

Timing of omitted events: An analysis of temporal control of inhibitory behavior

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Abstract

This paper reviews research designed to investigate the temporal control of inhibitory responding using rats as subjects. One area of investigation has focused on the role of temporal variables in conditioned inhibition produced using Pavlov's [Pavlov, I.P., 1927. *Conditioned Reflexes*. Oxford University Press, London, 430 pp.] procedure. These studies have found that evidence of conditioned inhibition obtained by negative summation testing is strongest when the conditioned inhibitor signals the omission of the unconditioned stimulus (US) at the same temporal location as a transfer excitator signals presentation of the US [e.g., Barnet, R.C., Miller, R.R., 1996. Temporal encoding as a determinant of inhibitory control. *Learn. Motiv.* 27, 73–91]. Similarly, retardation of acquisition of behavioral control by a previously inhibitory conditioned stimulus (CS) is maximal when the inhibitory CS is paired with the US at the same temporal location as the inhibitor had previously signaled US omission [Burger, D., Denniston, J.C., Miller, R.R., 2001. Temporal coding in condition inhibition: retardation tests. *Anim. Learn. Behav.* 29, 281–290]. Other lines of research designed to assess the associative structure of temporal control of inhibition [e.g., Denniston, J.C., Blaisdell, A.P., Miller, R.R., 2004. Temporal control in conditioned inhibition: analysis of associative structure of inhibition. *J. Exp. Psychol. Anim. Behav. Process.* 30, 190–202] are reviewed, as is the assessment of temporal control of inhibition produced through extinction [Denniston, J.C., Miller, R.R., 2003. The role of temporal variables in inhibition produced through extinction. *Learn. Behav.* 31, 35–48]. These collective observations are discussed in terms of the temporal coding hypothesis [Matzel, L.D., Held, F.P., Miller, R.R., 1988. Reexamination of simultaneous and backward conditioning: Implications for contiguity theory. *Learn. Motiv.* 19, 317–344].

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1. Introduction

The analysis of temporal variables in conditioned behavior has been widely studied since the pioneering work of Pavlov (1927). Pavlov's studies of inhibition of delay revealed that following conditioned stimulus (CS)–unconditioned stimulus (US) pairings with a CS of long duration, conditioned responding was maximal during the latter parts of the CS. Pavlov's early work both highlighted the importance of timing in conditioned behavior and provided the foundation for a thorough analysis of how animals both perceive and use temporal information. For the last 40 years, the study of animal timing has been inspired and led by Russell Church. A few of the many great contributions of Church's work include the development of the peak procedure

(Roberts and Church, 1978) and theorizing concerning internal clocks (Church, 1984) that model how animals learn about expected times of reinforcement and subsequently use this information in order to control conditioned responding. In contrast to this large literature, the present article summarizes the findings from a far smaller collection of research that has attempted to study analogous questions in inhibitory learning; specifically how animals temporally encode omitted events.

Despite the now vast literature on timing of excitatory behavior, relatively little emphasis has been placed on the temporal control of behavior indicative of conditioned inhibition. This deficit is likely due in large part to the difficulties in assessing expectations of event omission. Timing of excitatory behavior can be relatively easily assessed through measures such as the peak procedure, in which an animal is reinforced on a fixed-interval (FI) schedule of reinforcement and anticipatory responding is measured on probe trials in which the US is omitted (thereby producing a rise and fall in conditioned responding

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around the time at which reinforcement is expected; e.g., Roberts and Church, 1978). But assessment of inhibitory behavior is not as straightforward due to the lack of an overt response evoked by a conditioned inhibitor presented by itself (i.e., floor effects in conditioned responding). In a typical conditioned inhibition training situation using Pavlov's procedure, a training excitator is paired with the US, except when it is compounded with the intended inhibitor (e.g., $A \rightarrow US/XA - noUS$). The difficulty in assessing inhibitory behavior is differentiating between true inhibition (i.e., an expectation of non-reinforcement) and inattention. To overcome this difficulty, researchers (e.g., Barnet and Miller, 1996) have relied upon Rescorla's (1969) two-test strategy for assessing timing of inhibitory behavioral control. According to Rescorla, conditioned inhibition should be assessed through both a negative summation test and a retardation test. In a negative summation test, a putative inhibitor is tested in compound with an independently established excitator (called a transfer excitator). The putative inhibitor is said to pass the summation test for inhibition if the inhibitor attenuates conditioned responding to the transfer excitator, relative to the level of responding elicited by the transfer excitator alone or in compound with a neutral stimulus. Importantly, instead of conditioned inhibition, such a decrease in responding could be due to distraction from the transfer excitator by the inhibitor (i.e., enhanced attention to the inhibitor). To control for this possibility, Rescorla recommended the use of a retardation test, in which the putative inhibitor is paired with the US, in order to assess the rate of acquisition of stimulus control of behavior relative to that of a neutral stimulus. If the rate of acquisition of conditioned responding to the previously inhibitory CS is slow relative to that of the neutral stimulus, then the stimulus is said to pass the retardation test for inhibition. However, this test is similarly open to an alternative explanation, namely decreased attention to the putative inhibitor as a consequence of repeated non-reinforcement during inhibitory training. Notably, these alternative explanations (increased attention and decreased attention, respectively) are incompatible. Hence, passage of both tests provides a fairly compelling demonstration of inhibitory learning (but see Cole et al., 1997; Papini and Bitterman, 1993; Savastano et al., 1999 for further critiques of the two-test strategy).

In addition to providing a means for assessing the existence of inhibitory learning, Rescorla's (1969) two-test strategy has also led to the study of the temporal properties and associative structure of inhibitory learning (e.g., Barnet and Miller, 1996; Denniston et al., 2004). This line of research has been guided by the temporal coding hypothesis (Matzel et al., 1988; Miller and Barnet, 1993; Savastano and Miller, 1998) which states that: (1) learning is based upon spatio-temporal contiguity; (2) animals encode the temporal relationship between events (as a temporal map; Honig, 1981); (3) animals can integrate temporal maps from different phases of training when the maps contain a common stimulus element to anchor the integration; and (4) these simple and integrated temporal maps are used to determine the form and timing of the conditioned responding. Based on the temporal coding hypothesis, Barnet and Miller hypothesized that on a summation test behavior indicative of inhibition would be strongest when the conditioned inhibitor signals the omission of

the US at the same moment in time as the transfer excitator signals the occurrence of the US. These expectancies of US presentation and US omission are established during inhibition training and transfer excitator training, and can be further manipulated at or before the time of testing.

2. Temporal control of conditioned inhibition

The first set of experiments described in the present review systematically varied five temporal relationships in order to investigate the nature of temporal coding in conditioned inhibition (see Tables 1 and 2). During the procedure that Pavlov (1927) developed for conditioned inhibition training (i.e., $A \rightarrow US/XA - noUS$), the training excitator (A) is paired with the US except when compounded with the conditioned inhibitor (X). (There are other procedures for training conditioned inhibition, but most of them lack the potential for temporal learning that Pavlov's procedure has.) Toward investigating the representation of time in Pavlovian conditioned inhibition, both the temporal relationships between the training excitator (A) and the US (Variable 1 in Table 1) and between the inhibitor and the training excitator (X–A; Variable 2) may be manipulated. That is, during training the A–US association may be conditioned using either delay, simultaneous, or trace conditioning in order to vary the temporal expectation of the US provided by CS A. Similarly, during inhibitory training trials, presentations of X and A may be provided either simultaneously or serially in order to vary the expectation of US omission. Table 2 summarizes the systematic manipulation of these variables across a series of experiments performed by Miller and coworkers. Each experiment to be summarized in the following review manipulated two of the five variables while holding constant the remaining three variables. The purpose of manipulating these variables was to investigate how altering the temporal relationship between these pairs of stimuli influences the expression of behavior indicative of conditioned inhibition.

Table 1
Temporal variables in Pavlovian conditioned inhibition

Training	
Inhibition training	Transfer CS training
$A \rightarrow US^1/XA^2 - noUS$	$C \rightarrow US^3$
Testing	
Negative summation test	Retardation test
XC^4 relative to C alone or ZC	$X \rightarrow US^5$ relative to $Z \rightarrow US^5$

Notes. CS A represents the training excitator; CS X represents the conditioned inhibitor; CS C represents the transfer excitator; CS Z represents a previously neutral stimulus. Each of the potential temporal variables may be manipulated in order to assess temporal specificity of inhibitory behavioral control. Potential variables—(1) Variable 1: training excitator–US temporal interval; (2) Variable 2: inhibitor–training excitator temporal interval; (3) Variable 3: transfer excitator–US temporal interval; (4) Variable 4: inhibitor–transfer excitator temporal interval at summation test; (5) Variable 5: inhibitor–US temporal interval during retardation test pairings.

Table 2
Manipulation of temporal variables

Series	Manipulated Variables	Manipulated Temporal Relationship
1	1 and 2	A-->+ vs. B+ XA- vs. Y-->A- and YB- vs. Y-->B-
2	1 and 3	A-->+ vs. B----->+ C-->+ vs. D----->+
	2 and 3	XA- vs. Y-->A- C-->+ vs. D----->+
3a	2 and 4	XA- vs. Y-->A- XC vs. X-->C and YC vs. Y-->C
	1 and 4	A-->+ vs. B----->+ XC vs. X-->C and YC vs. Y-->C
3b	3 and 4	C-->+ vs. D----->+ XC vs. X-->C and XD vs. X-->D
4a	1 and 5	A-->+ vs. B----->+ X-->+ vs. X----->+ and Y-->+ vs. Y----->+
4b	2 and 5	XA- vs. Y-->A- X-->+ vs. X----->+ and Y-->+ vs. Y----->+
5a	1 and 3	A-->+ shifted to A----->+ C-->+ vs. D----->+
5b	1 and 3	A-->+ shifted to A+ C-->+ vs. D----->+

Notes. CSs A and B represent training excitors; CSs X and Y represent conditioned inhibitors; CSs C and D represent training excitors; '+' denotes presentation of the US; '-' represents omission of the US; '--->' denotes serial presentations with no gap between stimuli; '----->' denotes serial presentations with a 5-s gap between stimuli; omission of an arrow (e.g., A+) denotes simultaneous pairings. Potential variables—(1) Variable 1: training excitor–US temporal interval; (2) Variable 2: inhibitor–training excitor temporal interval; (3) Variable 3: transfer excitor–US temporal interval; (4) Variable 4: inhibitor–transfer excitor temporal interval at summation test; (5) Variable 5: inhibitor–US temporal interval during retardation test pairings.

For example, [Barnet and Miller \(1996\)](#) provided thirsty rats with conditioned inhibition training consisting of pairings of a 5-s audiovisual stimulus with a shock US (i.e., A → US pairings) using a delay conditioning procedure, in which termination of the CS coincided with onset of the US (see top panel of [Fig. 1](#)). On inhibitory training trials, CS A was presented coterminously (simultaneously) with CS X (i.e., XA–noUS). Based upon the temporal coding hypothesis, [Barnet and Miller](#) expected that CS A would become a signal for US presentation 5 s following CS onset and that, as a consequence of inhibitory training trials, CS X would become a signal for US omission 5 s following onset of CS X. This latter expectation was based upon the temporal coding hypothesis' assertion that animals encode the temporal relationships between events and that animals can integrate these temporal maps. In other words, the expectation of US omission activated by CS X is based upon both the temporal relationship between X and A on inhibitory training trials and upon

the temporal relationship between A and the US on reinforced trials. This reasoning follows from Principle 3 of the temporal coding hypothesis. As depicted in [Fig. 1](#), CS X (depicted in striped bars) should generate an expectation of the simultaneous presentation of CS A (depicted in stippled bars), which was otherwise immediately followed by the US (depicted in solid bars). Hence, integration of these two temporal maps (X–A and A–US) should now generate an expectation of US omission (depicted by open bars) following termination of CS X (i.e., 5 s following onset of X). Notably, the expectation of US omission (or of CS A presentation) could be based upon either the time following onset or termination of the CS ([Desmond and Moore, 1988](#)). For present purposes, we will describe this expectation as being based upon timing from the onset of a stimulus because the testing procedure used by [Barnet and Miller](#) to investigate timing of inhibition does not permit differentiation of these potential timing cues.

Toward assessing the representation of omitted events, **Barnet and Miller (1996)** established a second conditioned inhibitor (CS Y) with a different temporal expectancy for US omission. CS Y was established as a serial inhibitor through non-reinforced presentations of Y and A, in which presentation of CS Y was followed immediately by CS A (both CSs were 5 s in duration). By manipulating Variable 2 (in this case the Y–A temporal relationship), CS Y should become a signal for US omission 10 s following its onset because CS Y was followed by CS A (shown in parentheses in Fig. 1), which was otherwise followed by the US (see top panel of Fig. 1). For the purpose of negative summation testing, Barnet and Miller trained a 5-s transfer excitor, C, using a delay conditioning procedure in which CS C was immediately followed by the US. At test, the inhibitory potential of CS X was assessed through a negative summation test in which CS C was presented either alone or in simultaneous compound with CS X. Testing was conducted using a flooding measure in which stimuli were presented for 10 min while animals were drinking, and the time required to complete 5 cumulative seconds of drinking in the presence of the test stimuli served as the dependent measure. With this procedure, strong excitatory stimulus control (indicative of conditioned fear) is evidenced by longer times to resume drinking (denoted in Fig. 1 by ‘CR’), whereas behavior indicative of inhibition is evidenced by shorter times to resume drinking (denoted by ‘CI’). Barnet and Miller observed strong conditioned suppression when subjects were presented with CS C alone, and attenuated conditioned suppression when subjects were presented with the XC compound (see Fig. 1, top panel). This attenuation of fear is indicative of conditioned inhibition. As shown in Fig. 1, CS C was anticipated to generate an expectation of US presentation 5 s following CS onset, and CS X was anticipated to generate an expectation of US omission 5 s following onset of CS X (based upon the X–A and A–US temporal relationships described above). Another group of subjects was tested with a YC simultaneous compound in order to assess

the temporal specificity of inhibitory behavioral control. These subjects showed a strong conditioned response at test, indicating that CS Y failed the negative summation test for inhibition when tested with CS C. This failure was presumably a consequence of a mismatch of temporal expectancies, in that CS Y was anticipated to generate an expectancy of US omission 10 s following its onset because it was trained as a serial inhibitor, whereas CS C was anticipated to generate an expectancy of US presentation 5 s following its onset. Thus, simultaneous expectancies of US presentation (as signaled by the transfer excitor) and US omission (as signaled by the conditioned inhibitor) appear to be necessary for generating maximal inhibitory behavioral control.

In a further test of temporal control of inhibition, **Barnet and Miller (1996)** additionally manipulated the training excitor–US temporal relationship (Variable 1 from Table 1). During inhibition training, CS B was conditioned through simultaneous pairings of B and the US (see the bottom panel of Fig. 1) and all other training procedures were analogous to those described above (i.e., X and B were presented simultaneously and Y was presented serially immediately before B). As a consequence of this training, CS B was expected to generate an expectation of US presentation at onset of CS B due to the simultaneous training procedure. This manipulation of Variable 1 should have provided different expectations of US omission based upon CSs X and Y trained with CS B. That is, CS X should have now predicted omission of the US at its onset due to the simultaneous non-reinforced presentations of X and B, whereas CS Y should have predicted US omission 5 s following its onset due to the serial presentations of CSs Y and B in which CS Y was presented 5 s before CS B. Transfer excitor C was trained with a delay procedure such that presentation of the US was expected 5 s after C’s onset. At test, attenuated conditioned suppression was observed when CS Y was compounded with CS C, but not when CS X was compounded with CS C. This opposite pattern of responding, relative to that described above when X and Y were trained with CS A, was presumably the consequence of the manipulation of the training excitor–US temporal relationship in conjunction with CS C signaling US presentation 5 s following its onset and only CS Y now signaling US omission at the same temporal location. These findings confirm that maximal inhibition tends to be observed when the inhibitor and the transfer excitor signal US omission and presentation, respectively, at the same temporal location.

In another series of experiments, **Denniston et al. (1998b)** manipulated Variables 1 and 3 (top panel of Fig. 2) and Variables 2 and 3 (bottom panel of Fig. 2) in order to investigate the role of the transfer excitor–US temporal relationship on timing of inhibitory behavioral control. In their Experiment 1, Denniston et al. provided rats with training similar to that provided by **Barnet and Miller (1996)** in order to establish two conditioned inhibitors with different temporal expectancies for US omission. Inhibitor X was trained as a simultaneous inhibitor for delay training excitor (A) in order to establish X as a signal for US omission 5 s following its onset. Inhibitor Y was similarly trained as a simultaneous inhibitor, but in this instance was presented with trace training excitor B, which was otherwise paired with the US 5 s following termination of CS B (again,

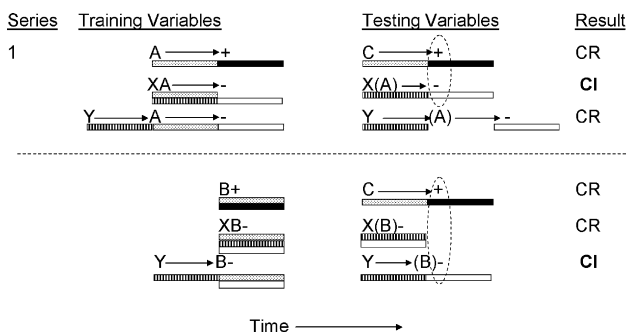


Fig. 1. Inhibitory training provided by **Barnet and Miller (1996)**. CSs A, B, C, X, and Y, were 5-s audiovisual stimuli; ‘+’ denotes a footshock; ‘-’ denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. At test, animals received presentations of C, XC, or YC. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitor and the omission of the US by the conditioned inhibitor. CR’s denote the observation at test of strong conditioned behavior and CI’s denote behavior indicative of conditioned inhibition.

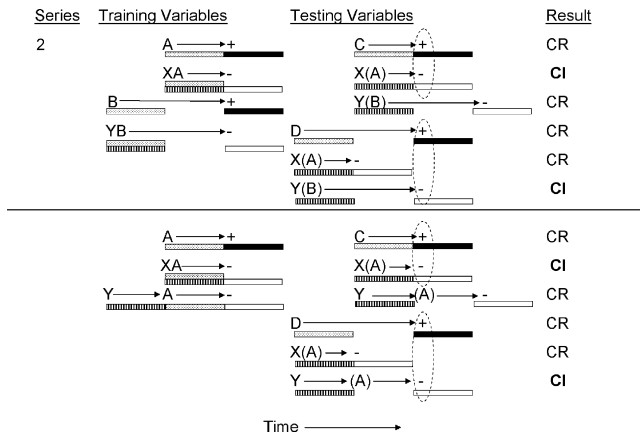


Fig. 2. Inhibitory training provided by Denniston et al. (1998b). CSs A, B, C, D, X, and Y, were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. At test, animals received presentations of C, XC, YC, D, XD, or YD. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitor and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition.

all stimuli were 5 s in duration). As a consequence of this training, CS Y was anticipated to signal US omission 10 s following its onset (due to manipulation of Variable 1). To assess these temporal expectancies of US omission, two transfer excitors were established for the purpose of negative summation testing. CS C was trained as a delay CS which was expected to signal US presentation 5 s following its onset, and CS D was trained as a trace transfer excitor, which was expected to signal US omission 10 s following its onset (a manipulation of Variable 3). At test, maximal conditioned inhibition was observed when inhibitor X was compounded with transfer excitor C, but not D, and when inhibitor Y was compounded with transfer excitor D, but not C. Denniston et al. explained this pattern of responding as being the result of inhibitor X signaling US omission 5 s following its onset which corresponds to the temporal expectancy for US presentation provided by transfer excitor C and inhibitor Y signaling US omission 10 s following its onset which corresponds to the temporal expectancy for US presentation provided by transfer excitor D. When the inhibitor and transfer excitor produced incongruent temporal expectancies for US omission and presentation, respectively, less inhibition was observed.

In their Experiment 2 (see Fig. 2, bottom panel), Denniston et al. (1998b) manipulated both the inhibitor–training excitor (Variable 2) and the transfer excitor–US (Variable 3) temporal relationships while holding constant the training excitor–US (Variable 1) temporal relationship. In this experiment, two conditioned inhibitors were separately established with a single delay training excitor (CS A, which was paired with the US 5 s following its onset). Inhibitor X was trained as a simultaneous inhibitor through coterminous non-reinforced presentations of X and A, whereas inhibitor Y was trained as a serial inhibitor through successive non-reinforced presentations of Y and A (see

Fig. 2, bottom panel). At test, the inhibitory potentials of X and Y were assessed through negative summation tests with two different transfer excitors, C and D, which were previously paired with the US 5 s following onset of C, and 10 s following onset of D (again, all stimuli were 5 s in duration, so C was a delay excitor and D was a trace excitor with a 5 s gap between termination of D and onset of the US). Negative summation testing revealed greater inhibition when inhibitor X was compounded with transfer excitor C than with transfer excitor D, and when inhibitor Y was compounded with transfer excitor D than with transfer excitor C. As depicted in Fig. 2 (bottom panel), inhibitor X was predicted to signal US omission 5 s following its onset, which corresponds to the expectancy of US presentation provided by transfer excitor C, but not D. In contrast, inhibitor Y was predicted to signal US omission 10 s following its onset because it was trained in a serial conditioning procedure. This corresponds to the expectancy of US presentation provided by transfer excitor D, but not C. The results of these experiments conceptually replicated and extended those of Barnet and Miller (1996) by demonstrating that timing of inhibitory behavioral control is sensitive not only to the training excitor–US and inhibitor–training excitor temporal relationships, but also to the expectation for US presentation provided by the transfer excitor at test.

The final series of experiments designed to assess temporal control in inhibition using summation tests for conditioned inhibition explored the role of the inhibitor–transfer excitor temporal relationship at test (Variable 4; Denniston et al., 1998a). In their Experiment 1, Denniston et al., established two conditioned inhibitors with different temporal expectancies for US omission (see Fig. 3a, top panel). In the absence of reinforcement, inhibitor X was presented simultaneously with delay excitor A in order to generate an expectation of omission of the US 5 s following onset of inhibitor X. Inhibitor Y was separately presented with CS A, using serial non-reinforced pairings with no gap between termination of Y and onset of A in order to generate an expectation of omission of the US 10 s following onset of inhibitor Y. Manipulation of the inhibitor–training excitor temporal interval (Variable 2) was intended to assess not only temporal control of inhibition, but also transfer of serial versus simultaneous inhibitors. That is, Holland (1984), Holland and Lamarre (1984), and Lamarre and Holland (1987) have found that simultaneous inhibitors readily transfer inhibitory control to independently trained excitors, whereas the transfer of serial inhibitors is restricted to other stimuli that were the target of discrimination training. Specifically, serial inhibitors appear to function as negative occasion setters (see Miller and Oberling, 1998, for a discussion) and only transfer to other targets of occasion setting training and to a lesser degree to stimuli that were partially reinforced. However, unlike Holland's procedure, in Denniston et al.'s procedure there was no gap between termination of the inhibitor and onset of the training excitor, which may be one factor that determines whether the stimulus will function as an occasion setter as opposed to a simple conditioned inhibitor.

For the purpose of negative summation testing, a transfer excitor, C, was established as a delay CS in order to produce an expectancy of US presentation 5 s following its onset. At test, inhibitors X and Y were separately compounded with

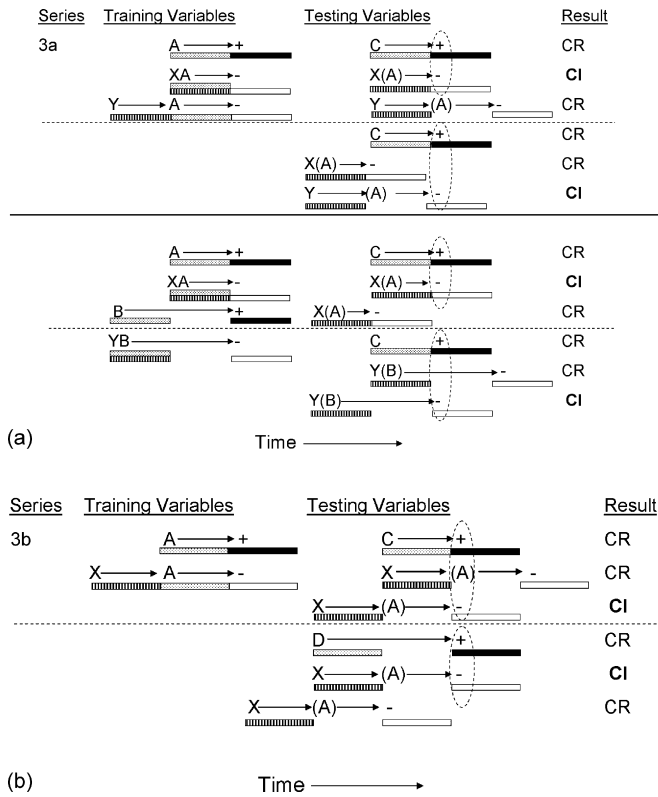


Fig. 3. (a) Inhibitory training provided by Denniston et al. (1998a). CSs A, B, C, X, and Y, were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; filled bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. At test, animals received either serial or simultaneous presentations of C, XC, or YC. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitator and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition. (b) Inhibitory training provided by Denniston et al. (1998a). CSs A, C, D, and X were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. At test, animals received either serial or simultaneous presentations of C, XC, D, or XD. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitator and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition.

transfer excitator C using either serial or simultaneous pairings (see Fig. 3a, top). Variable 4 was manipulated in order to vary the temporal expectations for US presentation and omission at test. Simultaneous presentations of X and C were expected to produce temporally congruent expectations of US omission and presentation. In contrast, serial presentations of X and C were expected to produce a mismatch of temporal expectancies of US omission and presentation because inhibitor X was anticipated to generate an expectation of US omission 5 s following its onset whereas transfer excitator C was anticipated to generate an expectation of US presentation 5 s following its onset. By providing a serial X → C presentation, in which X was presented

5 s prior to the onset of CS C, the temporal expectation of US omission was expected to occur 5 s prior to the expectation of US presentation anticipated based on transfer excitator C. At test, reduced inhibition (i.e., stronger conditioned suppression) was observed to the serial X → C compound relative to the simultaneous XC compound which resulted in robust inhibition. An opposite pattern of responding was observed when testing was conducted with the YC serial and simultaneous compounds. At test, strong inhibition (i.e., weak conditioned suppression) was observed to the serial Y → C compound relative to the YC simultaneous compound. This pattern of results was described as being a consequence of the inhibitor Y signaling US omission 10 s following its onset, which produced a matched temporal expectation of US omission and US presentation only when presented in a serial compound with transfer excitator C at test.

One potential concern with the preceding studies is that rather than the findings representing control of inhibition through different temporal expectancies for US omission, the results may be explained more simply through different degrees of inhibitory behavioral control (e.g., Williams et al., submitted for publication). That is, a delay training excitator may produce an acute pattern of responding, whereas a trace training excitator may produce a more diffuse pattern of responding. Likewise, a simultaneous inhibitor established with a delay training excitator may produce an acute pattern of inhibition that may then maximally inhibit a transfer excitator that generates an acute pattern of responding (i.e., a delay transfer excitator), whereas an inhibitor established with a trace training excitator may generate a more diffuse pattern of inhibition that best inhibits a diffuse pattern of responding generated by a trace transfer CS. However, Denniston et al.'s (1998a) Experiment 2 (see Fig. 3a, bottom panel) suggests that this alternative explanation of the previously described results is not the primary determinant of when transfer of inhibition will be observed. In their Experiment 2, Denniston et al. provided rats with training intended to produce two conditioned inhibitors with different temporal expectancies for US omission. Inhibitor X was trained as a simultaneous inhibitor for delay excitator A and inhibitor Y was trained as a simultaneous inhibitor for trace excitator B. As a consequence of this training, inhibitor X was expected to signal US omission 5 s following its onset, whereas inhibitor Y was expected to signal US omission 10 s following its onset. Alternatively, inhibitor X might generate an acute pattern of inhibition as it was trained with a delay training excitator, whereas inhibitor Y might generate a more diffuse pattern of inhibition as a consequence of being trained with a trace training excitator. At test, inhibitors X and Y were tested in either serial or simultaneous compound with delay transfer CS C (a manipulation of Variable 4 in Table 1). If transfer of inhibition is a consequence of patterns of inhibition, as suggested by Williams et al., rather than temporal expectancies of US omission and presentation, then one would expect to observe inhibitory behavioral control only when inhibitor X was compounded with transfer excitator C, or when inhibitor Y was compounded with another diffuse signal for US presentation (e.g., a trace transfer CS). Consistent with this analysis, inhibitor X reduced responding to transfer excitator C when presented in a simultaneous, but not a serial

compound. However, inhibitor Y produced robust inhibition when presented in a serial, but not simultaneous compound with transfer excitator C. This latter pattern of results demonstrates that inhibitory behavioral control, as assessed through a summation test for conditioned inhibition, is the consequence of temporal expectancies, rather than acute vs. diffuse patterns of inhibition, because according to Williams et al. inhibitor Y should have generated a diffuse pattern of inhibition that would not be anticipated to attenuate the acute pattern of responding generated by a delay transfer CS. Instead, these results appear to be a consequence of inhibitor Y signaling US omission 10 s following its onset, which by presenting inhibitor Y 5 s prior to CS C (which signaled US presentation 5 s following its onset) produced temporally matched expectations of US omission and presentation, respectively. Presenting Y and C in a simultaneous compound produced a mismatch in temporal expectancies because the expectations of US omission would be shifted by 5 s, such that the expectation of US omission would occur 5 s following the expectation of US presentation (see Fig. 3a, bottom panel).

Denniston et al.'s (1998a) Experiment 3 further explored this alternative account of temporal control of inhibition. In that experiment, rats received training intended to establish a single serial inhibitor for a delay trained excitator through serial compound non-reinforced presentations of inhibitor X with delay trained excitator A (see Fig. 3b). At test, inhibitor X was presented in either serial or simultaneous compound with either delay transfer excitator C or trace transfer excitator D. These four test conditions were intended to manipulate the temporal expectancies of US presentation and omission generated by the transfer excitators and the conditioned inhibitor, respectively. Serial presentation of inhibitor X and delay transfer excitator C (i.e., $X \rightarrow A$) was expected to generate maximal inhibition as a consequence of inhibitor X signaling US omission 10 s following its onset, which corresponded to the expectation of US presentation generated by transfer excitator C, provided that the inhibitor is presented 5 s prior to CS C. Likewise, simultaneous presentations of inhibitor X and trace transfer excitator D were expected to generate maximal inhibition as the expectation of US omission evoked by inhibitor X corresponded to the expectation of US presentation generated by transfer excitator D, provided that the inhibitor was presented simultaneously with CS D (which signaled US presentation 10 s following its onset). If transfer of inhibition is a consequence of patterns of inhibition, then maximal inhibition by an acute inhibitor (X) should be restricted to testing with a transfer excitator that produced an acute pattern of responding (i.e., transfer excitator C, but not D), a prediction that was not confirmed. At test, greater inhibition was observed with the $X \rightarrow C$ and XD compounds, relative to the XC and $X \rightarrow D$ compounds, thereby confirming that passage of a summation test is the consequence of temporal expectancies rather than patterns of inhibition.

The previously discussed studies of the timing of inhibitory behavioral control investigated the interaction of temporal expectancies generated by the conditioned inhibitor and transfer excitator at the time of negative summation testing. These studies demonstrated that behavior indicative of inhibitory behavioral control is sensitive to the temporal expectancies for US omission. However, they employed only one of the two tests recommended

by Rescorla (1969) for assessing the inhibitory properties of a CS. The following series of experiments were designed to investigate whether evidence of temporal control of inhibition could be obtained with retardation tests for conditioned inhibition. Burger et al. (2001) provided rats with inhibitory training in which two conditioned inhibitors were established as signals for the omission of the US at different temporal locations (see Fig. 4a). Inhibitor X was trained as a simultaneous inhibitor through non-reinforced pairings with a delay training excitator (A) to establish a temporal expectancy of US omission 5 s following onset of inhibitor X. Inhibitor Y was similarly trained as a simultaneous inhibitor through non-reinforced pairings with a trace training excitator (B) in order to establish a temporal expectancy of US omission 10 s following onset of inhibitor Y. Prior to testing, inhibitors X and Y were separately paired with the US to assess retardation of acquisition of behavioral control. Different groups of subjects received retardation pairings in which an inhibitor was paired with the US using either trace or delay conditioning (a manipulation of Variable 5, see Table 1). At test, conditioned responding was assessed using a flooding measure to assess degrees of retardation of acquisition of behavioral control. Maximal inhibition (i.e., retardation) was expected when the inhibitor was paired with the US at the same temporal location as the inhibitor had previously signaled omission of the US (e.g., delay $X \rightarrow US$ and trace $Y \rightarrow US$ pairings). Results indicated a greater attenuation of conditioned responding in these groups relative to that observed to a previously neutral CS, Z, and to trace $X \rightarrow US$ or delay $Y \rightarrow US$ pairings. These findings suggest that passage of a retardation test for conditioned inhibition is influenced by the temporal expectancies of US omission and the temporal location of the US on the retardation pairings. When these temporal expectancies of reinforcement and non-reinforcement were temporally consistent, greater retardation was observed.

In a second experiment, Burger et al. (2001) manipulated the inhibitor–training excitator temporal relationship (Variable 2, Table 1) to assess temporal control of simultaneous and serial inhibitors using a retardation test for conditioned inhibition. In that study, rats received training to establish two conditioned inhibitors (X and Y) with a single delay excitator (CS A, see Fig. 4b). Inhibitor X was trained as a simultaneous inhibitor for delay excitator A in order to produce a temporal expectancy of US omission 5 s following onset of inhibitor X, whereas inhibitor Y was trained as a serial inhibitor for delay excitator A through serial pairings of Y and A (with no gap between stimuli) in order to produce a temporal expectancy of US omission 10 s following onset of inhibitor Y. As in the previously described experiment, subjects then received $X-US$ and $Y-US$ retardation test pairings in which the inhibitor–US temporal relationship was manipulated. Subjects that received delay $X-US$ pairings, but not those receiving delay $Y-US$ pairings, and subjects that received trace $Y-US$, but not those receiving trace $X-US$ pairings, demonstrated reduced conditioned responding at test, thereby documenting retardation of acquisition of behavioral control. Again, these results demonstrate temporal control of inhibition through retardation tests, and they additionally extend the findings to serial inhibitors.

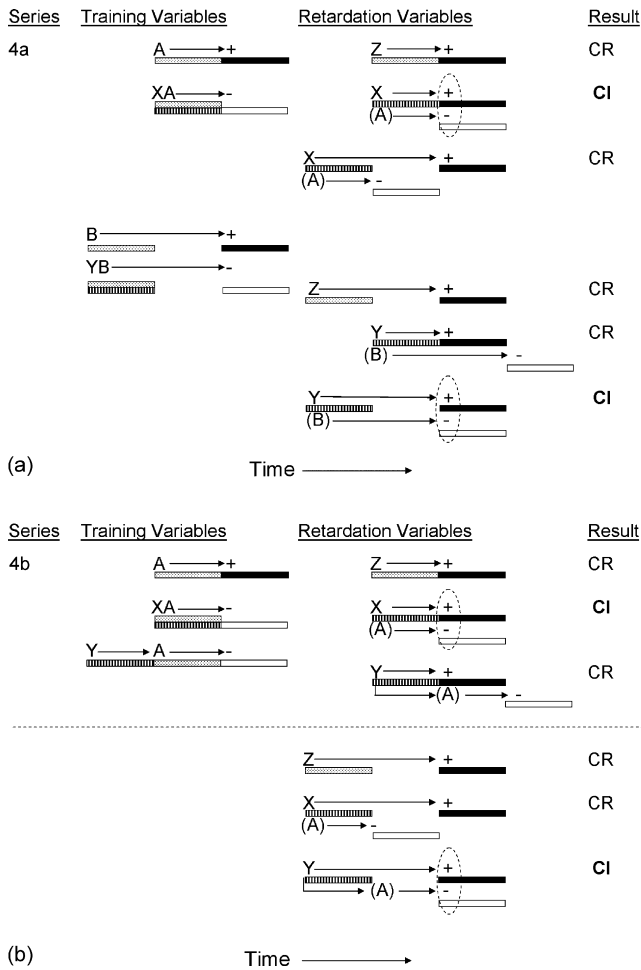


Fig. 4. (a) Inhibitory training provided by Burger et al. (2001). CSs A, B, X, Y, and Z were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. Prior to testing, animals received either delay or trace pairings of X, Y, or Z with the US. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitor and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition. (b) Inhibitory training provided by Burger et al. (2001). CSs A, X, Y, and Z were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. Prior to testing, animals received either delay or trace pairings of X, Y, or Z with the US. Stimuli in parentheses are hypothetical neural activations of the training excitors and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitor and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition.

One potential shortcoming of the previously described series of experiments is that they used a relatively gross measure of conditioned control of behavior (i.e., conditioned suppression). Although the patterns of inhibitory behavioral control demonstrated through both the retardation and summation tests for

conditioned inhibition provide seemingly compelling evidence for timing the omission of the US, the flooding test used to assess behavior indicative of inhibition does not provide a moment-by-moment measure of conditioned responding (e.g., such as that provided by the peak procedure, Roberts and Church, 1978). Furthermore, all of the previously reviewed experiments used an aversive conditioning procedure which potentially limits the generality of the findings. Toward addressing these concerns, Williams et al. (submitted for publication) used an appetitive nose poke procedure with rats in which food pellets were presented during a 30-s CS and conditioned responding was assessed by the number and timing of entries into the food cup. During conditioning, two training excitors (A1 and A2) were established as signals for US presentation through presentation of the US 30 s following onset of A1 and 10 s following onset of A2. On other trials, two other stimuli (V1 and V2) were each presented non-reinforced simultaneously with A1 and A2, respectively. This training was intended to establish V1 as a signal for omission of the US 30 s following onset of V1 and V2 as a signal for omission of the US 10 s following onset of V2. For the purpose of negative summation testing, a third excitor (A3) was established through pairings of A3 with the US at both 10 and 30 s following CS onset. At test, peak responding was observed to A3 alone around the times at which the US had previously been presented (10 and 30 s). However, when V1 was compounded with A3, reduced responding was observed 30 s, but not 10 s into the compound. Similarly, when V2 was compounded with A3, reduced responding was observed 10 s, but not 30 s into the compound. This pattern of results indicates that V1 and V2 produced maximal negative summation around the times at which their training excitors were otherwise paired with the US. This pattern of results replicates those of Miller and coworkers (Barnet and Miller, 1996; Denniston et al., 1998a,b) using a more fine grained analysis of the temporal control of inhibition made possible through the use of an appetitive conditioning preparation.

In a second experiment, Williams et al. (submitted for publication) assessed temporal specificity of inhibition using a retardation test for conditioned inhibition. Following training similar to that described above, in which V1 was established as a signal for US omission 30 s following its onset and V2 was established as a signal for US omission 10 s following its onset, retardation pairings were provided in which each stimulus was paired with the US either 10 or 30 s following CS onset. Results indicated decreased behavioral control by V1 when the US was presented 30 s, but not 10 s, following onset of V1 and by V2 when the US was presented 10 s, but not 30 s, following onset of V2. This pattern of responding during the retardation test indicates that maximal retardation is observed when the US is paired with the inhibitory CS at the same temporal location as the inhibitor signaled omission of the US, a result which replicates those of Burger et al. (2001).

3. Associative structure of temporal control of inhibition

The second line of experiments to be discussed in the present review investigated the mechanisms underlying temporal

control of conditioned inhibition. According to the temporal coding hypothesis (Matzel et al., 1988) animals form temporal maps linking events in memory and these temporal maps can be integrated when they contain a common element. Applied to inhibitory behavioral control, [Barnet and Miller's \(1996\)](#); see also [Denniston et al., 1998a,b](#)) findings suggest that inhibitory behavioral control is a consequence of animals forming temporal maps in which the temporal relationships between the inhibitor and the training excitator and between the training excitator and the US are encoded during training. During a negative summation test for inhibition, presentation of the inhibitor activates these temporal maps and produces an expectancy of US omission based upon integration of the inhibitor–training excitator and the training excitator–US temporal relationships. When this expectancy of US omission corresponds to the time at which the US is expected based upon the transfer excitator, maximal inhibition is observed. Although the previously described series of experiments obtained results consistent with this view, they do not directly assess whether the temporal expectancy of US omission is based upon a direct inhibitor–US inhibitory association, or one that is mediated by the inhibitor's training excitator (as hypothesized by [Barnet and Miller](#)).

To investigate the associative structure of temporal control of inhibition, [Denniston et al. \(2004\)](#) provided rats with conditioned inhibition training in which a simultaneous inhibitor was established with a delay training excitator (all CSs were 5 s in duration and the US was a brief, mild footshock, see [Fig. 5a](#)). This training was intended to establish inhibitor X as a signal for US omission 5 s following X's onset. Prior to negative summation testing, some subjects received further training with the training excitator, A, in order to manipulate the temporal expectancy of US omission (control subjects received equivalent training with a previously neutral stimulus, B, not shown in [Fig. 5a](#)). That is, if the temporal expectancy of US omission provided by inhibitor X is mediated by both the X–A and the A–US temporal relationships that prevailed at test, then changes in the A–US temporal relationship implemented following completion of inhibition training should produce a corresponding shift in temporal control of inhibition. Alternatively, if temporal control of inhibition is based upon a direct X–noUS association, then post-training manipulation of the A–US temporal relationship should have no effect. Following temporal shifting treatment in which CS A received trace pairings with a 5-s gap between termination of A and onset of the US, all subjects received negative summation testing with one of two transfer excitators. One transfer excitator, C, was trained as a delay excitator so that the US was expected 5 s after its onset, whereas a second transfer excitator, D, was trained as a delay excitator so that the US was expected 10 s after its onset. Subjects in the No-Shift control group displayed maximal inhibitory behavioral control when inhibitor X was compounded with a delay, but not a trace, transfer excitator. This finding replicated those of the previously described studies of timing of inhibitory behavioral control in that inhibitor X was expected to signal omission of the US 5 s following its onset which corresponds to the time at which transfer excitator C, the delay excitator, signaled US presentation. By contrast, subjects that received further training with training excitator A demon-

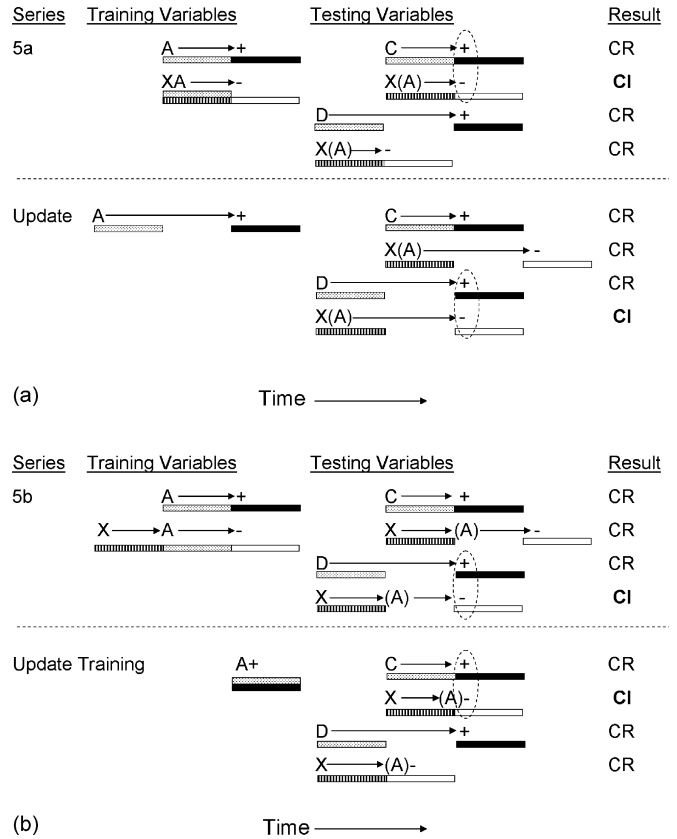


Fig. 5. (a) Inhibitory training provided by [Denniston et al. \(2004\)](#). CSs A, C, D, and X were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. Prior to testing, animals received additional training with CS A (or a previously neutral stimulus, B) in which the CS was conditioned as a trace excitator. At test, animals received presentations of C, XC, D, or XD. Stimuli in parentheses are hypothetical neural activations of the training excitators and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitator and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition. (b) Inhibitory training provided by [Denniston et al. \(2004\)](#). CSs A, C, D, and X were 5-s audiovisual stimuli; '+' denotes a footshock; '-' denotes non-reinforcement. Stippled bars indicate presentation of an excitatory CS; filled bars depict presentation of the US; striped bars depict presentation of the conditioned inhibitor; and open bars depict expectation of the omission of the US. Prior to testing, animals received additional training with CS A (or a previously neutral stimulus, B) in which the CS was conditioned as a simultaneous excitator. At test, animals received presentations of C, XC, D, or XD. Stimuli in parentheses are hypothetical neural activations of the training excitators and their associated USs. Dashed ovals represent simultaneous activation of the US by the transfer excitator and the omission of the US by the conditioned inhibitor. CR's denote the observation at test of strong conditioned behavior and CI's denote behavior indicative of conditioned inhibition.

strated maximal inhibition when inhibitor X was compounded with trace transfer excitator D, but not delay transfer excitator C. This finding suggests that the expectation of the omission of the US is mediated by the inhibitor's training excitator at the time of testing in that changes in the temporal expectancy of the US after completion of inhibition training (based upon CS A) produced a corresponding shift in the temporal expectancy of the omission

of the US. In other words, shifting the A–US temporal relationship from delay to trace allowed the simultaneous inhibitor to attenuate responding to the trace, but not delay transfer excitor. In the absence of this manipulation, the opposite pattern of results was obtained.

In a second study, Denniston et al. (2004) investigated the effect of shortening the A–US temporal relationship from delay to simultaneous. As in the previous experiment, a single inhibitor was established through non-reinforced pairings of inhibitor X with training excitor A (which was paired with a 5-s foot-shock US), but in this experiment inhibitor X was trained as a serial inhibitor in order to generate an expectancy of omission of the US 10 s following onset of inhibitor X (see Fig. 5b). Following inhibitory training, some subjects received further training with training excitor A (or a previously neutral stimulus, B) in which the temporal relationship of A was shifted from delay to simultaneous (i.e., the CS–US interval was shortened by 5 s). As a consequence of this manipulation, it was expected that the temporal expectancy of US omission based upon inhibitor X would be similarly shortened by 5 s (i.e., X should now signal US omission 5 s following its onset). At test, subjects lacking the A–US update training demonstrated maximal inhibition when inhibitor X was compounded with a trace transfer excitor D (which signaled US presentation 10 s following its onset), but not a delay transfer excitor C (which signaled US presentation 5 s following its onset). By contrast, subjects that received post-training temporal shifting of the A–US association demonstrated strong inhibition when inhibitor X was compounded with the delay, but not the trace transfer exciters. These results support the view that temporal control of inhibition is dependent upon both the inhibitor–training excitor and the training excitor–US temporal relationships in effect at the time of testing. In other words, the temporal expectancy of US omission appears to be mediated by its training excitor. Furthermore, these findings are consistent with the temporal coding hypothesis' assertion that animals form temporal maps linking events in memory and that these temporal maps can be integrated when they have common associates. For example, presentation of inhibitor X activates a temporal map containing training excitor A (in the absence of reinforcement), which in turn activates a representation of the US not occurring at a specific moment in time. When this temporal expectancy of the absence of the US is temporally consistent with the temporal expectancy of the US activated by the transfer excitor, maximal inhibition is observed.

It is important to note that similar additional reinforcement of the training excitor A without any change in the temporal location of the US can result in enhancement of Pavlovian conditioned inhibition (Amundson et al., 2005). Presumably, in the studies by Denniston et al. (2004) additional reinforcement of the training excitor decreased behavior indicative of inhibition because the temporal relationship between A and the US was altered. This suggests that, as others have noted (e.g., Lysle and Fowler, 1985), behavior indicative of inhibition depends on both the associative strength of training excitor A and the temporal information, provided through inhibitor X, of the training excitor's temporal relationship with the US.

4. Temporal control of inhibition produced through extinction

The prior discussion focused on conditioned inhibition produced using Pavlov's procedure. This was done because temporal relationships between stimuli are more clearly defined within Pavlov's procedure than with most other procedures for inducing conditioned inhibition (e.g., explicitly unpaired inhibition, differential inhibition, and backward inhibition). However, experimental extinction offers the possibility of producing conditioned inhibition in a situation in which all stimuli have clear temporal relationships. Many mechanisms have been proposed to underlie the phenomenon of experimental extinction. For example, Pavlov (1927) viewed the loss of responding to previously conditioned CS following non-reinforced exposure to the CS as being due to the acquisition of an inhibitory association. However, despite numerous attempts to demonstrate that an extinguished CS possesses net inhibitory strength (e.g., Bouton and Swartzentruber, 1989; Hendry, 1982; Konorski and Szwejkowska, 1950, 1952; Macrae and Kehoe, 1999; Reberg, 1972), most prior studies have found either positive summation by an extinguished CS when compounded with a transfer excitor (e.g., Hendry, 1982; Reberg, 1972) or facilitated reacquisition during a retardation test for conditioned inhibition (Konorski and Szwejkowska, 1950, 1952). Although these studies have failed to obtain evidence that an extinguished CS can pass the traditional tests for conditioned inhibition, this does not necessarily indicate that inhibition is not involved in the loss of responding indicative of extinction.

Based upon Pavlov's (1927) view of extinction, one might expect inhibition to accrue only until the strength of the inhibitory association matches that of the previously acquired excitatory association, thereby leading to a cessation of responding. Therefore, following extinction treatment it is not surprising that an extinguished CS fails both retardation and summation tests for conditioned inhibition, as the inhibitory and excitatory associations should offset each other, thereby leading to no net inhibitory effect. However, recent research has found that an extinguished CS can pass both summation and retardation tests for conditioned inhibition, provided that a sufficiently large number of extinction trials are provided (Calton et al., 1996; Hart et al., 1995; Schachtman et al., 2000). One potential explanation for the effect of massive extinction apparently resulting in net inhibition is that massive extinction may lead to superior retrieval of the inhibitory association over the excitatory association (Denniston and Miller, 2003). However, it is also possible that after massive extinction some loss of excitation occurs, thereby allowing the inhibitory potential to be more readily expressed. In either case, that a massively extinguished CS can pass both summation and retardation tests for conditioned inhibition raises the question as to whether this form of inhibition can display the same temporal characteristics as traditional conditioned inhibitors.

Research on the temporal properties of extinguished stimuli has revealed that animals can separate the decisions of whether and when to respond to a CS, in a manner similar to that observed with the acquisition of conditioned responding (Ohyama et al.,

1999). For example, Ohyama et al. used an autoshaping procedure with ring doves (*Streptopelia risoria*) in which subjects received exposure to a 4, 8, or 16-s keylight followed by access to food. On non-reinforced probe trials, peak responding was observed around that time at which food had normally been presented (i.e., 4, 8, or 16 s). In a second experiment, similar training to that described above was provided with the addition of an extinction phase in which subjects were exposed to 40-s non-reinforced presentations of the keylight CS. During extinction, conditioned responding steadily decreased; however, peak responding was maintained near the time at which the US had previously been presented. Ohyama et al. concluded that these results support the view that the decision of whether to respond is independent from the decision of when to respond. In other words, the timing of the conditioned response during extinction is independent from the absolute level of conditioned responding (see also Drew et al., 2004).

Given these two separate lines of research: one investigating whether an extinguished CS can pass the traditional tests for conditioned inhibition (e.g., Calton et al., 1996; Hart et al., 1995; Schachtman et al., 2000); and a second investigating the timing of responding during extinction, Denniston and Miller (2003) investigated whether an extinguished CS could exhibit temporal control of behavior indicative of inhibition in a manner analogous to the studies previously described (e.g., Barnett and Miller, 1996). In their Experiment 1, rats received conditioning with two excitors, X and Y, which were conditioned as delay and trace CSs, respectively, through pairings with a brief, mild footshock either immediately or 5 s following termination of the CS. Following acquisition treatment, subjects received massive extinction treatment of X and Y (1000 non-reinforced presentations of each stimulus, across groups). At test, the inhibitory potential of the extinguished CS was assessed through a negative summation test in which the ability of X and Y to attenuate responding to each of two transfer excitors, one delay and one trace, was assessed. Results indicated that the extinguished delay excitor, X, maximally inhibited the delay, but not trace transfer excitor and that the extinguished trace excitor, Y, maximally inhibited the trace, but not delay transfer excitor. In their Experiment 2, Denniston and Miller assessed the potential of these extinguished CSs to pass a retardation test for conditioned inhibition. Following analogous training to that described above, extinguished CSs X and Y were each paired with the US in order to assess temporal control of inhibition. During the retardation pairings, the temporal location of the US was manipulated such that it was presented either at the same or different temporal location as it was previously expected based on pre-extinction reinforced training. For example, subjects that had received extinction of CS X, the delay excitor, now received either delay or trace X–US retardation pairings. Similarly, subjects that had received extinction of CS Y, the trace excitor, received either delay or trace Y–US retardation pairings. Results indicated greater retardation when the US was presented at the same temporal location as it had been previously presented during acquisition training. That is, greater retardation was observed when the extinguished delay excitor was retrained as a delay, but not a trace CS, and when the extinguished trace excitor was

retrained as a trace, but not a delay CS. These findings suggest that an extinguished CS, at least with massive extinction treatment, can pass both summation and retardation tests for conditioned inhibition provided that the temporal expectancy of US omission coincides with the temporal expectancy of US presentation provided by either the transfer excitor (in a summation test) or the CS–US pairings (in a retardation test). More generally, these results extend the observations of temporal control of inhibition to inhibition produced through extinction.

5. Summary

The previously described lines of investigation were designed to assess the nature of temporal control of inhibitory responding. The first series of experiments reviewed the timing of inhibitory behavioral control through both summation and retardation tests for conditioned inhibition established using Pavlov's (1927) procedure. These experiments demonstrated that inhibitory behavioral control is influenced by temporal expectancies of non-reinforcement, which are based upon the temporal relationships between the inhibitor and the training excitor and between the training excitor and the US (e.g., Denniston et al., 2004). Such findings are consistent with the temporal coding hypothesis (Matzel et al., 1988; Savastano and Miller, 1998), which posits that animals encode the temporal relationship between events as a temporal map and can integrate these temporal maps when the maps include common stimuli. Applied to inhibitory behavioral control, presentation of the conditioned inhibitor activates a representation of the training excitor (without reinforcement) which in turn activates a representation of absence of the US. These representations include the temporal relationships between events and generate a temporal expectancy of the omission of the US based upon these temporal maps. Notably, the findings of Miller and coworkers have been replicated using an appetitive nose-poke procedure which provided a second-by-second analysis of inhibitory behavioral control (Williams et al., submitted for publication).

The second line of experiments described in the present review was designed to explore the nature of inhibition involved in extinction (Denniston and Miller, 2003). This series of experiments found that an excitor subjected to massive extinction treatment was capable of passing both summation and retardation tests for conditioned inhibition. Of greater interest, temporal control of inhibition produced through extinction was influenced by temporal expectancies of non-reinforcement. This effect mirrored that observed with more traditional inhibitors and suggests that an extinguished CS can pass a summation test for conditioned inhibition when the transfer excitor signals US presentation at the same temporal location as the extinguished CS previously signaled US presentation. Hence, extinction appears to result in an expectation of non-reinforcement at a particular point in time, which is consistent with the observations of Balsam and coworkers (Drew et al., 2004; Ohyama et al., 1999) who found continued temporal control of conditioned responding despite non-reinforcement of a CS. The results of Denniston and Miller suggest that this temporal information is maintained and that the decision of how to respond (i.e., either excitatory or

inhibitory) is influenced by the magnitude and nature of training (i.e., extinction).

Collectively, these studies point to temporal attributes being included in what is learned during inhibitory learning that results from either Pavlov's (1927) procedure or extinction of a simple excitator. Through assessment of inhibition using the two-test strategy (Rescorla, 1969), much has been learned about the nature of inhibitory conditioning. These studies demonstrate temporal control of inhibitory conditioned responding that is analogous to that observed in excitatory behavioral control, a finding complementary to those of Church's highly productive career.

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