Revusky argued that Ss are more likely to encounter exteroceptive stimuli (e.g., visual, auditory, and tactile stimuli) that can cause concurrent interference. Thus, a short ISI is required to produce conditioning because short ISIs limit the opportunity for interference.

Revusky (1971) presented several lines of evidence in support of his theory. For example, novel flavors placed between a CS and US presentation interfere with CS-US conditioning. Nonetheless, this theory cannot fully account for the long delays possible in CTA. Wilcoxon, Dragoin, and Kral (1970) used a taste aversion paradigm in bobwhite quail to associate a blue drinking tube with illness over a 30-min ISI. The birds undoubtedly experienced many other visual stimuli during the 30-min interim, so an explanation based primarily on interference poorly explains these results. Also, Kalat and Rozin (1971) were able to condition relatively strong aversions to sucrose even when three other novel tastes were presented between the CS and toxicosis. Further, Kalat and Rozin (1971) found an orderly decline in conditionability of the CS when no interfering taste stimuli (either food or fluid) where presented during the ISI. Revusky's concurrent interference (1971) theory has difficulty explaining why CTA shows this decline in conditionability when no interfering stimuli were present.

As an alternative to theories that try to find a common basis for the apparent differences in the effects of ISI manipulations in CTA and other conditions, Kalat and Rozin (1971) argued that taste aversion learning represents a special evolutionary adaptation. The illness produced by toxic foods can occur hours after ingestion. It would therefore be adaptive for animals to develop a special form of learning about food stuffs that allowed them to learn to avoid toxic foods even if hours separate its ingestion and its consequences. Thus, according to this view, taste aversion learning evolved into a separate learning mechanism governed by different rules from other types of learning. To account for the fact that even taste aversion conditioning declines as ISI length increases, they proposed that the CS gradually becomes less likely to be associated with the target US because the S actively learns that the CS is "safe." That is to say that over a long CS-US interval, the reaction to a novel taste CS's internal representation is given the opportunity gradually to change from being reacted to as "'possibly dangerous, associable with poison' to 'probably safe, relatively unassociable with poison'" (Kalat & Rozin, 1971, p. 199). Once the animal has learned that a flavor is "probably safe," that flavor will not be readily associated with a toxic event under conditions in which the temporal relationship between the flavor and toxin normally support learning.

Kalat and Rozin (1973) demonstrated that this attenuating effect can develop readily: just one, 20-minute taste exposure weeks before conditioning is sufficient to attenuate conditioning when the flavor was subsequently paired with illness (see also Best & Gemberling, 1977; Revusky & Bedarf, 1967). In fact, it appears that attenuation develops within hours of exposure to a taste CS. Kalat and Rozin (1973) clearly demonstrated this in an experiment in which rats were preexposed to the CS for 30 min 3.5 h before a second exposure to the taste CS was given that was closely paired with illness. Conditioning in these animals was compared with conditioning developed in a group that did not receive a

taste preexposure before the taste was presented and paired with the illness. They found that the preexposed rats displayed less aversion than a group that received no preexposure and only the CS-US pairing. That the preexposed group showed less aversion, Kalat and Rozin (1973) argued, implies that it actively learned something (viz., that the taste was "safe") about the CS at the preexposure that hampered conditioning when the taste was later paired with illness. In their view, transitory mechanisms are unlikely to last long enough to bridge this gap. They argue that only learning would be expected to endure this interval (Garcia, McGowan, & Green, 1972).

Kalat and Rozin (1973) recognized that the Ss might actually be learning that the taste is "meaningless" and not "safe" per se. While they preferred "learned safety" to "learned meaninglessness," they contended that in either case the important point is that later testing performance is mediated by what the Ss are learning about the CS during the CS-US interim.

Best (1975) preferred the "learned meaninglessness" alternative. He argued that the theoretical concepts behind learned safety more resemble conditioned inhibition (CI) while the procedures employed by Kalat and Rozin (1971) more closely resembled those used to create latent inhibition (LI). CI requires that both the CS and US be presented to the animal, but in a fashion in which the occurrence of the CS is predictive of the absence of the US (e.g., in an expressly unpaired manner). In contrast to procedures producing conditioned inhibition, latent inhibition is produced by exposing the subject to the CS without any presentations to the US. So, unlike a conditioned inhibition procedure, no relationship is arranged between the CS and US (Rescorla, 1971).

One widely held conception of CI is that it is a state that actively opposes conditioned excitatory effects of the US. Rescorla (1971) proposed two tests that jointly allow determination of whether a stimulus has anit-excitatory properties. First (the

retardation test), a suspected inhibitory stimulus must show retarded development of a conditioned excitatory response compared to the stimulus when it is neutral. Second (the summation test), the stimulus must reduce conditioned responding to a known excitatory stimulus when the two are presented together.

The pattern of results from retardation and summation tests with LI stimuli strongly indicates that LI and CI are very different processes. A principle defining character of a latently inhibitory stimulus is that it is slower to condition, an attribute it shares with conditioned inhibitor. However, unlike a conditioned inhibitor, a latently inhibitory stimulus does not subtract from the excitation in a summation test. For example, using a CER procedure, Rescorla (1971) paired a light with shock. He preexposed half of the animals to a tone alone. This tone was then presented simultaneously with a light. He found no difference in responding to the light between the tone-preexposed and tone-non-preexposed groups. This implies that preexposing the tone did not affect the tone's ability to become a CI. This strongly suggests that LI and CI are different and independent processes. Moreover, Reiss and Wagner (1972), in a rabbit nictitating membrane procedure, found that preexposing a stimulus retarded rather than facilitated inhibitory conditioning with that stimulus. One would expect that if a LI procedure actually gave a stimulus conditioned inhibitory properties the opposite should have occurred. Similar results have been obtained by others (e.g., Halgren, 1974; Solomon, Lohr, & Moore, 1974).

Thus, there is ample reason to believe that simple exposure to a CS does not give it inhibitory properties. Best (1975) confirmed this notion in CTA learning, demonstrating that preexposing a taste not only makes it generally less conditionable but also makes it less able to acquire conditioned inhibitory properties. First, he established that a flavor could acquire CI properties when it signals that an expected toxicosis will not occur. To do this, Best conditioned a flavor by pairing it with toxicosis. He then added trials on which the illness

was omitted after the flavor was presented; these no-illness trials were signaled by a second flavored fluid. Preference for the second flavor was then tested against the preference over another (third) flavor that was previously paired with illness or against water. When made a signal for no illness using this procedure, the second flavor was preferred both over the third flavor and over water. The second flavor was not preferred over the third or water if it had not been made a signal for no illness. Best argued that this implies that making the second flavor signal no illness allows it to acquire conditioned inhibitory properties.

Having established conditioned inhibition in a CTA procedure, Best conducted an experiment in which the flavor stimulus that was to signal nonreinforced CS+ trials was preexposed prior to training. He found that preexposure greatly reduced conditioned inhibition. In effect, Best demonstrated that CI does not arise as a consequence of simple exposure to a taste stimulus in CTA. Preexposing a taste makes it generally less conditionable—either as a conditioned inhibitor or as a predictor of illness. He thus concluded that "learned meaninglessness" or "learned irrelevance" may be a more appropriate term than "learned safety."

It has been suggested that LI developing over long ISIs may reduce the ability of a taste CS to acquire associative strength (e.g., De la Casa & Lubow, 1995; Kalat, 1977; Kalat & Rozin, 1973; Lubow, Weiner, & Schnur, 1981). It is therefore important to understand what, if anything, is learned during the LI procedure because similar processes may be at work during the long ISI in CTA.

However, more than forty years after the first documented account of LI, there is still disagreement about its underlying mechanisms. For much of its history, research directed towards finding what LI is has mostly seemed to find what it is not. Lubow and Moore (1959), who coined the term latent inhibition, tested if LI could be explained as the learning

of responses incompatible to the CR during the nonreinforcement phase. They did not find evidence that LI was caused by the acquisition of incompatible responses.

LI also has prima facie similarity to habituation as it involves a reduction in responsiveness to a stimulus after it has been repeatedly presented without subsequent consequences. However, habituation reduces the probability of a specific response whereas LI creates a general decline in the ability of the CS to condition a variety of reactions (Lubow, 1989).

While habituation of a reflexive response may not account for LI, habituation of the orienting response (OR) may. Sokolov (1963) argued that the presence of the OR greatly facilitates conditioning and the absence of the OR hinders the development of a conditioned response. Thus, Sokolov predicted that if a stimulus were preexposed until the OR is habituated, then efforts to condition that stimulus would be affected adversely. However, if the OR was dishabituated after preexposure to the stimulus, Sokolov predicted that LI would disappear. To test this, Sokolov preexposed a tone many times without reinforcement. This tone was then presented in compound with a light. The addition of the light served to dishabituate the OR to the stimulus. Sokolov found that with the reestablishment of the OR he was able to reverse the adverse effects of the stimulus preexposure.

Domjan and Seigel (1971) offered direct reasons to suppose that habituation and LI are independent phenomena by demonstrating that habituation of the OR to a tone is obtained in five presentations, but that it is not until the twenty-fifth tone presentation that conditioning of the tone is adversely affected.

Hall and Schachtman (1987) demonstrated that LI can persist over longer intervals than habituation of an OR, implying that habituation of the OR is not the basis of LI effects. They presented a localized light several times. The rats demonstrated an OR to the light that habituated during these presentations. After sixteen days, they tested these rats by

representing them with the light. The OR reemerged to levels similar to that displayed when the rats were presented with the light for the first time. On the day following this test, the rats began a training phase in which the light predicted access to food. Rats who had been preexposed to the light showed retarded learning compared with rats who had not received light preexposures (i.e., the preexposed rats demonstrated LI). Therefore, LI persisted for the preexposed rats even after habituation to the OR had abated.

Another approach to understanding the process of LI grew out of Rescorla and Wagner's (1972) model of associative learning. Rescorla and Wagner's model was created to address the possible associative mechanisms at play when several stimuli, perhaps with different histories, are presented together, and are reinforced or not reinforced. Despite its sophisticated treatment of various phenomena, Wagner and Rescorla (1972) note that the Rescorla and Wagner (1972) model does not provide a formal method by which nonreinforced CS preexposures can attenuate CS conditioning.

Wagner expanded and modified these concepts of the mechanisms of conditioning beyond those expressed in the Rescorla-Wagner model, and arrived at a model he labeled the sometimes opponent process (SOP) model (e.g., Wagner, 1981). The SOP model postulated a short-term (STM) and a long-term memory (LTM). STM was defined as a rather limited subset of elements or nodes that are currently active (i.e., that are currently attended to by the learner). Elements may become activated into STM either from the environment (i.e., entry via the animal's sensoria) or as a result of retrieval from LTM. LTM was defined as a vast, interconnected, inactive, relatively permanent reservoir of memory elements. According to the model, units in the STM can be in either one of two states, A1 or A2. Presentation of a previously encountered stimulus will tend to cause the representations of the elements of that stimulus to become active in the A1 state in STM. With the passage of time, elements in the A1 state rapidly decay into the A2 state, and elements in the A2

decay more slowly into the inactive state. Activation in the A1 state is short-lasting while activation in the A2 state is relatively long. Elements in the A1 state are capable of priming (and thus retrieving) other, associated elements in LTM via spreading activation. However, such primed elements are retrieved into the A2 state.

Two additional propositions of SOP give it much of its explanatory power. First, the model holds that excitatory associations between two elements will develop to the extent that their representations overlap in the A1 state. Thus any process that prevents a stimulus from having access to the A1 state will block its ability to develop excitatory links with other events. The second proposition offered by SOP concerns the conditions under which an event will not be represented in the A1 state. Specifically, it is proposed that, while an event is active in the A2 state, it cannot be activated into the A1 state. This means that while a CS or an US is being processed in the A2 state, actual occurrences of these events will not result in their representation in A1—which will prevent excitatory connections involving them from developing.

These two propositions figure centrally in the model's account of various phenomena, including LI. Wagner (1981) suggested that on preexposure trials in which the CS is presented "alone," it may form associations with the context (i.e., situational and environmental cues) in which it is presented, as both the CS and the context will be in the A1 state. Both being in the A1 state, they will form an excitatory association such that when the animal is reintroduced to the context, these context cues will prime the memory of the CS, activating it into the A2 state. Therefore, since the context cues have already primed most of the CS elements, the CS will not gain access to the A1 state and thus will not be associable with other elements in the A1 state. In other words, activation of the CS by the context prevents most of its nodes from being activated into the A1 state, and since only

elements in the A1 state form associations, none of these primed elements are predicted to form an association with the US when it is presented in this context.

Critical tests of this theory depend, then, on whether manipulations of the context affect the conditionability of CSs given nonreinforced exposures in it. He theorized that preexposure impedes conditioning to the CS because associations it has formed with contextual cues already prime the CS. Therefore, a manipulation that prevents the contextual cues from being able to prime the CS should eliminate the reduced conditionability of the CS.

Two lines of experimentation have examined this aspect of Wagner's (1981) theory. First, it follows from the theory that if the context is changed after preexposure and then conditioning is implemented in the presence of different context cues, LI should be attenuated as the context cues that could activate the stimulus into the A2 state would not be present. There are in fact numerous demonstrations that changing the contextual cues present during preexposure and conditioning strongly attenuates LI (Channell & Hall, 1981; Dexter & Merrill, 1969; Hall & Minor, 1984; Lantz, 1973; Pfautz & Wagner, 1976; Rosas & Bouton, 1997).

Second, if the context-CS excitatory association is somehow extinguished, then the context will no longer prime the CS representation into A2 and interference with conditioning should be reduced. Wagner, Pfautz, and Donegan (1977, cited in Wagner, 1979) reported results consistent with this prediction. In both an eyelid conditioning and a CER procedure, a CS was first repeatedly presented without reinforcement in the context in which it would later be paired with the US. Between the CS preexposure and conditioning phases, half of the animals in each experiment were presented with context "extinction" trials in which they were exposed to the context without the CS or US. Subjects that were exposed to the context extinction displayed less LI to the CS than rats who did not receive

this context extinction. Therefore, it would appear that the LI-causing associations between the CS and the context could be rendered less effective by context-alone exposure. However, these results have not gone undisputed. In a conditioned suppression procedure, Hall and Minor (1984) failed to find that context-alone exposure between CS preexposure and conditioning attenuated LI.

A different perspective on LI has been offered by Mackintosh (1975) in another broad theory of associative learning. He proposed instead that the associability of a stimulus is determined by how well it predicts it consequences. More specifically, Mackintosh argued that the level of attention devoted to a stimulus is directly related to how well it predicts subsequent events relative to other concurrently presented stimuli. Specifically, he claimed that attention increases toward CSs that predict important outcomes better than alternative cues and wanes to relatively unpredictive ones.

If the CS is presented in the absence of reinforcement (as happens in a LI procedure), then both it and contextual cues are equally predictive of subsequent consequences, in this case nonreinforcement. Mackintosh assumed that under these conditions, where the CS is no better a predictor of consequences than other stimuli, then attention to it will decrease, thereby making it less conditionable when later paired with the US.

Mackintosh's (1975) model predicted that if the CS predicts some event better than other stimuli, then it would lose associability more slowly. Hall and Pearce (1979) addressed this prediction in an experiment in which instead of following a CS with nothing in the first phase, it was followed by a mild foot shock. In the second phase, the CS was followed by a stronger foot shock. Mackintosh's (1975) theory would predict that this treatment would preserve much of the CS's associability and allow it to condition well with the stronger shock in phase two. This was not found; the CS conditioned poorly with the stronger shock.

To account for such data, Hall and Pearce (1980) offered an alternative theory of

associative learning. Generally, they accepted Mackintosh's proposition that changes in CS effectiveness play a strong role in conditioning, but presented a different conception of the nature of these changes. They asserted that any time a CS accurately predicts its consequences it will not be processed, even during conditioning. It is only when—and to the extent that—the CS does not predict its consequences that it will be processed. Thus while Mackintosh argued that a CS will only be processed if it predicts its consequences better than other stimuli, Pearce and Hall's model holds that a CS will only be processed to the extent it does not predict its consequences.

Pearce and Hall (1980) adopted the position that stimuli become associated with each other if both achieve conjoint access to some limited-capacity memory system. They define associability then as a stimulus' ability to compete successfully for access to this system. Stimuli that completely predict their consequences are denied access to this memory system. Stimuli are admitted into the memory system to the extent to which they do not adequately predict their consequences. Thus when a stimulus' predictability does not change over trials, its associability will decrease. However, when the events following a CS change, so that the CS no longer accurately predicts them, the CS's associability will increase.

Concerning LI, Pearce and Hall (1980) predict that with each nonreinforced preexposure, the CS will loose associability because it accurately predicts its outcome: nothing. In other words, they argue that LI effects are a result of learning during nonreinforced CS presentations, that the CS gradually comes to predict no consequence. On the first trial when this CS is paired with the US, it will not form an association with the US as the associability of the CS depends on its predictability on the *previous* trial, in a manner similar to that proposed by Mackintosh (1975). However, the surprising presentation of the US will increase the associability of the CS on the subsequent trial, causing it to slowly lose its association with no consequence and replace it with an association with the US.

Another explanation of LI that also emphasizes attentional processes, the Conditioned Attention Theory (CAT), has been proposed by Lubow and his colleagues (Lubow, 1989; Lubow, Schnur, & Rifkin, 1976; Lubow, Weiner, & Schnur, 1981). Simply stated in regards to CS preexposure, the theory claims that nonreinforced CS exposures serve to reduce attention invested in the CS which later impairs conditioning.

More specifically, CAT begins by assuming that attention is a conditionable response governed by the same laws as other conditionable responses. Like other responses, attention is elicited by the presentation of a stimulus, and its frequency and intensity are conditionable depending on the circumstances in which the stimulus is presented. Following the attentional response (R_a) to a stimulus with reinforcement will serve to maintain the R_a, while following it with no reinforcement will decrease its probability of occurrence. When a stimulus is presented, it will elicit an R_a. If the stimulus is followed by some significant event, this is hypothesized to reinforce the R_a, thus maintaining it. Following the stimulus instead with no event will not reinforce the R_a to that stimulus and the R_a will decline.

According to Lubow (1989), the attentional response to the stimulus is necessary in order for it to condition. The greater the R_a, the better the opportunity for that stimulus to be conditioned. The likelihood of forming an association of the stimulus rises and falls as R_a increases and decreases respectively.

The applicability of CAT to LI is obvious: nonreinforced presentations of a CS condition a decline in attention to that CS, reducing its conditionability. The extent to which the R_a is reduced from nonreinforced exposures is a function of the number and intensity of the exposures. Attention to the CS increases when a US later follows it, but a preexposed CS will condition more poorly than a nonpreexposed CS as the preexposed CS has experienced a decline in its R_a.

Note that the one theme common to all of these theories—associative and attentional—is the expectation that a latently inhibited CS does not readily become associated with the US with which it is paired. In other words, these theorists take the position that the difficulty in developing a CR to a latently inhibited CS is an associative failure; that preexposure—be it through conventional preexposure or simply inordinately long ISIs—impairs development of associative links between the preexposed CS and a subsequently paired US. However, it is possible that acquisition failures do not fully explain the effects of LI procedures. Retrieval failures may contribute to the LI phenomenon. Recently, numerous investigators have found evidence that the effects of CS preexposures are not always permanent. Context switches (Bouton, 1993), post-conditioning extinction of the conditioning context (Grahame, Barnet, Gunther, & Miller, 1994; Wagner, Pfautz, & Donegan 1977 (cited in Wagner, 1979)), and delayed testing (Batsell & Best, 1992; Biederman, Milgram, Heighington, & Stockman, 1974; Kraemer & Ossenkopp, 1985; Kraemer, Randall, & Carbary, 1991; Kraemer & Roberts, 1984; McIntosh & Tarpy, 1977) have provided evidence that LI may depend on retrieval processes.

In light of this data, then, it is not surprising that another approach to LI has grown from the general idea that the expression of conditioned responding depends most strongly on memory retrieval processes. Miller and his associates are leading proponents of this view. They argue (e.g., Miller, Kasprow, & Schachtman, 1986) that animals encode and store virtually all experiences they encounter. However, they contend that whether the knowledge is expressed depends on retrieval processes that are subject to interference.

Following Miller et al. (1986), Kraemer et al. (Kraemer & Roberts, 1984; Kraemer & Ossenkopp, 1985) have provided evidence that, in taste aversion conditioning, LI may induce retrieval failure. They found that Ss showed little evidence of conditioning to a preexposed flavor when tests for the aversion were conducted shortly after conditioning.

However, if the Ss were tested after a long post-conditioning interval (e.g., 10 or 21 days), then the aversion to the flavor was displayed more strongly. Clearly, Ss in these studies formed an association between the flavor and illness that was not fully expressed when only a short amount of time separated conditioning and test. Similar results have been obtained by Biederman, Milgram, Heighington, and Stockman (1974) and McIntosh and Tarpy (1977).

Such data lead Kraemer and Roberts (1984) to argue that LI is not the result of the lessened ability of the CS to form associations, but reflects competition between the two different memories associated with the flavor—one formed during preexposure, the other formed when the flavor was paired with illness. They suggested that during preexposure to the taste, the rats associate it with the event of "no consequence." When the flavor is later paired with illness, they argue that the flavor also becomes associated with that event, resulting in the flavor having associations with two separate and mutually interfering memories, memories of no consequence and of illness. On the assumption that excitatory associations (e.g., taste-illness) are less subject to forgetting than are taste-no consequence associations, they argue that greater interference should be observed between these two memories as a short conditioning-to-test interval than at a long.

However, some of the empirical support for their retrieval failure hypothesis has been questioned by Batsell and Best (1994; see also Batsell & George, 1996). Generally, they find that rats receiving a single pairing of a novel flavor with LiCl displayed weaker aversions one day after conditioning than they do two or ten days later. This strengthening of CTA over time may have little to do with forgetting of no consequences as the procedures followed in their work should minimize the opportunity for LI to develop (a novel flavor and short ISIs are used). They argued that this growth in the expressed strength of the CTA over time may be common to all CTAs, regardless of whether or not preexposure to the CS is

given. Batsell and Best (1994) hypothesize that the change in the strength of the avoidance reflects changes in a performance interference process produced by the effects of the US. They claim that the novel illness event remains in the animal's STM for up to 24 h. During its residency in STM, it interferes with retrieval of other events, such as the conditioning episode.

It should be noted that the effect described by Batsell and Best (1994) may account for some of the findings of an attenuation of conditioned responding at a short retention interval in CTA procedures. The experiments reported by De la Casa and Lubow (1995), Kraemer et al. (Kraemer & Roberts, 1984; Kraemer & Ossenkopp, 1986), and McIntosh and Tarpy (1977) compared performance 1 day after conditioning with performance measured later (e.g., 10 or 21 days post conditioning). Clearly, the poorer avoidance at the 1-day interval relative to the longer intervals could be attributed to processes described by Batsell and Best (1994) instead of processes relating to the expression and loss of LI over time. However, Backner, Strohen, Nordeen, and Riccio (1991) and Marcant, Schmaltz, Roy, and Leconte (1985) both found conditioned taste aversions attenuated at two, but not at seven or more, days post conditioning.

To test their theory, they conditioned an aversion by injecting LiCl into rats 15 min after saccharin solution consumption. They also injected some of the animals with LiCl four days before this CS-US paring. They predicted that this US preexposure four days before the conditioning episode would serve to reduce the novelty of the US at conditioning, reducing any disruptive effects a novel US may have for these preexposed animals at a short retention interval, and thereby allowing these US-preexposed animals to more fully express their conditioned aversion one day after conditioning. Their results supported their hypothesis. US-preexposed Ss showed stronger aversions than nonpreexposed at a one—but not a five—day retention interval. In addition, though, all 5-day Ss showed stronger aversions than all 1-

day Ss. Perhaps one US preexposure was not sufficient to entirely eliminate short-term disruption of the aversion at the 1-day retention interval.

Data from studies by Kraemer et al. (Kraemer & Roberts, 1984; Kraemer & Ossenkopp, 1986) and Batsell and Best (1994) raise the possibility that expression of a CTA produced by a long delay conditioning procedure may strengthen over time. From Kraemer et al.'s perspective, if LI developed during the long ISI, test performance will improve over time as the event-no consequence memory becomes less available for interference. Batsell and Best (1994) also anticipate better performance over time as the harmful effects of the surprisingness of the US diminishes. In contrast, theories that propose that LI develops during the long ISI reduces the ability of the CS to enter into association with toxicosis (and don't instead interfere with retrieval) suggest regardless of when tests are conducted that there should be little difference in performance.

In a preliminary investigation of performance changes in long delay CTA learning over time, we conditioned a taste aversion by injecting 52 adult, male, water-deprived rats with 1.25 ml/kg 0.6 M LiCl three hours after ingestion of a novel 0.1% sodium saccharide solution. Control rats were injected with isotonic saline three hours after saccharin presentation when the experimental rats were injected with LiCl. These control animals were given an unpaired injection of LiCl 24 h prior to the conditioning trial with saccharin. The Ss were tested either 2, 10, 21 or 45 days after conditioning. Testing consisted of 20-minute preference tests in which rats were presented with a choice between plain water and the saccharin solution with which they were conditioned. Testing continued for four consecutive days. Saccharin preference was measured as the amount of saccharin solution drunk versus the total amount of fluid drunk. Figure 1 plots these preferences over the four days of testing. A few inferences can be made about the data from this figure. First, the rats tested two days after conditioning showed no significant aversion compared to the rats in the

unpaired control group. Such a result could entirely reflect poor associative learning resulting from delay between the presentation of the CS and US. However, the data from Ss tested at the 10-day retention interval suggest otherwise. An aversion emerged by the tenth post-conditioning day as rats that were given a paired presentation of saccharin and toxicosis showed a greater aversion than the unpaired rats. The difference between the paired and unpaired groups then appears to weaken at the 21- and 45-day intervals, perhaps due to forgetting of the mild taste aversion.

The main findings of this preliminary experiment lead to the conclusion that at least part of the weakness in avoidance seen at the 2-day retention interval can be interpreted as a performance, not an associative, deficit. Two experiments were subsequently conducted to investigate the parametric factors necessary for this phenomenon.

2. EXPERIMENT 1

The extent to which aversive responding is attenuated at a short versus a long retention interval may be influenced by the particular flavor used in conditioning. Most of the evidence reported by Kraemer and Roberts (1984) and by Kraemer and Ossenkopp (1986) indicating that LI affects performance of CTA was obtained from a procedure in which they preexposed one flavor but then conditioned and tested with a different flavor. The strength of the aversion to saccharin conditioned and tested in this fashion was not affected by the passage of time. Only when the preexposure and the conditioning flavors were both chocolate milk did the aversion recover over time (Kraemer and Roberts, 1984, Experiment 3). Nonetheless, not all researchers have used different solutions for preexposure and conditioning. Backner, Strohen, Nordeen, and Riccio (1991) found that extensive preexposure attenuated aversive responding to sucrose at two and five days post-conditioning. Batsell and Best (1992a, 1992b, and 1994), Biederman, Milgram, Heighington, Stockman, and O'Neil (1974), and Marcant, Schmaltz, Roy, and Leconte (1985) observed that aversions to saccharin solutions were weaker when tested shortly after they were conditioned than when they were tested at a later point in time.

One possible source of the varying successes of these researchers may be the flavors used. Perhaps unknown qualities of the flavors are differentially modulating performance. The results of Kraemer and Roberts (1984) and Kraemer and Ossenkopp (1986) suggest that how these flavors generalize—to the same flavor in different circumstances and to other flavors—may be complex.

Experiment 1 was conducted in order to replicate the results of the preliminary study and to determine whether the phenomenon observed is shaped by the specific taste used as

CS. Independent groups of rats had one of three tastes paired with drug-induced illness over a 3-h ISI and then were tested either two or ten days later. The three tastes used were a chocolate milk, a saccharin, and a sucrose solution. Control animals were given both the flavor and illness, but in an explicitly unpaired fashion. These unpaired Ss were used to control for non-associative factors. Since we expected these non-associative factors to be stronger earlier to the conditioning episode, the control animals were tested at the two-day retention interval.

Methods

Subjects

The subjects were 81 naïve, adult, Sprague-Dawley-derived rats, weighing between 311 and 455 grams. They were born and raised at the University of Texas at Arlington. The subjects were maintained on a 12:12-h light:dark schedule, with light on at 0700 h, and were given Purina Rat Chow ad libitum at all times during the experiment except as described herein.

The subjects were matched into 13 groups based on the mean water consumption during the three days before the first US injection (i.e., before the 7-day retention interval groups, the first groups to receive a US injection, are so injected). Each group contained nine rats. Three groups received a chocolate milk solution as tastant, three received a saccharin solution, and three a sucrose solution. Of the three groups that received a given tastant, two of these received a paired presentation of this taste and LiCl and were tested two or ten days after taste-LiCl conditioning. The third group received the taste and illness, but in an expressly unpaired fashion and was tested two days after conditioning.

Apparatus

The Ss were housed in stainless steel cages 20 x 25 x 20 cm with ambient temperature maintained at about 22° C. Water was presented in polypropylene graduated cylinders with rubber stoppers and straight, stainless steel sipper tubes. The "mock injections" were performed by using the same type of needle and syringe that was used later to inject the subjects, however, the needle remained capped. The flavors used were a 50% (v/v) chocolate milk solution using Nestlé Quick chocolate milk (4% butterfat), a 10% (w/v) sucrose solution, and a 0.1% (w/v) saccharin solution. All fluids were prepared using normal tap water and presented at room temperature.

Procedure

Preconditioning Acclimation and Water Deprivation

All experimental phases were carried out in the rats' home cages. After three day's acclimation to their home cages, subjects were handled for thirty seconds every day for one week. Following this week of handling, the subjects were put on a water deprivation schedule for eight days. During this time, subjects were on 23.5-h water deprivation. Food was removed from the hoppers before the Ss were given a thirty-minute access to room-temperature tap water. Starting on the left on the first day, the position of the bottle alternated from the left to right side of the food hopper on each subsequent day.

After the amount of water consumed was measured and the bottles removed from the cages, each rat was weighed and returned to its home cage. After all the rats were weighed, they received a mock injection that was intended to habituate them to the injection procedure. The blunt tip of a capped needle was gently pressed against the lower abdomen for five seconds while the subject was held vertically. The food was returned to the hoppers after all rats had been mock injected.

Conditioning

The subjects were matched into nine groups based on mean water consumption during the last three days of the eight-day water deprivation phase. Any ties were broken by matching weight as well.

On the day before conditioning, all rats received 30-min access to water and were weighed as usual. Three hours after the bottles were first presented, intraperitoneal (ip) injections were administered. Animals in the unpaired control groups (C-Na, Su-Na, and Sacc-Na) were given an ip injection of 0.6M LiCl (1.25 ml/kg). The animals in the paired groups (C-2, C-10, Su-2, Su-10, Sacc-2, and Sacc-10) were injected with the same amount of isotonic (9% w/v) saline.

On the next day, subjects in the chocolate milk groups (C-2, C-10, and C-Na) received the chocolate milk solution instead of plain water for 30 min. Those in the sucrose groups (Su-2, Su-10, and Su-Na) received the sucrose solution instead of water and those in the saccharin groups (Sacc-2, Sacc-10, and Sacc-Na) were given the saccharin solution. Three hours after the bottles were first presented, the Ss were again injected. This time unpaired control groups (C-Na, Su-Na, and Sacc-Na) were injected with isotonic saline while the other groups (C-2, C-10, Su-2, Su-10, Sacc-2, and Sacc-10) received 1.25 ml/kg of 0.6M LiCl.

On the day after conditioning, the Ss were watered and their intakes recorded, but they were not handled or weighed. From this time onward, the Ss were weighed once a week. Groups C-2, C-Na, Su-2, Su-Na, Sacc-2, and Sacc-Na began testing two days after the conditioning day whereas testing began ten days post-conditioning in groups C-10, Su-10, and Sacc-10. Subjects in the ten-day groups were maintained on the water deprivation schedule throughout the experiment. Aversions to the flavors were assessed with two-bottle tests. One bottle contained the flavor solution to which that animal was conditioned (e.g., a

50% chocolate milk solution for groups C-2 and C-Na), the other contained plain water. The initial position of the flavor solution bottle was counterbalanced across days and subjects. The left bottle (whatever solution it contained) was inserted and the S was allowed briefly to sample from it. The bottle was then swiftly removed and the rat was allowed to sample the right bottle in the same manner. When the rat was roughly equidistant from the entry points of the two bottles, both bottles were inserted simultaneously and their quantities measured. The Ss were then permitted access to the two bottles for 30 min before their final volumes were measured and they were simultaneously removed. Four tests were administered, each separated by 24 h.

Results

An alpha level of .05 was used for all tests in all experiments. A one-way ANOVA on all groups' conditioning day consumptions revealed no significant differences (F (8,19) < 1.0).

Aversions were recorded as saccharin solution preferences calculated as saccharin consumption divided by total consumption (i.e., consmumption of both sacchrin and water) multiplied by 100%.

Figure 2 plots the effect of retention interval on the flavor preferences. Inspection suggests that regardless of the particular CS, avoidance was weaker two days after conditioning than it was ten days later. Thus, under these conditions, the specific properties of the flavors seem to have little influence on the change in performance over time. Separate 3 (group; two-day paired, ten-day paired, and 2-day unpaired) x 4 (test day) repeated measures ANOVAs confirmed this impression. In the case of chocolate milk, the effects of group (F (2, 24) = 16.80, MSE = 884.007, p < .05) and test day (F (3, 72) = 43.74, MSE = 232.184, p < .05) were significant as was the group x test day interaction (F (6, 72) = 43.74, MSE = 232.184, p < .05). REGW, post hoc comparisons verified that the two-day paired

group showed no evidence of an aversion; it did not differ from the unpaired control. The ten-day paired group did show a significantly greater aversion than the unpaired group.

Similarly, the sucrose solution groups also showed significant group (F (2, 24) = 4.30, MSE = 1172.274, $p < .05$), test day (F (3, 72) = 7.42, MSE = 270.50, $p < .05$), and group x test day interaction (F (6, 72) = 3.10, MSE = 270.50, $p < .05$) effects. REGW, post hoc comparisons revealed that for the sucrose groups, like the chocolate milk conditioned rats, there was no reliable aversion expressed by the paired animals at the two-day retention interval but that an aversion emerged10 days post conditioning.

The data for the animals given saccharin solution followed the same pattern as that of the other two flavors. Again, there was no noticeable difference between the flavor preferences expressed by the animals in the two-day paired and the unpaired groups. A 3 (group, Sacc-2, Sacc-10, Sacc-Na) x 4 (test day) repeated measures ANOVA for the saccharin solution groups showed that there was a marginally significant difference between the groups (F (2, 24) = 3.09, MSE = 1497.64, $p = .0641$). The test day effect was significant (F (3, 72) = 3.72, MSE = 625.62, $p < .05$), though the group x test day interaction was not (F (6, 72) < 1.0). The test day effect was most likely due to extinction of the aversions. Planned comparisons used the first test day mean preferences as it can be assumed that the effect of retention interval was least mitigated by extraneous factors on this day. These planned comparisons demonstrated that the groups followed the predicted pattern before extinction obscured them on later test days. On the first test day, the animals tested ten days after conditioning showed stronger avoidance of saccharin than the two-day, unpaired animals (t (9, 72) = 2.160, MSE = 1184.64, $p < .05$). In addition, the rats in the two-day paired and two-day unpaired groups did not show significantly different saccharin preferences (t (9, 72) < 1.0).

Discussion

Chocolate milk, sucrose, and saccharin all produced weak aversive responding at a short retention interval after long-delay taste aversion conditioning. This weak avoidance is due to more than just an acquisition deficit as animals tested at a long retention interval tended to show a relatively strong flavor avoidance.

It is not surprising that the absolute magnitude of the preferences, and thus the differences between them, was contingent on the given flavor used. The inherent preferences for different flavors will vary—as will their conditionability (e.g., Kalat & Rozin, 1970). Qualities of the stimulus may affect other processes that may be relevant to understanding the retention interval effect. For example, the propensity for different flavors to become latently inhibited may vary. It may be, as Kraemer and Roberts (1984) found, that flavors differ in their capacity to create an attenuation of conditioned responding and might more easily develop LI than do other flavors. They would thus better interfere with the expression of an aversion at the short retention interval. Be this as it may, despite that flavors possess unique characteristics that may influence performance, the factors which cause a weakened avoidance at a short but not a long retention interval are still robust enough to obtain for different flavors.

3. EXPERIMENT 2

Previous work in our laboratory has indicated that conditioned responding strengthens between the second and tenth day after conditioning. In Experiment 2, we continued to investigate when this strengthening begins to be expressed, testing our animals at 2, 5, and 10 days post-conditioning. These intervals span the range over which effects emerged in our previous research.

Additionally, Experiment 2 included groups which were tested one day after conditioning. Many of the researchers who report that CTA strengthens over retention intervals compared aversions measured one day after conditioning with aversions measured at later times (e.g., Batsell & Best, 1986; Batsell & Best, 1992b; Batsell & Best, 1994; Kraemer, Larviere, & Spear, 1980; Kraemer, Randall, & Carbary, 1991; Kraemer & Roberts, 1989; McIntosh & Tarpy, 1977). One explanation for this improved performance over time was proposed by Batsell and Best (1986, 1992b, 1994). As noted earlier, Batsell and Best have reported a short-lived, non-associative effect that masks the expression of the conditioned taste aversions' strengths. Their evidence revealed that this source of interference completely dissipated within 48 h after conditioning. The present experiment examined groups tested when the non-associative effect described by Batsell and Best should be strong and groups tested 48 (or more) h after conditioning, when such effects should be negligible, in order to determine what this short-lived process contributes to the effects observed in the present studies.

Methods

Subjects

The subjects were 71 male, naïve, Sprague-Dawley rats, weighing between 290 and 407 grams at the beginning of the experiment. The Ss were housed in conditions and circumstances identical to those in Experiment 1.

The subjects were matched into eight groups based on mean water consumption during the last three days of preconditioning water deprivation. All groups originally contained nine Ss; however, one animal in group Li2 was eliminated from the experiment due to illness and one animal's data from group Na5 were excluded due to a procedural error during conditioning. These animals were not replaced. Two groups, Li1 and Na1, were tested beginning one day after saccharin/lithium pairing, Li2 and Na2 were tested beginning two days after pairing; Li5 and Na5, five days after pairing; groups Li10 and Na10, ten days after pairing.

Apparatus

The Ss were housed in conditions identical to those in Experiment 1. One-bottle tests were used.

Procedure

Preconditioning Acclimation and Water Deprivation

The procedure for this phase was the same as that for Experiment 1.

Conditioning

The conditioning procedure was identical to that of Experiment 1 in all details except that the animals in the Li and Na groups were tested at either a 1-, 2-, 5-, or 10-day test interval and all animals were given saccharin as the CS.

Results

A one-way ANOVA revealed that the conditioning day saccharin consumptions were not significantly different between any of the groups (F (7,69) < 1.0). The types one through four sums of squares were not different for any of the ANOVAs conducted on the data from Experiment 2. Thus the unequal sample sizes in groups Li2 and Na5 did not bias these analyses (Hayes, 1994; SAS/STAT, 1994).

The effects of the manipulation of retention interval are illustrated in figure 3. Consistent with the results of previous work in our lab, conditioned avoidance was weak at the shorter retention intervals and strengthened as the retention intervals lengthened. A 2 (treatment; Li vs. Na) x 4 (retention interval; 1, 2, 5, and 10) x 4 (test day) repeated measures ANOVA indicated that there were significant treatment ($F(1, 62) = 32.71$, $MSE = 1260.55$, $p < .05$) and test day ($F(3, 186) = 6.82$, $MSE = 611.81$, $p < .05$) effects. REGW, post hoc comparisons were performed on the four-day means. These comparisons indicated that groups Li1 and Li2 failed to display conditioned aversions as neither groups' preference for saccharin differed from their unpaired controls. Moreover, the Li1 and Li2 mean saccharin preference ratios did not differ from each other (t (15) < 1.0) which supports the conclusion that the CTA did not strengthen over the 2-day retention interval as would be expected if interference dissappears within 48 h as Batsell and Best (1994) contended. The post hoc comparisons also confirmed that the animals in both of the paired groups tested at five and ten days after conditioning showed significantly stronger aversions than the rats in their respective unpaired control groups.

Discussion

Animals tested at the 1- and 2-day retention intervals showed little evidence of an aversion while those tested at the 5- and 10-day retention intervals did. These results

replicate and expand the results of our previous work. Also, the aversions expressed on the first two days after conditioning were weaker than those expressed at five and ten days post-conditioning.

Batsell and Best (1986, 1992b, 1994) have provided ample evidence that a short-lived process temporarily interferes with the expression of taste aversions. However, the results of this experiment do not directly speak to this possibility. Experiment 3 was conducted to address this issue more directly. In this study, US preexposure was used to eliminate the interference effect described by Batsell and Best. Long ISI conditioning was then scheduled to be conducted. If interference CTA strength is found to increase across retention intervals when the Batsell and Best interference effect is eliminated, we would have to conclude that performance was strongly affected by another process.

4. EXPERIMENT 3

Experiments 1 and 2 demonstrated that the measured strength of a CTA conditioned over a long delay is underestimated when animals are tested shortly after conditioning. When tests are conducted 5-10 days after conditioning, stronger conditioned avoidance is seen than when tests are conducted 1 or 2 days after conditioning. Experiment 3 was undertaken to examine possible reasons why aversive reactions tend to strengthen over the conditioning-test intervals.

Two possibilities suggest themselves. First, it is possible that LI develops during the ISI and interferes with the display of conditioned taste aversions at short retention intervals; LI may then dissipate with time, allowing a fuller expression of the aversion at a longer interval. Kraemer and Roberts (1984; Kraemer, Larviere, & Spear, 1988a; Kraemer, Larviere, & Spear, 1988b; Kraemer, Hoffman, & Spear, 1988; Kraemer & Ossenkopp, 1986; Kraemer, Randall, & Carbary, 1991) contend that poor conditioning of a latently inhibited CS at least partly reflects the transient effect of CS preexposure on performance.

A second possibility is suggested by the work of Batsell and Best (1994). They propose that a novel or surprising illness disrupts conditioned responding for about 24 h after presentation. Specifically, they argued that after a paired presentation of a novel taste and novel illness, animals continue to process the novel illness experience for a period of time. This processing is believed to interfere with the retrieval of the association between taste and illness via priming-like effects (e.g., Wagner, 1978).

However, the process proposed by Batsell and Best (1994) may not be a relevant factor in the experiments reported here, or in all cases in which conditioned performance increases over time. One reason for this doubt is the fact that Batsell and Best found that the

interference they described does not persist for more than 30 h, yet poor performance was observed in the present experiments, as well as in other investigations of changes in performance in CTA (Backner, Strohen, Nordeen, & Riccio, 1991; De La Casa & Lubow, 1995), beyond the first day post-conditioning. Another reason that militates against explaining the present data as an outcome of the Batsell and Best phenomenon is that Batsell and Best show that the effect is highly sensitive to the manner in which a CTA is measured; they do not find interference at 1 day when 2-bottle tests are used (Batsell & Best, 1993)—only during 1-bottle tests are sufficiently sensitive for their effects. The fact that the change in avoidance over time was observed under two-bottle test conditions in the present experiments (as it was by Kraemer & Ossenkopp, 1986; Marcant, Schmaltz, & Leconte, 1985) does not fit the known characteristics of the Batsell and Best effect.

As Batsell and Best's (1994) effects do not seem to affect performance measured two or more days after conditioning, and as two-bottle tests are not optimal for observing their effect even one day after conditioning, it may be that some other, longer-lived mechanism is responsible for the improvement in performance over time. The variation in the effects of LI over time, as raised by Kraemer and his associates (e.g., Kraemer & Roberts, 1984) is one possible alternative. Nevertheless, it must be acknowledged that the evidence contrary to Batsell and Best's hypothesis is not entirely persuasive as it is unknown whether differences in drug dose, flavor, test conditions, or other methodological factors may affect the durability of their phenomenon and allow it to affect two-bottle tests two days post-conditioning.

Experiment 3 was undertaken to begin assessing more directly the contribution of the phenomenon described by Batsell and Best (1994) to the change over time in the strength of CTAs. Batsell and Best maintain that it is the novelty or surprisingness of the US that initiates the process that interferes with retrieval of flavor-illness associations for about 24 h.

One implication of this idea is that short-term interference effects should be reduced if animals are familiarized with the US prior to conditioning. If the US were not surprising, it would be less likely to be actively processed over time and thus should be less likely to interfere with the expression of the CTA. Evidence supporting this reason was provided in a series of experiments by Batsell and Best (1994) who found that prior exposure to the illness eliminated the performance deficit typically observed one day after conditioning.

These findings imply that if the retention interval effects observed in our studies of long delay learning reflect the same processes described by Batsell and Best, then US preexposure should eliminate the short-term deficit, improving performance of such animals to the level observed in animals tested after a long delay.

Experiment 3 was initially conceived of being the first of two experiments which together constituted an investigation into the contribution of Batsell and Best's (1994) US novelty effect on CTA conditioned at both a short and a long ISI. Experiment 3 was intended merely to replicate the US preexposure effect in a procedure similar to that used by Batsell and Best (1994). The subsequent experiment would have utilized the same procedure as Experiment 3, except that a 3 h ISI would have separated the taste and illness at conditioning.

In Experiment 3, animals were preexposed to illness twice before the CS was immediately followed by the US, or received saline injections at these times. Unlike Batsell and Best (1994), the US was preexposed twice instead of once because a study conducted earlier in our laboratory failed to find any effect of one preexposure to LiCl on later performance. As it is possible that one exposure did not induce sufficient familiarity with LiCl, two exposures were given in the present study in an effort to enhance this effect. Giving more than two US preexposures was considered, but rejected, because of concerns about introducing a conventional US preexposure effect (Braveman, 1975; Randich &

LoLordo, 1979) into an already complex situation.

These US preexposures occurred two and four days before the conditioning day. The Ss were tested at either 1, 2, or 7 days post-conditioning for their level of taste aversion. To minimize confounding effects of amount of water deprivation, all animals began water deprivation at the same time and were tested at the same time. This time line is outlined in table 2. As one-bottle tests may be better suited to detect differences in degrees of aversion (Batsell & Best, 1993), we used them instead of two-bottle tests.

Methods

Subjects

The subjects were 56 male, naïve, Sprague-Dawley rats, weighing between 305 and 436 grams at the beginning of the experiment. The subjects were matched into 7 groups based on their mean water consumption during the three days before the first US injection. The procedure for the groups in this experiment is outlined in tables 1 and 2.

Apparatus

The Ss were housed in conditions identical to those in Experiment 1. One-bottle tests were used.

Procedure

Preconditioning Acclimation and Water Deprivation

The procedure for this phase was the same as that for Experiment 1 except that the length of time before the first US injection was varied between the groups. There were a total of 13 days of water deprivation prior to the conditioning trial. The rats were weighed and mock-injected on each of these water deprivation days as described in Experiment 1. The US preexposures and CS-US pairings occurred during this water deprivation period.

US Preexposure

On the fifth day of the experiment (i.e., on the fifth day of water deprivation), the animals the illness preexposure group (P-7) were injected with 0.11 M LiCl, whereas the Ss in the group that were not to receive an illness preexposure (NP-7) were injected with isotonic saline.

On the seventh day of the experiment, the animals in groups P-2 and NP-2 (i.e,. the animals to be tested two days after conditioning) were injected with either 1.25 ml/kg of 0.11 M LiCl, or saline, respectively. The animals in groups P1 and NP1 received LiCl or saline on the eighth experimental day.

Two days after the first injection each group of Ss received a second injection identical to the first.

Conditioning

Two days after the second preexposure injection, Ss received a 0.1% (w/v) sodium saccharide/tap water solution for 0.5 h instead of their regular water ration. Immediately following the saccharin presentation, the Ss were injected with 1.25 ml/kg of 0.11 M LiCl. The rats in group NP-UP were injected with an equal amount of saline on their respective conditioning day.

Testing

All animals were tested the day after they were conditioned. The rats were given a one-bottle test containing a 0.1% w/v saccharin/water solution for 0.5 h. Testing proceeded for three days.

The rats were maintained on the water deprivation diet throughout the experiment. However, after their respective conditioning day, they were no longer handled, mock injected or removed from their home cages.

Results

Figure 4 displays the volumes of saccharin-flavored water consumed by the Ss in Experiment 3. Inspection of this figure does not to indicate any substantial differences among the groups' consumptions. A 2 (US preexposure) x 3 (retention interval) x 4 (test day) repeated measures ANOVA indicated that the only significant effect was the main effect for test day ($F(1, 46) = 21.84$, $MSE = 20.33$, $p < .05$). None of the other main effects or interactions approached significance (all F's < 1.0). Planned comparisons also indicated that there were no significant differences between each of the experimental groups (i.e., 1-P, 1-NP, 2-P, 2-NP, 7-P, and 7-NP) and NP-UP (all t's (14) < 1.0).

Discussion

Experiment 3 failed to find a significant effect of US preexposure or retention interval. Since there was no effect of retention interval in the nonpreexposed groups (NP1, NP2, and NP7), we cannot conclude that we succeeded in obtaining an attenuation of the CTA at a short retention interval.

The lack of evidence of an effect of US preexposure or retention interval under these conditions is not readily explainable. Coupled with the earlier failures in our laboratory to replicate Batsell and Best's (1994) US preexposure effect and the surprising absence of a retention interval effect, we thought it is possible that some subtle difference between Batsell and Best's procedure and those used by us have contributed to the differences in our results.

If Experiment 3 had succeeded in replicating the findings that US preexposure reduces the performance deficit observed 1 or 2 days post conditioning, the next experiment would have been conducted identically to Experiment 3 except that the CS and US were to be separated by a 3-h ISI on the conditioning day. This would have allowed us to investigate

the effects of US preexposure on aversions developed with a long ISI and interpret the two most likely outcomes. More critically, if it were found that US familiarity had little of no effect on aversions conditioned over long ISIs, yet eliminated the effects obtained with short ISIs, we would be able to argue that the performance deficits produced under these conditioning procedures were mediated by different processes.

However, the results of Experiment 3 did not replicate those obtained by Batsell and Best (1994). Therefore, instead of conducting an experiment like Experiment 3, but with taste and illness paired over a 3 h ISI, another attempt was made to replicate Batsell and Best's findings using a procedure that followed theirs as closely as possible.

5. EXPERIMENT 4

As Experiment 3 did not follow Batsell and Best's (1994) procedure precisely, it is possible that the US preexposure effect they reported is unexpectedly sensitive to some detail particular to their design. Therefore, Experiment 4 sought to replicate their findings when we replicating their procedures exactly. The principle differences between their study and Experiment 3 were (1) flavor concentration, (2) duration of exposure to the flavor at conditioning and at test, (3) amount of CS consumption on the conditioning day, (4) length of water deprivation before initiation of experimental manipulations, (5) dose of LiCl, (6) number of US preexposures, (7) number of days between US preexposure and conditioning, and (8) whether the rats were mock-injected to minimize the impact of injection cues. The method followed in Experiment 4 was altered to eliminate these differences.

Methods

Subjects

The subjects were 40 male, naïve, Sprague-Dawley rats, weighing between 288 and 437 grams at the beginning of the experiment. They were assigned to each of the groups based on their mean water consumption during the two weeks of water deprivation prior to any experimental manipulations. Each group was comprised of ten animals.

Apparatus

The Ss were housed in conditions identical to those in Experiment 1, which resembled those described by Batsell and Best (1994). The bottles, syringes, and needles were identical to those used in Experiment 1. The concentration of the sodium saccharide/tap water solution used as the CS in this experiment was increased to 0.15%

(w/v). The US dose was changed to 12 mg/kg (1.887 ml/kg) of 0.15 M LiCl. This dose of LiCl was 2.831 x 10^{-4} mol LiCl per kg rat; the dose used in Experiment 3 was 1.375 x 10^{-4} mol/kg. One-bottle tests were used.

Procedure

After three days of acclimation to their home cage, the rats were put on a water deprivation regimen that was extended to last for three weeks prior to the conditioning day. The rats were also maintained on the water deprivation schedule throughout the experiment. The length of time during which water was provided was reduced to 20 min each day. Rats were not mock-injected. The Ss did not receive replacement fluids at any time during the experiment.

The rats in groups 5-P and 1-P were given one US preexposure (not two as in Experiment 3), four days (not two) before they were given CS-US pairing. The rats in group 5-P were injected with 1.887 ml/kg LiCl 15 min after their daily water ration on the 17th day of the water deprivation.

Four days later (i.e., five days before all groups began testing), rats in groups 5-P and 5-NP were presented with 8 ml of the saccharin solution for 10 min. Fifteen min later, these rats were injected with the LiCl solution. On this same day, the rats in group 1-P were also injected with the LiCl solution, fifteen minutes after their daily watering.

Four days later (i.e., one day before testing began), the Ss in groups 1-P and 1-NP were conditioned using Batsell and Best's (1994) procedure. The rats were given 8 ml of the saccharin solution for 10 min (instead of ad lib saccharin for 30 min) followed 15 min later (instead of immediately) with an injection of the LiCl solution. To equate for levels of dehydration, the rats in the other groups (i.e., in groups 5-P and 5-NP) were given only 8 ml of water on this day for 10 min.

On the day following conditioning of the 1-day groups, the levels of aversion in all rats were tested by presenting them with the saccharin solution. The length of this presentation was reduced from 30 to 20 min.

Results

All Ss drank all of the 8 ml of saccharin solution on the conditioning day. Figure 5, which presents the consumptions during the first test day, suggests that the rats in group 5-NP drank less saccharin solution than the rats in the other three groups. A 2 (US preexposure) x 2 (retention interval) ANOVA and REGW post hoc comparisons confirmed this observation. The ANOVA revealed a significant main effect for retention interval ($F(1, 39) = 8.71$, $MSE = 7.610$, $p < .05$). The main effect for preexposure was not significant ($F(1, 39) = 3.06$, $MSE = 7.610$, n.s.). The retention interval by preexposure interaction approached significance ($F(1, 39) = 3.69$, $MSE = 7.610$, $p = .0628$). The post hoc analyses indicated that indeed the rats in group 5-NP drank less at test than the other three groups which, in turn, did not differ. Planned comparisons revealed that, of the experimental groups (i.e., 1-P, 1-NP, 5-P, and 5-NP), only 5-NP consumed significantly less saccharin on the first test day than NP-UP, the nonpreexposed, unpaired control (for 1-P, 1-NP, 5-P, and 5-NP all t's $(18) < 1.0$; for 5-NP $t(18) = -2.244$, $MSE = 12.16$, $p < .05$).

Discussion

Batsell and Best (1994) report that performance one day after conditioning is worse than performance measured five days after conditioning. This finding was replicated in the present study. However, the US preexposure effects they reported were not obtained.

While the US preexposure manipulation did not produce results corresponding to those reported by Batsell and Best (1994), the apparent interference with the CTA expressed in group 5-P produced by the US preexposure is not unusual. The effect of a preexposure of

an illness US is typically to attenuate taste aversion conditioning (Berman & Cannon, 1974; Braveman, 1975; Brookshire & Brackbill, 1971; Domjan & Best, 1977; Elkins, 1974), presumably by interfering with US processing or perception (Braveman, 1975; Randich & LoLordo, 1979).

However, the US preexposure had no effect on the 1-day groups. The most likely explanation is that a ceiling effect reflecting weak avoidance as short intervals obscured the effect of US exposure.

The rats in group 1-NP showed less aversion than did the rats in group 5-NP. That is to say, there was an attenuation of the CTA at the shorter retention interval. Why the aversion strengthened over time in this experiment are not clear. Not withstanding the failure to replicate their US preexposure results, Batsell and Best's (1994) hypothesized process remains a possibility. Latent inhibition remains another possible explanation.

It is possible that LI could form even during the brief exposure to the CS prior to illness in this study, although the little research that we know of that might support this possibility is not directly comparable. Best and Gemberling (1977) found that one presentation of casein hydrolysate solution 15 min before casein-LiCl pairing was sufficient to mitigate conditioned, aversive responding. In an odor-illness study, Rudy and Cheatle (1977) found that a 10 min preexposure to lemon odor 20 min before conditioning weakened the aversion. Thus it is possible that variation in LI may have contributed to the changes in performance over time that were observed in this experiment.

6. GENERAL DISCUSSION

Previous research in our laboratory indicated that rats can express an aversion to a flavored solution conditioned over a 3 h ISI with illness when tested 10 days post-conditioning. The expression of this aversion was relatively weak, however, when testing occurred only two days after conditioning. Since control animals administered the flavor and toxicosis in a unpaired fashion failed to display an aversion to the flavor at any of the tested retention intervals, we conclude that this aversion was due to associative mechanisms.

In Experiment 1, rats showed a similar—though not identical—pattern of responding (i.e., a weaker aversion two days, compared to ten days, after conditioning) when the flavor used was chocolate milk, sucrose, or saccharin. Therefore, we conclude that the weaker 2-day retention interval aversion relative to later retention days is a robust effect that is not entirely a result of some unique properties of the tastants.

Experiment 2 investigated more precisely when the aversion emerges as the dominant response. The results indicated that it was not until the fifth day after conditioning that rats who recieved saccharin followed 3 h later by illness showed reliably stronger aversions than unpaired control rats tested at the same retention interval. Rats tested at one or two days after conditioning showed similarly weak aversions while those tested at five and ten days after conditioning showed reliably strong aversions.

There are at least two explanations for what causes the reduced aversive responding at the shorter retention intervals. Batsell and Best (1994) argue that a novel toxicosis event, such as typically happens during a CTA procedure, disrupts retrieval of the conditioned aversion for up to 24 h. Thus, they argue, when the Ss are tested for aversive responding on the day after conditioning, they evince a weaker aversion than they do at later test

intervals. An alternative theory, following from Kraemer and his associates (e.g., Kraemer & Roberts, 1984), states that during the long taste-illness ISI the Ss is afforded the opportunity to learn that the taste is innocuous. This memory competes at retrieval with the taste-illness memory when the Ss are tested shortly after conditioning, and the net results of this is weaker aversive responding. This taste-no consequence association competes less successfully at later test intervals, allowing a stronger aversion to be expressed. Experiment 3 was conducted to address this issue.

Experients 3 manipulated the novelty of the US via preexposures. Experiment 3 was originally designed to establish the presence of Batsell and Best's (1994) US novelty effect using the same CS and US employed in our long-delay experiment. Upon establishment of this effect, a subsequent experiment was going to investigate the ability of a US novelty effect to account for variation in long-delay conditioned responding over short and long retention intervals.

However, Experiment 3 failed to replicate Batsell and Best's (1994) results. A possible reason for this failure was that Experiemnt 3 did not strictly follow the procedure outlined by Batsell and Best (1994). Therefore, Experiment 4 duplicated Batsell and Best's procedure as closely as possible. This experiment failed to replicate their US preexposure findings. US preexposure did not restore responding at a short retention interval. In fact, the only detectable effect of the treatment was to impair responding when it otherwise would have been strong.

Batsell and Best (1994) agued that their effect is driven by the degree of US novelty. We know of no other way to directly manipulate US novelty except by manipulating US preexposures. Therefore, since we could not manipulate their effect, we were unable to measure its impact on the expression of conditioned aversions in long delay conditioning

directly. It is possible that the effect they describe is influencing the outcomes of our experiments. We simply do not know of any way of confirming this.

Attention instead will focus on the contribution of LI to the poorer performance found at short retention intervals. The argument that LI develops during long delay conditioning and gradually loses its deleterious effect on performance over time requires two assumptions. It presumes, first, that LI does occur during the conditioning trial and, second, that LI's effects dissipate over a 5 to 10 day retention interval.

Other researchers have demonstrated LI can develop very quickly, even after one preexposure to a flavor or odor (for a review see Lubow, 1989). For example, Rudy and Cheatle (1978) demonstrated that a 10-min exposure to lemon odor 45 min before odor-illness pairing sufficed to reduce aversive responding. Best and Gemberling (1977) reported that preexposure to casein 15 min before casein-illness pairing reduced the measured aversion, and that increasing the time between preexposure and conditioning up to 3.5 h resulted in increasingly weaker aversions. Such evidence makes this assumption that LI may develope during long delay conditioning quite plausible.

To assess the notion that LI develops during the CS-US ISI more directly, we can take advantage of the finding that LI is more sensitive to certain context shifts than is CTA (Archer, Mohammed, & Järbe, 1986; Archer, Järbe, Mohammed, & Predite, 1985; Mitchell, Winter, & Moffitt, 1980). These investigators found that the effects of CS preexposure on conditioning were attenuated when preexposure and conditioning were conducted in different contexts. Expression of CTA was unaffected by context shifts that attenuated LI. Thus, if we condition and test in different contexts, we would expect long-delay conditioned taste aversion to remain relatively strong, while LI should suffer. Therefore, if the poorer short retention interval performance is at least partially due to LI, a change in context between conditioning and test should improve performance at this interval. A changed

context during tests at longer retention intervals should have much less of an effect on performance.

The second assumption, that LI developed after one exposure to a taste dissipates as the retention interval lengthens, can also be examined by giving rats a single unreinforced exposure to saccharin 1 or 10 days prior to a single conditioning trial. If LI produced by a limited preexposure weakens over a 10-day period, as we have proposed, we would expect poorer performance when the preexposure to conditioning interval is short, relative to a longer preexposure to conditioning interval. Such a finding would increase the plausibility of the argument that LI can develop and mask performance in long delay learning, and a failure to observe this effect would reduce it.

An interesting issue concerns whether the effects we observed in long delay CTA learning occur in trace conditioning procedures in other paradigms. Kraemer, Randall, and Carbary (1991) found the CS preexposure attenuated conditioned responding on tests conducted at a one day after CER conditioning, relative to tests conducted 7 to 10 days after conditioning. Thus, they found a release from LI in another conditioning paradigm. It would be interesting to discover if true conditioned CERs also strengthen across retention intervals with longer ISIs. Or if other procedures, for example appetitive conditioning, followed a similar pattern of performance attenuation at shorter retention intervals.

Whatever the mechanism by which conditioned responding is attenuated at short retention intervals, these results demonstrate the aversive responding to the CS was typically attenuated at short, but not longer, retention intervals implying that the S did learn the CTA but was unable to demonstrate this aversion shortly after conditioning. Had we tested at only a short retention interval, we would have seriously underestimated our Ss' abilities to form associations. At least in CTA, these results suggest that an animal's ability to associate

events across relatively large temporal intervals may be most clearly revealed by tests conducted 5 to 10 days after conditioning.

ILLUSTRATIONS

Figure 1.: Pilot Study Saccharin Preference Ratios as a Function of Retention Interval

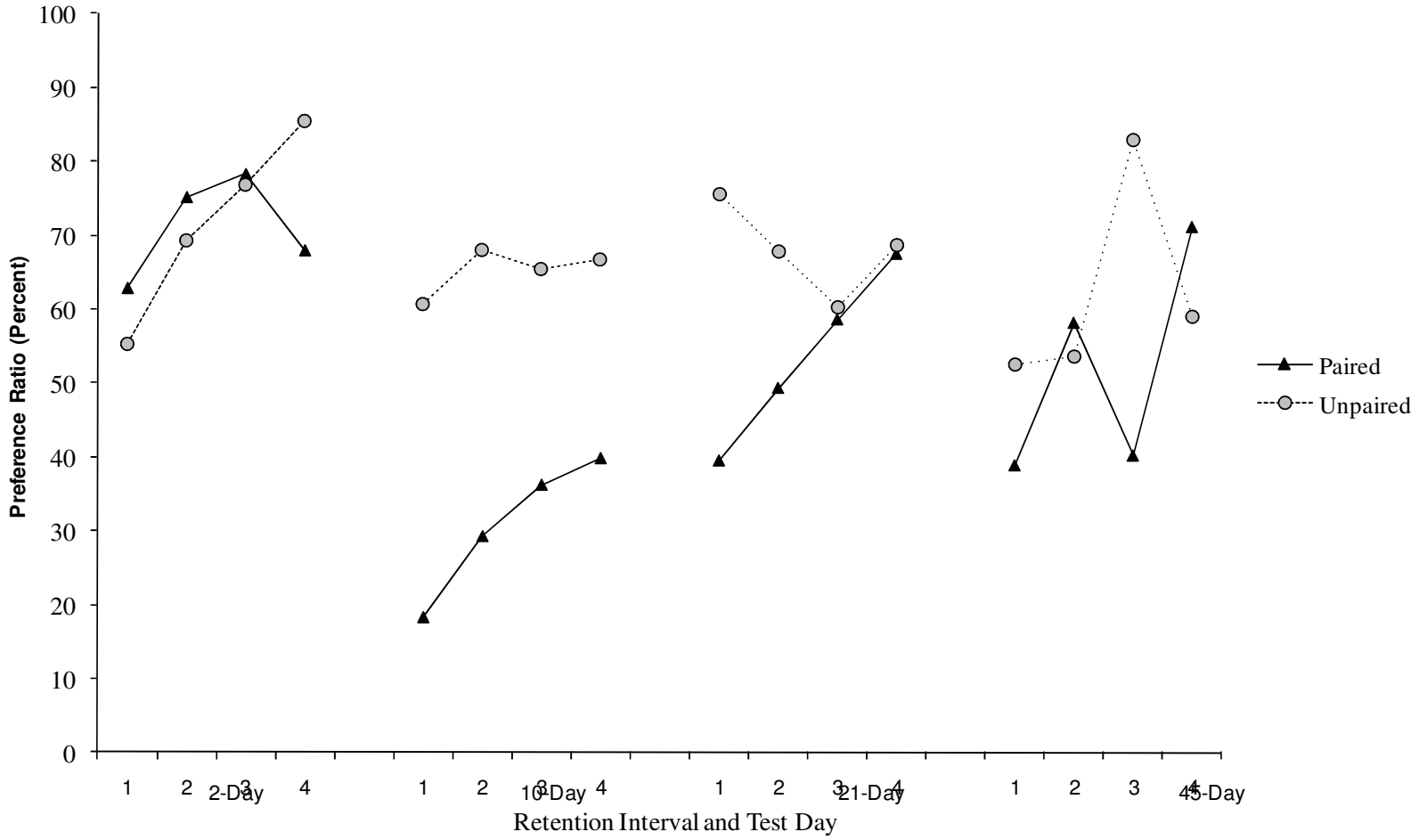


Figure 2.: Experiment 1 Fluid Preference Ratios as a Function of Test Day

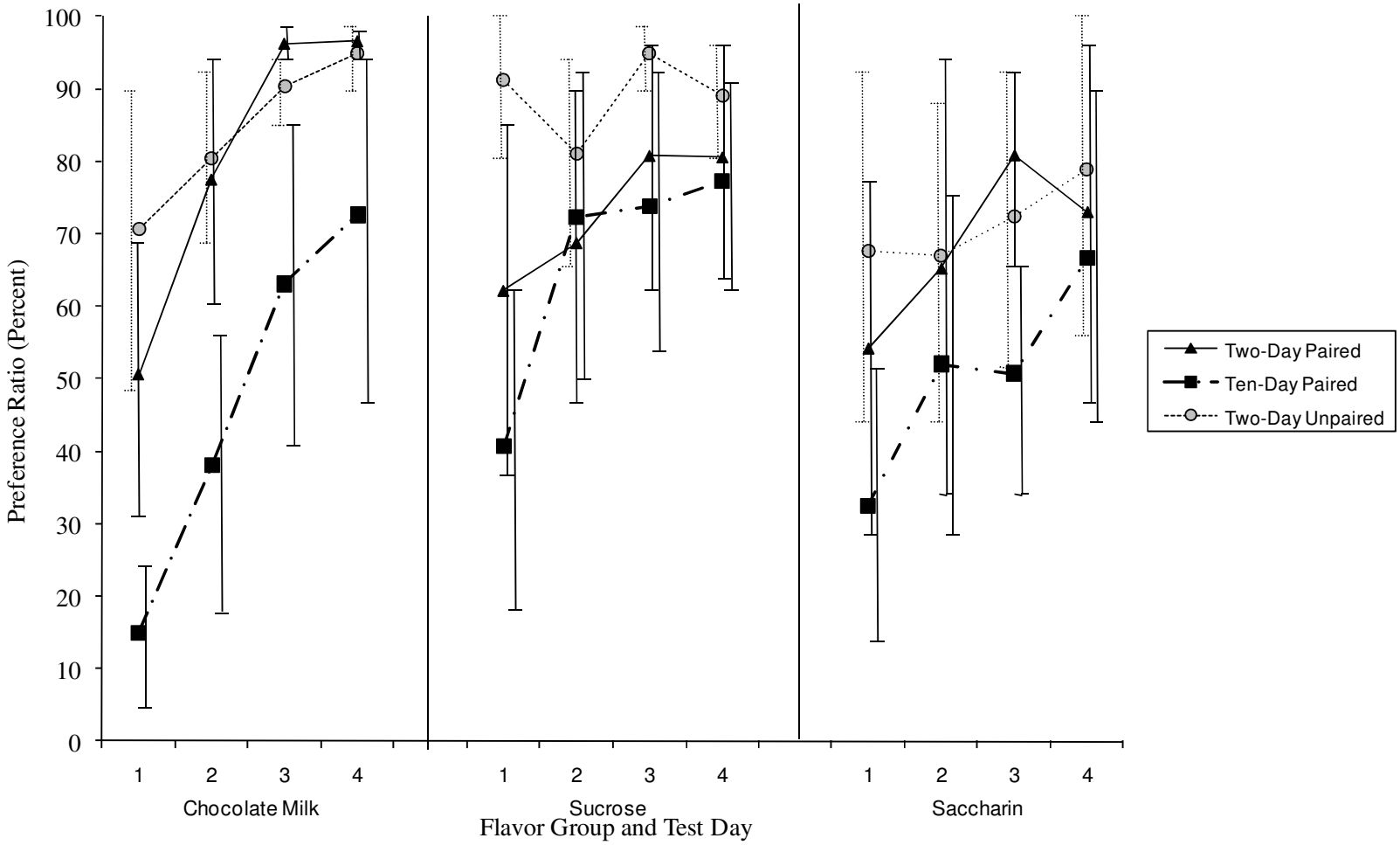


Figure 3.: Experiment 2 Saccharin Preference as a Functin of Retention Interval and Test Day

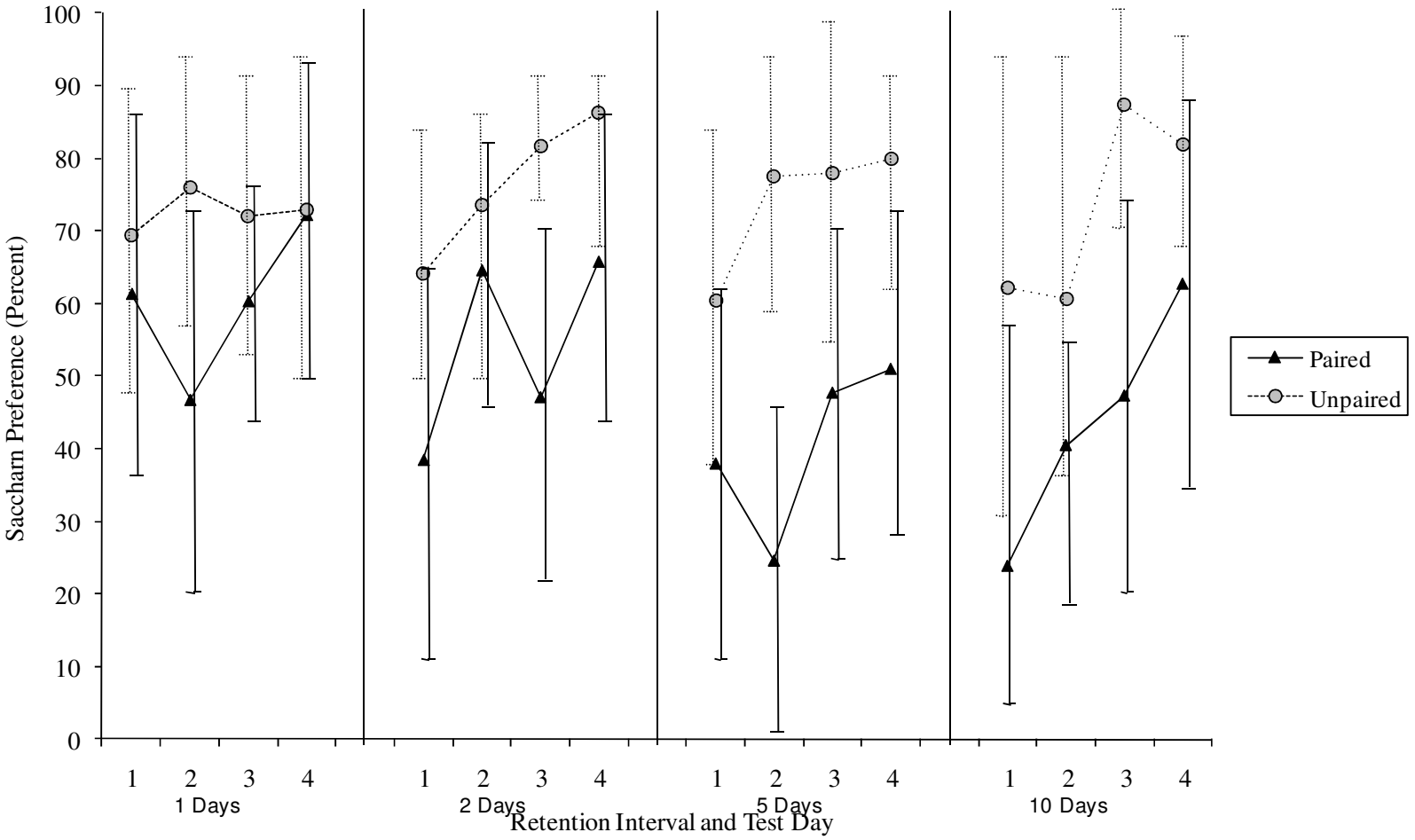


Figure 4.: Experiment 3 Saccharin Consumptions

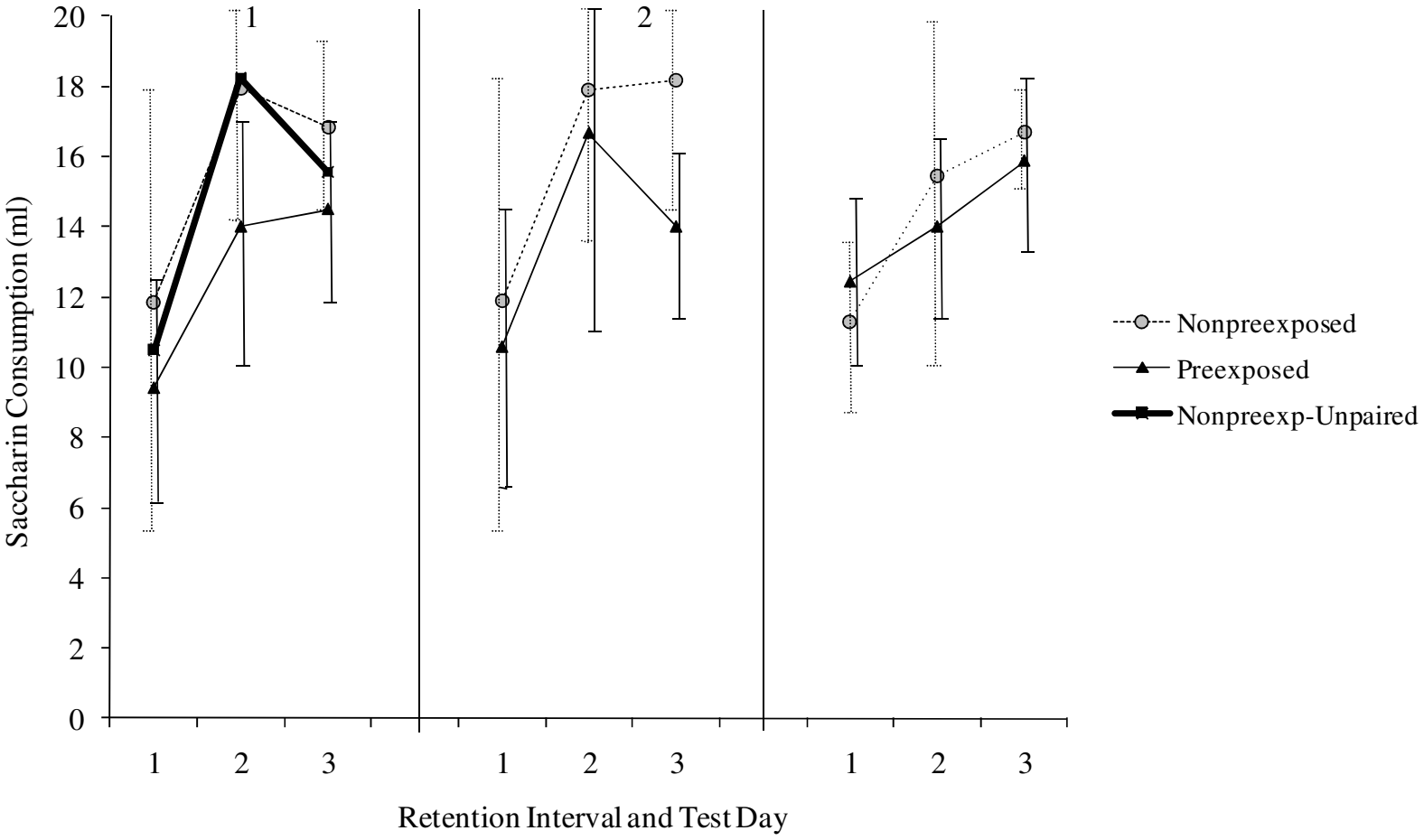


Figure 5: Experiment 4 Saccharin Consumptions

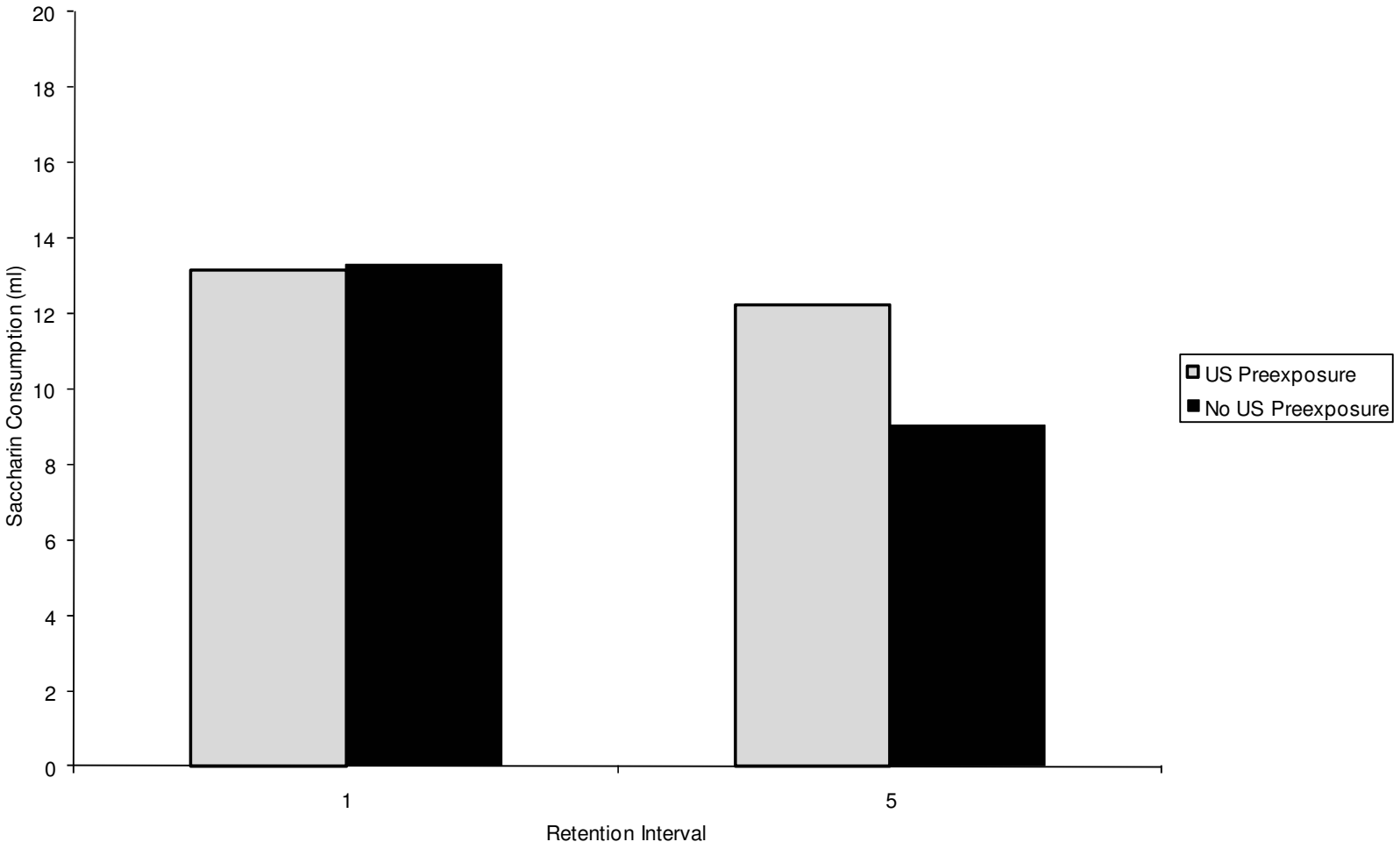
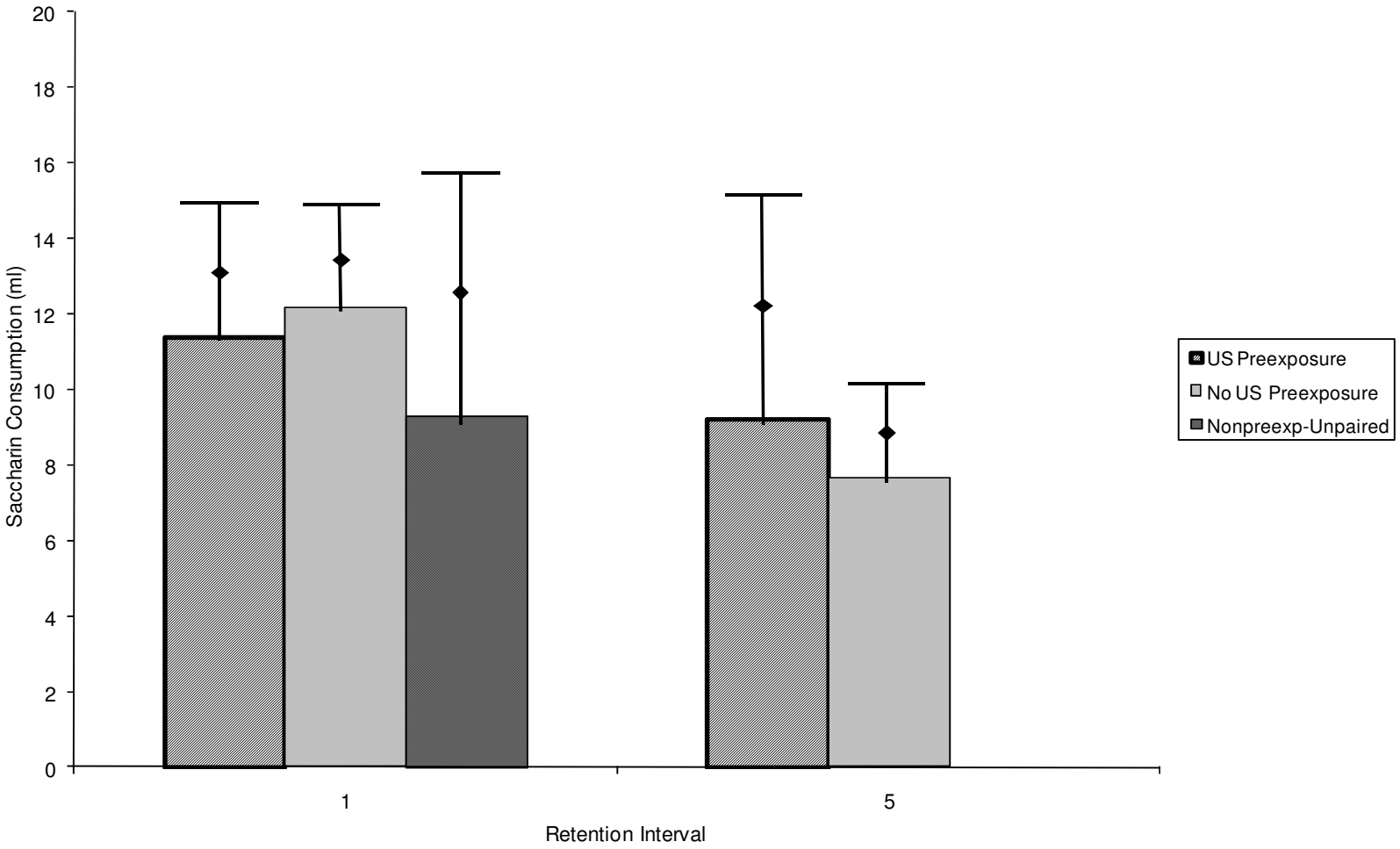


Figure 6: Experiment 5Saccharin Consumptions



TABLES

Table 1.: Outline of Experiment 3

Experiment 3A							
Group Name	Day 1 - First Preexposure	Day 3 - Second Preexposure	Day 5 - Conditioning Day	Day 5 - ISI	Day 6	Day 7	Day 15
P-I-1	LiCl	LiCl	CS-US	Immediate	Test		
P-I-2	LiCl	LiCl	CS-US	Immediate		Test	
P-I-5	LiCl	LiCl	CS-US	Immediate			Test
NP-I-1	Saline	Saline	CS-US	Immediate	Test		
NP-I-2	Saline	Saline	CS-US	Immediate		Test	
NP-I-5	Saline	Saline	CS-US	Immediate			Test

Experiment 3B							
Group Name	Day 1 - First Preexposure	Day 3 - Second Preexposure	Day 5 - Conditioning Day	Day 5 ISI	Day 6	Day 7	Day 15
P-3h-1	LiCl	LiCl	CS-US	3 hours	Test		
P-3h-2	LiCl	LiCl	CS-US	3 hours		Test	
P-3h-5	LiCl	LiCl	CS-US	3 hours			Test
NP-3h-1	Saline	Saline	CS-US	3 hours	Test		
NP-3h-2	Saline	Saline	CS-US	3 hours		Test	
NP-3h-5	Saline	Saline	CS-US	3 hours			Test

NP-UP	Saline	Saline	CS-Saline	Immediate	Test

Table 2.: Time Line for Experiment 3

	Activities											
Group	Day 1	Day 5	Day 7	Day 8	Day 9	Day 10	Day 11	Day 12	Day 13	Day 14	Day 15	Day 16
P-I-1	Start Water Deprivation				LiCl Injection		LiCl Injection		CS-US Pairing	One-bottle Test	One-bottle Test	One-bottle Test
P-I-2				LiCl Injection		LiCl Injection		CS-US Pairing		One-bottle Test	One-bottle Test	One-bottle Test
P-I-5		LiCl Injection	LiCl Injection		CS-US Pairing					One-bottle Test	One-bottle Test	One-bottle Test
NP-I-1					Saline Injection		Saline Injection		CS-US Pairing	One-bottle Test	One-bottle Test	One-bottle Test
NP-I-2				Saline Injection		Saline Injection		CS-US Pairing		One-bottle Test	One-bottle Test	One-bottle Test
NP-I-5		Saline Injection	Saline Injection		CS-US Pairing					One-bottle Test	One-bottle Test	One-bottle Test
P-3h-1					LiCl Injection		LiCl Injection		CS-US Pairing	One-bottle Test	One-bottle Test	One-bottle Test
P-3h-2				LiCl Injection		LiCl Injection		CS-US Pairing		One-bottle Test	One-bottle Test	One-bottle Test
P-3h-5		LiCl Injection	LiCl Injection		CS-US Pairing					One-bottle Test	One-bottle Test	One-bottle Test
NP-3h-1					Saline Injection		Saline Injection		CS-US Pairing	One-bottle Test	One-bottle Test	One-bottle Test
NP-3h-2				Saline Injection		Saline Injection		CS-US Pairing		One-bottle Test	One-bottle Test	One-bottle Test
NP-3h-5		Saline Injection	Saline Injection		CS-US Pairing					One-bottle Test	One-bottle Test	One-bottle Test
NP-UP									CS-Saline Pairing	One-bottle Test	One-bottle Test	One-bottle Test

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