EXPLORING TEMPORAL PROPERTIES OF THE OVEREXPECTATION EFFECT

by

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Exploring Temporal Properties of the Overexpectation Effect

During Pavlovian conditioning, repeated pairings of an unconditioned stimulus (US; e.g., sucrose) with an initially neutral, conditioned stimulus (e.g., a tone) alter the magnitude of a conditioned response (CR; e.g., searching for food) across training (Mackintosh, 1975; Pavlov, 1927; Pearce, 1987; Pearce & Hall, 1980; Rescorla & Wagner, 1972). In one conditioning procedure, overexpectation (OX), animals are trained to expect a common US following the presentation of two conditioned stimuli (i.e., elements). If the two elements are then placed in compound and followed by the same US from before, trial 1 of compound training should be an instance of predication error (e.g., animals expect two USs but only receive one). Proper adjustment to each element's diminished value would manifest as a diminished CR magnitude to either element alone. The temporal relationship between an element and the US can also modify *when* a CR occurs (Pavlov, 1927). Given animals can elicit CRs at appropriate times in anticipation of food, we wondered whether adjustments in the magnitude of the CR in response to the Overexpectation treatment (OXT) could be as temporally sensitive as the mere elicitation of the CR.

The Rescorla-Wagner (R-W) model of learning (Rescorla & Wagner, 1972) proposes an equation for describing how an element (e.g., X), such as tone, comes to control a CR (e.g., approach food) by couching learning as trial by trial alterations to X's associative value. A hallmark of the R-W model is that when more than one element predicts the same US (e.g., X and A), the two elements compete for a finite amount of information value; the response elicited by each element, thus, can vary for X or A depending on the conditions in which they were trained. While the R-W model excels in operationalizing how elements modulate the magnitude or intensity of the CR, the model has little to say about how the element modifies other

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dimensions of the CR; for example, on a trial with X alone, changes in the associative value of X can be determined by the formula $\Delta V_X = \alpha x \cdot \beta \cdot (\lambda - \Sigma Vi)$. The associative value gained by X (V_X) on a trial is determined by the discrepancy ($\lambda - \Sigma Vi$) between what can be learned about the US (λ) and the sum of value already explained by all participating elements, ΣVi (e.g., $V_X + V_A$). The model assumes that the amount of associative value the US can support is finite. For example, when the associative value of all participating elements (e.g., $V_{XA}=1.00$) is equal to the total associative value supportable by the US (e.g., $\lambda = 1$), the discrepancy term is zero (e.g., $\lambda - \Sigma vi = 0$) and learning about the US is said to have reached asymptotic levels. In OX, X and A are trained to separately reach asymptotic values before they are able induce a marked overexpectation of the US when placed in compound.

We can apply the R-W model to the OXT to better understand the model and the finding. In OX, two elements are first asymptotically trained to a common US. Figure 1A shows separate acquisition curves for X and A. Given that each trial of X and A occur separately, the R-W model posits a summation rule; when X and A are placed in compound, their associative values sum together. It is on the initial compound trial, therefore, that animals should maximally over-expect the single US. Because of the finite amount of learning that can occur to a US, the model predicts that the associative value of each element following overexpectation should drop until each element predicts the appropriate amount of US (e.g., ΔV_X and ΔV_X both equal .5, assuming each element is of equal salience).

To compare the effects of placing two pretrained elements into compound, subjects are assigned in compound training (i.e., Phase 2) to either an OX condition, or a control (CTL) condition. Animals in the OX condition receive compound trials of pretrained X and A, co-terminating with the same US encountered during Phase 1. Animals in the CTL condition

typically receive additional trials of the target X alone, or receive multiple trials of the target X in

compound with a novel element (e.g., element C). Across phase 2, for subjects in group OX, the

prediction error corrects itself so that X and A readjust their values to correct for the single US.

Figure 1

The Overexpectation Effect According To:
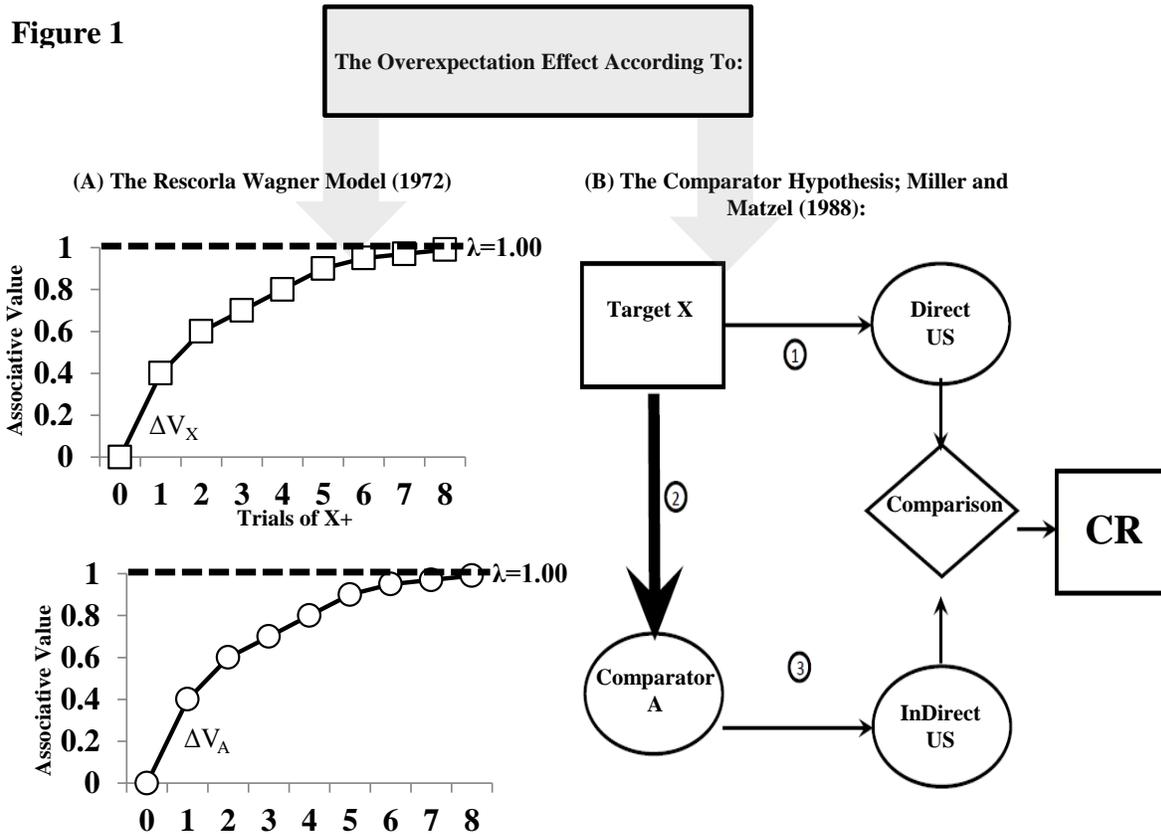
(A) The acquisition based R-W model: both X and A increase in associative strength (y-axis) as paired
trials with the US decrease the discrepancy between lambda (dotted line) and each element's current
associative value (i.e., the product ΔV). Across acquisition trials (x-axis), as does A (bottom left) on
separate trials. The R-W anticipates a decrement to X given X and A are placed compound, resulting in
a prediction error and subsequent decrements in responding to either participating element.
(B) The performance based comparator model: performance during the test of X, following OX: links
between X, the comparator, A, and the US are merely representations. Link 2 describes the possible
link in memory between X and A give the past pairings of A with X in the compound phase. Tests of X
elicits both a direct (link 1) and indirect (link 3) representation of the US in memory; competition
between what is elicited via the target, X, and its comparator, A, determines the degree of responding to
X at test.

Less associative value equates to CRs of lower magnitude; the OX effect (i.e, OXE), therefore, is

defined as a diminished CR during each tests of X for the OX group, when compared to a CTL

group that received either compounds with a neutral element (e.g., XC+)**,** or no compound at all (e.g., X+).

The discrepancy, or error-correction, driven R-W model has enjoyed considerable success, providing compelling explanations for reports of cue-competition between elements (e.g., blocking; Kamin, 1969; overshadowing; Pavlov, 1927). The R-W model, notably, described, *a priori,* a possible overexpectation scenario. The overexpectation scenario has been substantiated in the behavior of rats (Kamin & Gaioni, 1974; Kremer, 1978; Lattal & Nakijima, 1998; Levitan, 1975; Rescorla, 1970; Rescorla, 1999) and pigeons (Khallad & Moore, 1996) utilizing both aversive and appetitive USs. The finding of a reduced CR, however, following the compound trials of two asymptotic elements is not anticipated solely by the RW-model. Acquisition focused models like the R-W model are just one viable way to conceptualize the emergence of a conditioned response in Pavlovian conditioning (Miller & Escobar, 2001).

The comparator hypothesis (e.g., Miller & Matzel, 1988; Figure 1B), for instance, is a performance-based model that describes how responding to a target element can be influenced by the extent to which other stimuli or the context itself predict the same US. Thus, on any given conditioning trial (e.g., X+), responding is determined not solely by the strength with which X activates a direct representation of the US, but also by the extent that X activates the US indirectly through other stimuli it has become associated with (e.g., A, the comparator stimulus).

According to the comparator hypothesis, during the OXT, X and A in the OX group should develop similar affiliations with the US during element training. During compound training, X and A will also acquire a target-comparator relationship (link 2, Figure 1B). At test, activation of the target (X-US) will elicit less conditioned responding as a result of activation of the comparator stimulus, A, and indirectly, the US. This memory based deviation from the

acquisition based R-W model highly testable as only the comparator hypothesis predicts that post OXT manipulations to the comparator, A, would have effects on X. The existence of link 2 could therefore, be tested by presenting A without the US following the OXT (i.e., extinction of A). Using a fear conditioning paradigm, Blaisdell, Dennison, and Miller (2001) found that extinction of A, following the OXT, attenuated the decrement in conditioned responding observed during X. Blaisdell et al. (2001) interpreted that the extinction of the comparator element weakened the indirect activation of the US via the comparator, permitting un-attenuated responding to X. This result could not be accounted for via the traditional R-W model, thus, adding to the notion that the OXE may not be merely a result of trial by trial readjustments in learning to X and A.

Both the RW-model and comparator hypothesis make predictions about CR magnitudes following the OXT; however, we are also certain that animals can learn about the timing of crucial conditioning events, such as the onset of an element and the delivery of a US (e.g., Catania, 1970; Gibbon, Malapani, Dale, & Gallistel, 1997; Kirkpatrick & Church, 1998; Kirkpatrick & Church, 2000; Roberts, 1981) Roberts (1981), for example, trained rats that the US was to arrive at a certain time following the onset of the element. At test, the element was extended well beyond its normal length; rat's responding increased during the original duration of the element and peaked at the exact time the US was expected, before quickly dropping. The peak in responding was interpreted as the rats being sensitive to temporal components during excitatory conditioning. If animals can learn when to anticipate a US, can the decrement in responding induced by the OXT also reflect temporal properties?

To observe a timed OXE, animals would need to encode temporal information about both elements, when in isolation and in compound, and transfer this knowledge across separate phases of training. Savastano and Miller (1998) presented several experiments supporting the temporal

coding hypothesis (TCH; Barnet, Arnold, & Miller, 1991; Barnet, Cole, & Miller, 1997; Matzel,

Held, & Miller, 1988; Miller & Barnet, 1993). The TCH proposes that during conditioning the

temporal relationship between an element and the US is automatically encoded in association

and determines the magnitude and nature of any conditioned response. One important prediction,

temporal integration, follows from the fourth tenet of the TCH; animals can integrate temporal

information encoded in separate phases of conditioning when a common element is present

(Honig, 1981; Matzel et al, 1988; Miller & Barnet, 1993; Roberts, 1981; Savastano & Miller,

1998).

This type of integration has received much support in the fear conditioning paradigm

using rats (Savastano & Miller, 1998). Targeting the OXT, for example, Blaisdell and colleagues

(2001) showed that the temporal relationship between X, A, and the US modulated the strength

of the OXE. In Experiment 4 of Blaisdell et al. (2001), when X and A both terminated 5 s prior

to the delivery of shock (i.e., trace conditioning), the strongest decrement in conditioned

responding (i.e., less conditioned suppression) was observed during X compared to when the

timing of X and A were incongruent. Using fear conditioning in rats, Miller and colleagues have

also been able to show through a complex set of between-group comparisons, that temporal

factors play a prominent in conditioning procedures, such as blocking (Barnet, Grahame, &

Miller, 1993), sensory preconditioning (Cole, Barnet, & Miller, 1995b), and second-order

conditioning (Barnet, Arnold, & Miller, 1991).

Temporal specificity can, however, be monitored by measuring fine grained changes in

the time course of the CR (e.g., Leising, et al., 2007; Williams, Johns, & Bindras, 2008). While

recent research has elucidated several unique properties of the OXE during spontaneous recovery

(Rescorla, 2006), experimental renewal, (Rescorla, 2007), and trial massing (Sissons & Miller,

2009), measuring the magnitude of the CR has continued to be the primary measure for testing the response decrement induced by prior overexpectation. If associative cue-competition occurs against the backdrop of time, it should be possible to observe a temporally specific drop in CR due to readjustment of cues participating in the OXT. Modified models of the RW model describe how cue competition can still be operationalized within the backdrop of time. To illustrate the intersection of associative conditioning and response timing, however, a paradigm is needed that allows participating cues to communicate unique temporal information.

One such paradigm, the embedded procedure (e.g., Leising, Sawa, & Blaisdell, 2007), was recently introduced to study temporal integration in appetitive conditioning. Using a Pavlovian sensory-preconditioning procedure, a short (10 s in duration) element X was embedded within a long (40 s) element A, either early after its onset (5 s) or late (25 s) after its onset. Following these pairings, X was simultaneously paired with sucrose solution. If subjects had integrated the temporal information encountered during conditioning, then the peak response rate during A should have correlated with the maximal expectation of the US based on the relationship between stimuli in Phase 1 and 2 (e.g., Catania, 1970; Roberts 1981). During non-reinforced probes, rats in Group Early checked for sucrose more often in the early portion of A, while rats in Group Late checked more often in the latter portion of A. Tests of A showed that rats had successfully integrated temporal information acquired in Phase 1 (X-A) and Phase 2 (X-US) into a higher-order chain (A-X-US) that preserved the order and time between the paired events. Borrowing from the logic of Leising et al. (2007), it becomes possible to examine the response decrement imposed by the OXT if elements of separate durations are embedded into one another. The following experiments (Table 1) were designed to evaluate the generality of temporal integration by testing for temporal specificity of the OXE. We utilized a procedure

similar to Leising et al. (2007), in which a short stimulus was embedded into target periods of a longer stimulus.

Summary and Hypothesis

Imagine that two separate warning chimes (e.g., low tire pressure and low gas) on a race car drivers' headset indicated the need for the driver to make a pit stop. The low gas chime signaled the need for a pit-stop very soon in time, and lasted 2 minutes, whereas the low tire chime signaled the need for a pit-stop much later, and lasted 5 minutes. Imagine then that during a particularly unlucky race, the shorter chime began to co-signal for a pit-stop 4 min into the duration of the longer low-tire chime (i.e., compound training). Given enough compounds of the two chimes, would the driver be more or less liable to expect an upcoming pit-stop during the later period of the gas period when it chimed alone?

Following the compound of two pretrained, asymptotic elements, the R-W model describes how over-expectation might drive a diminished conditioned response to each element in isolation (i.e., the OXE). Adaptions on the original R-W model however, allowing for response acquisition to occur against the backdrop of time (Sutton & Barto, 1981). An adaptive, timing based model may be able to simulate a timed overexpectation event but the possibility has never been empirically tested. We might expect, assuming the original R-W model, that the decrement to X should be generalized across the element to the extent that the shorter A interacts with the entire element. The comparator hypothesis does not necessarily anticipate a timed decrement either, only that A causes interference to responding within X when it is added in compound. The comparator hypothesis does, however, recognize the importance of time as a factor in conditioning (Savastano & Miller, 1998). Thus, embedding pretrained A to coincide with the delivery of the US at the particular time it was expected during X, according to the

comparator hypothesis, should further enhance the decrement seen during X because of the comparison made between direct and indirect US representations at test (Figure 1B). Recovery from the response decrement occurring during X via the retrospective effects of extinguishing A, as well as the importance of timing during the OXT (Blaisdell et al., 2001; Experiments 3 and 4) indicates that the traditional R-W model interpretation of OX is incomplete. Furthermore, temporal expectancies are not captured by either model, but might be anticipated within the TCH.

We hypothesized that the response decrement induced by the OXT during target stimulus X would be exaggerated during the period that a short, pretrained A was previously embedded. Using a conditioned magazine approach paradigm with rats, in Experiment 1, we placed two forward-paired elements that differed in duration into compound, following a design approximating to a more traditional OXT. In Experiment 2, A was embedded directly in the middle of X and compared to a group receiving a similar pairing but with a novel element, C. In Experiment 3, two time periods of reward (early and late) within the 40-s X were trained, but A

Table 1: Experimental Design

Experiment	Group	Timing of US	Phase 1a	Phase 1b	Phase 2	Test
1	OX ($n = 16$)	After X	X+ B-	X+ A+ B-	XA+	X?
	CTL ($n = 16$)	After X	X+ B-	X+ A+ B-	X+	X?
2	OX ($n = 32$)	15 s into X	X+ B-	X+ A+ B-	XA+	X?
	CTL ($n = 32$)	15 s into X	X+ B-	X+ A+ B-	XC+	X?
3	OX ($n = 32$)	5 and 25 s into X	X+ B-	X+ A+ B-	XA+	X?
	CTL ($n = 32$)	5 and 25 s into X	X+ B-	X+ A+ B-	X+	X?

Table 1 displays the experimental design of Experiments 1 – 3. Trial types that coincided with the US are denoted by a (+), trial types with no US are denoted by a (-). In the group column, OX denotes groups receiving the OXT (e.g., XA+/ X?); CTL denotes groups receiving either X alone or a novel compound (e.g., XC+/X?) instead of the OXT. Concerning the timing of US column, in Experiment 1, X was forward paired with the US, in Experiments 2 and 3, the US was presented at different times within X. In all experiments, X and B were 40-s auditory stimuli, A was a 10-s visual stimulus.

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was embedded during only one of the time periods (e.g., 5 sec after the onset of X). Across the experiments, fitting the embedded procedure to the OXT indicated that the effect exerted an effect on temporally specific portions of X; therefore, embedding a shorter, separately pretrained A into X causes a temporally specific decrease in responding exaggerated during period that A or the US were previously expected to occur.

Experiment 1

A primary objective was to illustrate the OXE within an embedded, appetitive paradigm (e.g., rats approaching a sucrose well) utilizing elements of separate durations; thus, X was a 40-s element, and A was a 10-s element. Examining how embedding the 10-s A into the 40-s X during the OXT was of importance as the remainder the experiments featured a 10-s A being embedded into a specific time period of a 40-s X. Half of the rats received a compound manipulation (i.e., XA+), the remaining rats received repeated presentations of the target alone (i.e., X+). The effect of compounding the two asymptotic elements (i.e., the OXE) was measured by testing the target X.

Across element training, rats received extensive training; 184 with each stimulus, X, A, and B. X (an auditory stimulus) and A (a visual stimulus) were forward-paired with a common US, a 10-s opportunity to drink sucrose from a raised dipper. B, another auditory stimulus was never paired with sucrose The US was common throughout all 3 experiments Trials of X+, A+, and B- continued until rats demonstrated evidence of asymptotic responding to X+ and A+ (Rescorla & Wagner, 1972).

Upon reaching compound training, the training manipulation (AX+ vs. X+) effectively split the rats into 2 groups. Rats randomly assigned to the OX condition received compound trials of A embedded within the final 10 s of X, followed by the US (see Table 1). Rats assigned

to group CTL received trials of X alone (i.e., X+). No previous study has examined the distribution of conditioned responding during the OXT. Typically, the CR is averaged across the entire duration of element X and compared as a single value against the CTL group. Based on the results of Leising et al. (2007) and predictions derived from the R-W model (Rescorla & Wagner, 1972; Sutton & Barto, 1981), we anticipated that subjects would learn the X-A temporal relationship, integrate them to form an X-A-Sucrose temporal map, and over-expect the US towards the conclusion of X in phase 2.

Behavior congruent with this integrated map prediction would manifest as a drop in nose pokes during the final 10 s of X for group OX, relative to Group CTL.

Method

Subjects and Apparatus

The subjects were 16 female and 16 male Long-Evans rats bred in the TCU vivarium from parents obtained from Harlan Laboratories (Indianapolis, IN). Subjects were pair-housed in translucent plastic tubs with a substrate of wood shavings in a vivarium maintained on a 12 hr dark/12 hr light cycle. All experimental manipulations were conducted during the light portion of the cycle. A progressive food restriction schedule was imposed over the week prior to the beginning of the experiment, until each rat received 15 g of food each day. All animals were handled daily for 30 s, during the week prior to the initiation of the study. Subjects were randomly assigned to each group, however, one subject in the CTL group died prior to test making the final number of subjects in group OX ($n = 16$) slightly higher than group CTL ($n = 15$).

Each of eight experimental chambers measuring 30 x 25 x 20 cm (l x w x h) was housed in a separate sound and light-attenuating environmental isolation chest (Med Associates). The

walls and ceiling of the chamber were constructed of clear Plexiglas and the floor was constructed of stainless-steel rods measuring 0.5 cm in diameter, spaced 1.5 cm center-to-center. One wall of the chamber was equipped with a dipper that could deliver sucrose solution (16%). When in the raised position, a small well (0.05 cc) at the end of the dipper arm protruded up into the feeding niche. An infrared photo-detector was positioned across the entrance to the feeding niche. When a rat placed its nose into the feeding niche to lick the sucrose solution (i.e., a nose poke), the photo beam was disrupted measuring responding at a rate of 10 breaks per sec (i.e., dSec).

A ventilation fan in the enclosure and a white-noise generator on a shelf outside of the enclosure provided a constant 74-dB(A-Scale) background noise. Three speakers on the outside walls of the chamber delivered a high frequency tone (3000 Hz, 8 dB above background noise) or a low frequency tone (750 Hz, 8 dB above background noise). The 3000 Hz tone and 750 Hz tone served as elements X and B, and were counterbalanced across groups. A diffuse light was located 13 cm above the floor, on the same wall as the food magazine. A flashing light (0.25 s on/0.25 s off) stimulus could be presented by flashing the diffuse light; 10 sec of the flashing light stimulus served as element A for all subjects. The house light was turned off during the duration of the Experiment 1, 2, and 3. Box assignments were counterbalanced between groups.

Procedure

Acclimation. For 2 days, rats received un-signaled presentations of sucrose on a variable interval schedule of 20 s (Day1), followed by a 60 s variable interval schedule (Day 2).

Phase 1a (Element Training). On days 3 to 6, all rats received 8 trials each of auditory (High Tone vs. Low Tone, counterbalanced) stimuli X and B (see Table 1). Element training during Phase 1a was therefore composed of 16 trials per day. Phase 1a (e.g., 8 trials of X+, 8

trials of B-) was designed to encourage responding during the 40-s X, and to enhance

discrimination to X via exposure to non-reinforced B, a stimulus of identical (i.e., 40 s) duration.

The inter-trial interval during Phases 1a and 1b was set to a variable interval-50 s for the first two

days of 1a (days 3 and 4) and 1b (days 7 and 8). A variable interval-80 s ITI was implemented

for the remainder of the experiment (days 9-24).

Phase 1b (Element Training). On days 7 to 19, all rats received 8 trials each of 10 s A,

in addition to 8 trials each of 40 s X and B. Element training was therefore composed of 24 trials

per day.

Phase 2 (Compound Training). On days 20, 21, and 22, subjects in group OX ($n = 16$)

received 8 subsequent compound trials during which the onset of A was embedded 30 s after the

onset of X; co-terminating with the US 10 s later. Subjects in group CTL ($n = 15$) received 8

subsequent trials of X, identical to how X appeared in element training.

Test. On days 23 and 24, group OX received 8 more compound trials (XA+), while

group CTL received 8 more presentations of X+. All subjects then received 4 non-reinforced

probes of the target X.

Results and Discussion

Results
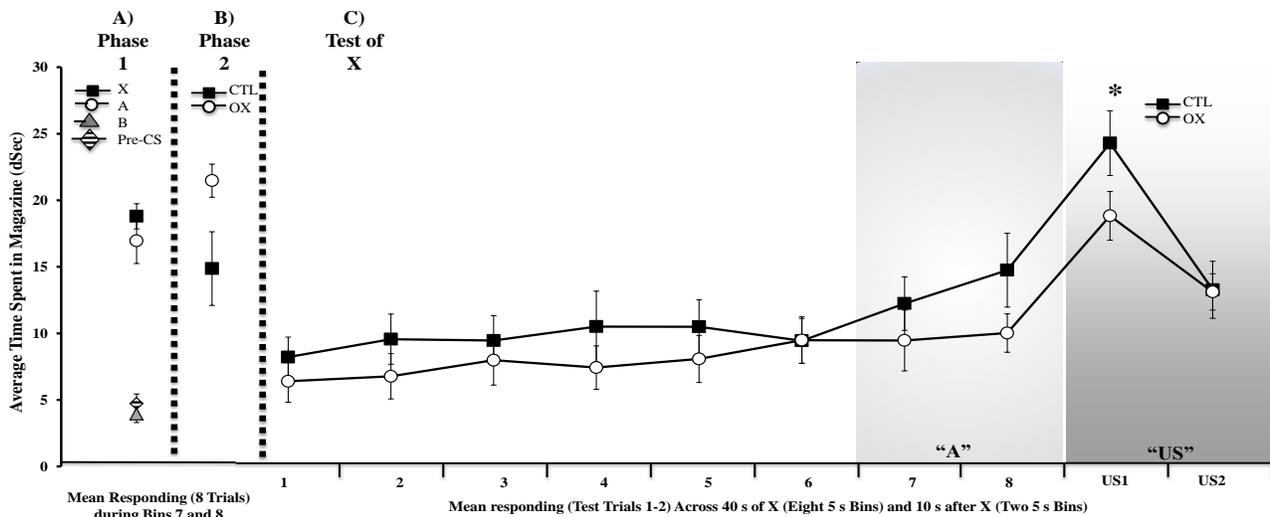
Element Training. Figure 2A shows average time spent in the magazine during elements

X, A, B and a 40 sec Pre-CS period (occurring before all 3 trial types). Given that X and A

differed in duration, we compared magazine entries during Bins 7 and 8 of 40-s X, and Bins 1

and 2 of 10-s A. The two time periods shared adjacent, temporal relationships to the US during

element training.

A probability value of $p > .05$ was used as a criterion for significance for all statistical analyses. To test for any preexisting relationships between groups prior to Phase 2, we conducted a 4 (Element: X vs. A vs. B vs. Pre-CS) X 2 (Stimulus: High Tone vs. Low Tone) X 2 (Gender: Male vs. Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable. As expected, there was significant main effect of stimulus, $F(3) = 54.62$, $p < .001$, all other main effects and interactions were *n.s.* Within the main effect of stimulus, Post-Hoc analysis (Tukey's HSD) revealed that X ($M = 16.95$, $SD = 1.70$) and A ($M = 18.8$, $SD = 0.94$) significantly differed from B ($M = 3.94$, $SD = .64$) and the Pre-CS ($M = 4.73$, $SD = .71$).

Compound Training. Figure 2B shows average time spent in the magazine during element X in rats assigned to the OX and CTL condition on the last day of compound training. Again, we compared magazine entries during Bins 7 and 8 of 40-s X, as the two time periods

Figure 2

Figure 2 Shows the Results from Experiment 1. The y-axis shows the average amount of time rats spent nose poking the magazine (in dSec).
A: Mean nose pokes during Bins 7 and 8 are plotted for the 40-s X, B, and Pre-CS period during Element training (Day 19).
B: Mean nose pokes during Bins 7 and 8 of X for groups OX and CTL during the final day of compound training (Day 22).
C: Mean nose pokes are charted across time for th3 40-s X and the 10-s US period after X for groups OX and CTL during test (Day 23 and 24). *= $p < .06$

shared adjacent, temporal relationships to the US during element training.

To test for any preexisting relationships between during the Phase 2 stimulus manipulation, we conducted a 2 (Stimulus: High Tone vs. Low Tone) X 2 (Gender: Male vs. Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable revealed a trending non-significant main effect of group, F (3) = 3.64, $p > .06$. The potentially problematic main effect of group during compound training may have been indicative of continued summation (A plus X), or merely indicate that the OX group was more excitable during Phase 2.

Test. Across all 4 test trials, and both test days, a 2 (Group: OX vs. CTL) X 8 (Time: Bins 1-8) mixed ANOVA revealed a significant main effect of time, F (9, 261) = 26.6, $p < .001$, but a non-significant interaction of time and group. All planned comparisons were non-significant. Using an similar preparation and procedure (i.e., magazine approach in rats), Lattal and Nakajima (1998, Figures 1 and 2) found that the decrement to X had disappeared by test trials 3 and 4, therefore, we chose to run similar analysis on average responding during trials 1 and 2 across the test days.

Figure 2C shows the main results of the test averaged across trials 1 and 2. The dependent variable was average magazine responding across all the first two test trials of stimulus X for two days (4 trials total). A 2 (Group: OX vs. CTL) X 8 (Time: Bins 1-8) mixed ANOVA revealed a significant main effect of time, $F(9, 261) = 30.1$, $p < .001$, but a non-significant interaction of time and group. The data, therefore, were not indicative of a widespread OXE across the entirety of element X, when it was compounded with a much shorter element A.

Due to the timing of X and A, we expected a difference between the groups to appear near the end of the X (specifically Bins 7 and 8, when A was previously embedded), and a

maximal difference during US-1, when sucrose was to arrive. Planned comparisons targeting group as a between subject variable at the target time period (Bins 7 and 8,), when A was embedded revealed a non-significant (i.e., *n.s.*) difference between groups (OX vs. CTL) when focusing on this time period, however, a planned comparison comparing groups at the US-1 Bin revealed a trending non-significant difference between groups, $F(1, 29) = 3.55$, $p < .06$.

Discussion

The data suggested a timed rather than generalized OXE occurred following a modified embedded procedure. The difference that emerges post Bin 7 supported the possibility that the response decrement due to the OXT exhibits temporal properties. If the decrement had generalized across X, it would support the notion that mechanisms driving the excitation to elements seem to operate independent of the mechanisms responsible for coordinating response timing.

Experiment 1 is the first reported experiment to track the CR throughout the duration of a target element, X, following the OXT. However, a serious limitation to the current data is the possibility of generalization decrement as an alternative cause for the response decrement that occurred during X for group OX. Generalization decrement describes how procedural differences in training of two elements hoping to be compared can alone foster a difference in CR at test. Specifically, because group OX experienced compound trials (i.e., AX+), and group CTL experienced individual trials (i.e., X+), their stands a risk that the response decrement occurring during X was not a result of the OXT but a result of responding in OX subjects being disrupted by the change from AX to X in isolation (e.g., generalization decrement). In other words, the excitatory properties associated with AX failed to generalize to X alone. In experiment 2, we addressed this concern with the addition of a novel control group (i.e., XC+).

Experiment 2

Experiment 1 obtained evidence that when A, a 10-s pretrained element was embedded into X, a 40-s pretrained element the decrement during X was confirmed to be temporally specific to the moment that A was embedded during Phase 2.One major limitation to the previous experiment, however, concerned the issue of generalization decrement. Experiment 2 attempted to answer this potential issue by altering training of the CTL group. We were also interested in further exploring the temporal properties of the OXE; therefore, we altered: 1) The arrival of the US during X was placed directly in the middle of the element (i.e., Bins 4 and 5, see Table 1). By placing the US 15 s after the onset of X, we hoped the US might still arrive at a discriminable time point during X but elicit a greater amount of excitation, given findings in delay conditioning that suggest shorter intervals between the element onset and US arrival support stronger responding (Konorski, 1967; Pavlov, 1927). 2) The US arrived simultaneously during A. We chose to alter the nature of A because during phase 2, A and US would co-occur at the precise time period we were targeting, whereas in Experiment 1, the excitation was spread across bins during and following A (e.g., Bins 7, 8, and US-1).

During element training, rats received extensive training with 40-s elements X, B, and 10-s A. During compound conditioning, a stimulus manipulation split the rats into two groups: group OX and group CTL. Rats assigned to group OX received simultaneous trials of AX+, with A and the US co-occurring during Bins 4 and 5. Rats assigned to group CTL received simultaneous trials of XC+. Finally, all rats were tested with 4 probes of X across two days.

Experiment 1 found a maximal difference immediately when the US was expected (i.e., Bin US-1, Figure 2C). It was hypothesized that the stimulus manipulation (OX vs. CTL) in addition to the placement of a US in the middle of X would cause a timed decrement during X

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right at Bin 4, with the co-onset of pretrained A and the US in phase 2. Rats in the OX condition were expected to nose poke less solely during the target period of X compared to rats in the CTL condition that should continue to nose poke similarly across the test of X.

Method

Subjects and Apparatus

Subjects included 32 female and 32 male Long-Evans rats obtained from the TCU breeding colony served as subjects in Experiment 2. Subjects were housed, fed, and maintained as in Experiment 1. The environmental apparatus was identical to that used in Experiment 1. The 3000 Hz high tone and 750 Hz low tone again served as the auditory stimuli X and B, counterbalanced across all subjects. The flashing light (e.g., Experiment 1) and a new steady house light stimulus, located on the wall opposite from the magazine, served as visual stimuli A and C, counterbalanced across all subjects. During the 10-s steady house light stimulus, the enclosure was illuminated by a 28-V, 100-mA shielded incandescent house light mounted on the top of the rear wall (i.e., the wall opposite of the food magazine) of the chamber, 2 cm below the ceiling.

Procedure

Acclimation. The two days of magazine approach acclimation were identical to the days mentioned in experiment 1.

Phase 1a (Element Training). Table 1 shows the schedule of experimental events. Phase 1a occurred across days 3 and 4 of the experiment. Training of the 40 s X and B proceeded in Phase 1a identical to Experiment 1 with the exception that a single US was delivered midway during X (15 s after the onset). There were a total of 16 trials a day with the same inter-trial interval and trial ordering constraints mentioned in Experiment 1.

Phase 1b (Element Training). Phase 1b occurred from days 5-19 of the experiment. Training of the 40 s X and B, and 10 s A proceeded in Phase 1b identical to Experiment 1: 128 total trials for each element, 24 trials a day with the same inter-trial intervals and constraints for trial type ordering.

Phase 2 (Compound Training). On days 20, 21, and 22, rats randomly assigned to the OX condition ($n = 32$) received 16 trials each of XA+, whereas rats randomly assigned to the CTL condition ($n = 16$) received 16 repeated trials of XC+.

Test. On days 23 and 24, rats in group OX and group CTL received 8 trials of XA+ or XC + respectively. All rats then received 4 tests of X.

Results and Discussion

Results

Element Training. Figure 3A shows average time spent in the magazine during elements X, A, B and a 40 sec Pre-CS period (occurring before all 3 trial types). Given that X and A differed in duration, we compared magazine entries during Bins 4 and 5 of 40-s X, and Bins 1 and 2 of 10-s A. Bins 4 and 5 of X were when A would be embedded into X during phase 2, and the two time periods shared identical temporal relationships to the US (i.e., both co-occurred with the US) during element training.

To test for any preexisting relationships between groups prior to the Phase 2 stimulus manipulation, we conducted a 4 (Element: X vs. A vs. B vs. Pre-CS) X 4 (Stimulus: High Tone vs. Low Tone vs. Flashing Light vs. Steady Light) X 2 (Gender: Male vs. Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable. As expected, there was significant main effect of stimulus, $F(3) = 627.4$, $p < .001$, all other main effects and interactions were *n.s.* Within the main effect of stimulus, Post-Hoc analysis (Tukey's HSD) revealed that X

(M = 42.03, SD = 0.98) and A (M = 39.30, SD = 0.36) significantly differed from B (M = 5.88,

SD = .80) and the Pre-CS (M = 5.91, SD = .79), p < .05.

Compound Training. Figure 3B shows average time spent in the magazine during

element X in rats assigned to the OX and CTL condition on the last day of compound training.

Again, we compared magazine entries during Bins 4 and 5 of 40-s X, as the two time periods had

shared identical relationships to the US during element training.
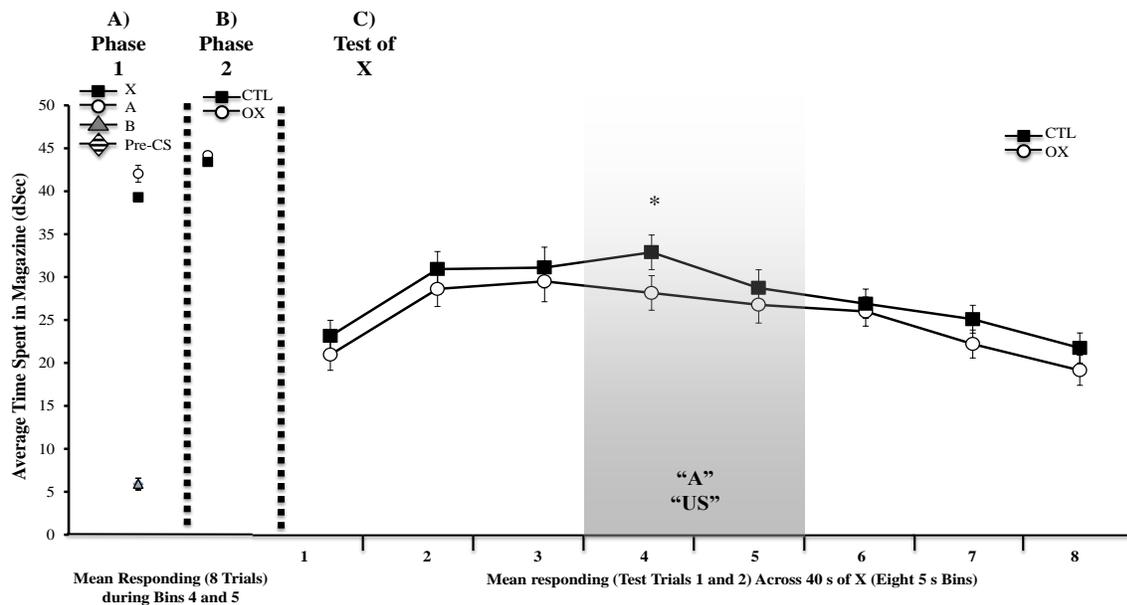
Figure 3

Figure 3 Shows the Results from Experiment 2. The y-axis shows the average amount of time rats spent nose poking the magazine (in dSec).
A: Mean nose pokes during Bins 7 and 8 are plotted for the 40-s X, B, and Pre-CS period during Element training (Day 19).
B: Mean nose pokes during Bins 7 and 8 of X for groups OX and CTL during the final day of compound training (Day 22).
C: Mean nose pokes are charted across time for th3 40-s X and the 10-s US period after X for groups OX and CTL during test (Day 23 and 24). *= p < .06

To test for any preexisting relationships between groups during the Phase 2 stimulus

manipulation, we conducted a 2 (Stimulus: High Tone vs. Low Tone) X 2 (Gender: Male vs.

Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable. As

expected, all main effects or interactions were *n.s.*

Test. A similar analysis was conducted on responding across the 4 test trials, across two days. The analysis revealed neither a significant main effect of group nor an interaction of group and time on responding. Recalling that OX tends to diminish following trials 1 and 2 (e.g., Lattal and Nakajima, 1998), we conducted the analysis on trials 1 and 2 across days.

Figure 3 shows the main results of testing, averaged across two days. The dependent variable was average magazine responding across all the first two test trials of stimulus X for two days (4 trials total). A 2 (Group: OX vs. CTL) X 8 (Time: Bins 1-8) mixed ANOVA revealed a significant main effect of time, $F(7, 434) = 22.9$, $p < .001$, but a non-significant main effect of group. The data, therefore, were again, not indicative of a generalized OXE across the entirety of stimulus X, when it was compounded with a 10-s element, A versus a novel element C.

Based on the results of Experiment 1, we predicted the largest difference would be in Bin 4. Planned comparisons compared group OX and CTL at the target time period when A and the upcoming sucrose delivery were expected; a trending non-significant difference between groups was obtained during Bin 4, $F(1, 62) = 3.97$, $p < .06$.

Perhaps the consequence of using a single US and a 10-s element A (e.g., experiment 1 and 2) was that overexpectation across the entirety of X was not obtained. The only reliable difference emerged at Bin 4, bolstering the notion that the response decrement due to overexpectation exhibited temporal properties.

Discussion

Experiment 2 was able to show that embedding a 10-s pretrained A into a 40-s pretrained X caused a decrement during Bin 4 of X, independent of the possibility that there was generalization decrement to X from Phase 2 to Phase 3 for the OX group. Experiment 2 stood as a novel experiment that tracked the CR throughout the duration of a target element, X after being

compounded with either a pretrained X, or a novel element C. Compared to experiment 1 (e.g., Figure 2C, Bin 7), embedding X and the US at the same time seemed to encourage timing of the decrement precisely when A was expected. Of theoretical importance, a question remained as to whether the arrival of A or the US precisely exerted the most control over when the response decrement occurs during X.

Experiment 3

Experiment 2 obtained evidence that when A, a 10-s pretrained element was embedded into X, a longer, pretrained element that made delayed predictions about a US arriving 15 s later, the decrement seen during X seemed to be greatest 15 sec after the onset of X when compared to a group receiving an embedded, novel stimulus. Experiment 3 served two purposes.

First, we aimed at enhancing responding to X while still being able to enquire about the nature of embedding an asymptotic A into a temporally distinct region of X. To this effect, we altered the Phase 1 timing manipulation from Experiment 2 and trained all rats to expect sucrose during X at an early (i.e., 5 s after onset of X) and late (i.e., 25 s after the onset of X) time period. While adding a second US presentation was expected to increase responding to X, it also allowed an opportunity to assess the unique contribution that embedding A into one time period (e.g., the early period) of X versus a non-embedded US delivery (e.g., the late period) during X.

During element training, rats received extensive training with 40-s elements X, B, and 10-s A. The onset of X preceded two US arrivals, one early within X and one late within X. B was non-reinforced and A was simultaneously paired with sucrose as in Experiment 2. During compound conditioning, the rats were split into two groups: group OX ($n =16$) and group CTL ($n =16$). Rats assigned to group OX received simultaneous trials of AX+, with X embedded only

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during the early period. Rats assigned to group CTL received simultaneous trials of A+. Finally, all rats were tested with 4 probes of X across two days.

Having X make delayed predictions about two USs (i.e., early and late) should enhance responding to X during test, compared to the probes of X made in experiment 1 and 2 when X made a delayed prediction about a single US delivery. In particular, for the experimental condition (OX), we anticipated that subjects would learn the X-A temporal relationship, integrate them to form an X-A-Sucrose temporal map, and over-expect the US during the targeted early period (Bins 2 and 3) of X but not the within-cue comparison period (Bins 6 and 7) of X. For the control condition (CTL), we anticipated that subjects would continue to show timed, asymptotic like behavior during both the target (Bins 2 and 3) and comparison (Bins 6 and 7) periods of X. Rats in the OX condition should nose poke less solely during the early period of X compared to rat in the CTL condition that should continue to nose poke similarly across the probe of X.

Method

Subjects and Apparatus

Subjects included 16 female and 16 male Long-Evans rats obtained from the TCU breeding colony served as subjects in this study. Subjects were housed and maintained as in Experiment 1and 2. The environmental chest and experimental chamber were the same as described in Experiment 1, 2, and 3a. The 3000Hz high tone and 750Hz low tone served as the auditory stimuli X and B, counterbalanced within each subject. The flashing light again served as a visual stimulus, A, for all subjects.

Procedure

Acclimation. The two days of magazine approach acclimation were identical to the days mentioned in experiment 1 and 2.

Phase 1a (Element Training). Table 1 shows the schedule of experimental events. Training of the 40 s elements X and B proceeded identical to experiment 2. Phase 1a occurred on days 3 and 4, a total of 16 trials a day with the same inter-trial intervals and constraints on trial ordering mentioned in experiments 1 and 2.

Phase 1a (Element Training). Training of 40-s elements X, and B and 10-s element A proceeded identical to experiment 2. Phase 1b lasted from Day 5-19, a total of 24 trials a day with the same inter-trial intervals and constraints on trial ordering mentioned in experiments 1 and 2.

Phase 2 (Compound Training). On days 20, 21, and 22, rats assigned to the OX condition ($n = 16$) received 16 trials each of XA + whereas rats assigned to the CTL condition ($n = 16$), received 16 repeated trials of X+.

**Testing.** On days 23 and 24, rats received 8 trials of AX+ or A + respectively, followed by 4 probes of X.

Results and Discussion

Results

Element Training. Figure 4A shows average time spent in the magazine during elements X, A, B and a 40 sec Pre-CS period (occurring before all 3 trial types) on the last day of element training (Day 19). Given that X and A differed in duration, we compared magazine entries during Bins 2 and 3 of 40-s X, and Bins 1 and 2 of 10-s A. Bins 2 and 3 of X and Bins 1 and 2 of A shared identical temporal relationships to the US (i.e., both presented simultaneously with the US) during element training.

To test for any preexisting relationships between groups prior to the Phase 2 stimulus manipulation, we conducted a 4 (Element: X vs. A vs. B vs. Pre-CS) X 2 (Stimulus: High Tone vs. Low Tone) X 2 (Gender: Male vs. Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable. As expected, there was significant main effect of stimulus, $F(3) = 417.8$, $p < .001$, but unexpectedly, a main effect of gender $F(3) = 8.64$, $p < .01$, the stimulus and group assignments were fully counterbalanced by box. Within the main effect of gender, Post-Hoc analysis (Tukey's HSD) revealed that females ($M = 26.86$, $SD = 1.12$) nose poked more than males ($M = 23.75$, $SD = .1.34$) across all 4 stimuli (X,A, B and the Pre-CS period). Within the main effect of stimulus, Post-Hoc analysis (Tukey's HSD) revealed that X ($M = 44.03$, $SD = 0.66$) differed from A ($M = 39.11$, $SD = 0.72$), and both X and A significantly differed from B ($M = 7.62$, $SD = 1.34$) and the Pre-CS ($M = 10.47$, $SD = 1.18$), $p < .05$.

Figure 4
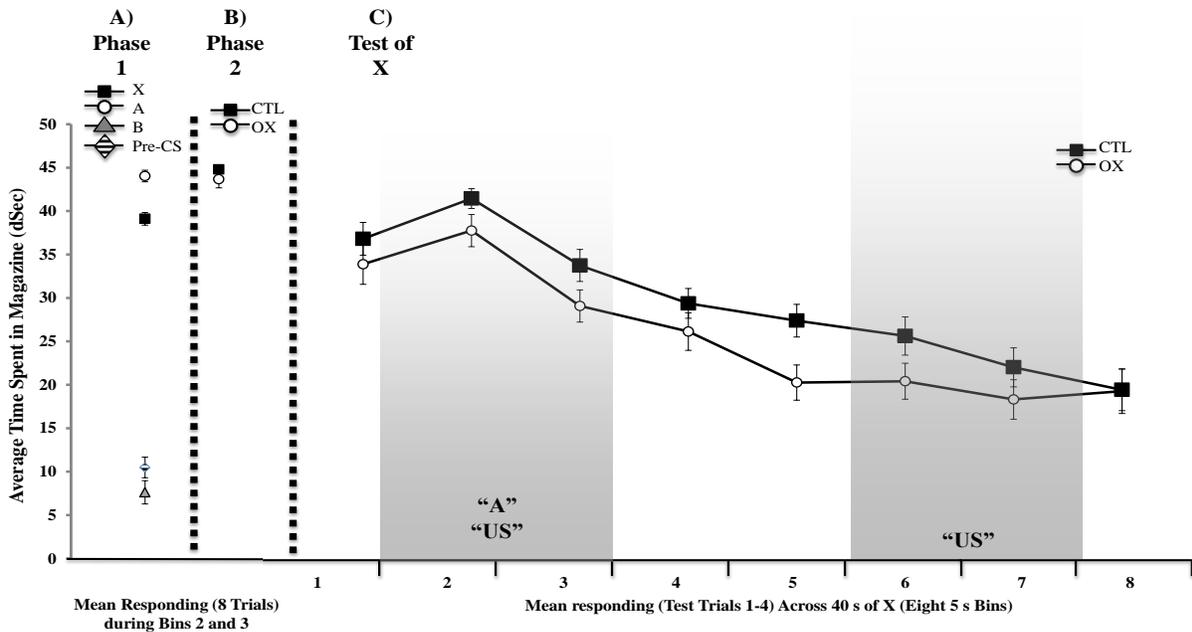
Figure 4 Shows the Results from Experiment 3. The y-axis shows the average amount of time rats spent nose poking the magazine (in dSec).
A: Mean nose pokes during Bins 7 and 8 are plotted for the 40-s X, B, and Pre-CS period during Element training (Day 19).
B: Mean nose pokes during Bins 7 and 8 of X for groups OX and CTL during the final day of compound training (Day 22).
C: Mean nose pokes are charted across time for th3 40-s X and the 10-s US period after X for groups OX and CTL during test (Day 23 and 24).

Compound Training. Figure 4B shows average time spent in the magazine during element X in rats assigned to the OX and CTL condition on the last day of compound training. Again, we compared magazine entries during Bins 2 and 3 of 40-s X, as the two time periods had shared identical relationships to the US during element training.

To test for any preexisting relationships between groups during Phase 2, we conducted a 2 (Stimulus: High Tone vs. Low Tone) X 2 (Gender: Male vs. Female) X 2 (Group: OX vs. CTL) factorial ANOVA with mag time as the outcome variable. As expected, all main effects or interactions were *n.s.*

Test. Figure 4C shows magazine behavior during all 4 test trials of X. A 2 x 8 mixed design ANOVA revealed a significant effect of time, $F(7, 210) = 50.96$, $p < .001$, group and the time X group interaction were *n.s.* Given the results of experiment 1 and 2, we ran planned comparisons at bin 2 and bin 6. The comparison at bin two was non-significant ($p < .09$), and the comparison at Bin 6 was non-significant.

Given the findings of Lattal and Nakajima (1998), we analyzed the first and second trials as in Experiments 1 and 2. A 2 x 8 mixed design ANOVA revealed a significant main effect of group, $F(1, 30) = 4.83$, $p < .05$, time, $F(7, 210) = 50.96$, $p < .001$, and a significant interaction of group x time, $F(7, 210) = 3.28$, $p < .01$. Planned comparisons comparing the target early period were *n.s.,* a planned comparison of the comparison period (during which the US was embedded, but not X), however, revealed that rats in the OX group ($M = 22.40$, $SD = 7.57$) nose poked less than rats in the CTL condition ($M = 28.53$, $SD = 8.05$; $F(1, 30) = 6.82$, $p < .01$).

Discussion

The target time period (i.e., the early period) failed to differ, whereas, responding across the entirety of X differed between the groups during trials 1 and 2 (e.g., Experiment 2). The

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results indicate that the decrement to X targeted via the OXT seemed to be more widespread rather than temporally specific.

The analysis of the first two test trials revealed no difference during the period (Bins 2 and 3) that A had been embedded in Phase 2.One possibility to consider is that there may have been overshadowing of X by A. A, being a shorter stimulus, acquired more strength than X during element training (Figure 4A), and possibly overshadowed X during compound training.

A potential caveat to adding two USs during X in Experiment 3 was that it was unclear what level of US (i.e., λ) X is predicting. The original R-W model wasn't particularly clear about what might happen, however, a model that incorporates real time into associative acquisition (e.g., Sutton and Barto, 1981) would interpret that each US delivery is independent of one other, given its different placements in time. Therefore, as X was only added to the US at one time period, the decrement should have occurred during this time period to the extent that rats discriminated the two deliveries as being independent events. Future studies may wish to embed A during both the early and late periods, to see if the decrement is maximized during X in a timely fashion. Furthermore, one may wish to further distance the two US deliveries in time, to allow each event to have a greater chance of being encoded as an independent associative event in time.

General Discussion

The present studies examined if an embedded procedure modified for the OXT would reveal whether elements over-predicting sucrose at specific time periods might lead to a timed decrement in responding to one of the elements after compound training had occurred. The results, as a whole, indicated that using the embedded procedure to obtain timed response decrements resulted in a more generalized decrement in responding to the target element when

more than one US was used (e.g., Experiment 3), and a weaker, temporally specific decrement in responding when only one US was predicted by X (e.g., Experiments 1 and 2). The central question of what, precisely, animals encode about each pretrained element during the OXT becomes even more tantalizing given the present findings. Much like the timed response peaks described by Roberts (1981), in all three experiments, the decrement to X peaked at the moment the US, more so than the pretrained element, was expected to arrive. The success of finding a timed decrement only in certain scenarios, in contrast to alternative studies that have been able to observe temporally specific (e.g., Leising et al., 2007) and spatially specific (e.g., Sawa, Leising, & Blaisdell, 2005) amplifications in responding transferred across separate phases of training, and sensitive to the placement of the element (e.g., A) more so than the placement of the indicates that perhaps there is something unique about the OXE induced response decrement that separates it from other instances of excitatory and inhibitory responding .

The OXE is the result of two stages, the initial OX event, when two pertained elements over-predict the US followed by the subsequent readjustment of value to each participating element. Although the OXE is the direct result of an adjustment in US expectation, much attention has also been given to the significance of the first event, which is an instance of prediction error. Instances of prediction error are common in studies targeting learning and memory. During trial 1 of extinction, for example, animals learn that a CS no longer predicts a US ($\lambda = 0$), even though a single US ($\lambda = 1.00$) was previously anticipated. The commonality between the OXT and extinction has not been ignored. Rescorla (2006, 2007) was recently able to show that the OXE behaves similarly to extinction by being equally susceptible to memory decay phenomenon such as spontaneous recovery and renewal.

Neurobiological evidence suggests a common activation of GABA$_A$ receptors following instances of negative prediction error (McNally, Pigg, & Weideman, 2004; Garfield & McNally, 2009). Moreover, in the overexpectation of a fearful stimulus, McNally et al. (2004, Experiment 2) were able to show that administration of the opioid receptor antagonist naloxone abolished the OXE. Therefore, opioid activation may play a role in the reaction and abolishment of conditioned responding when animals receive the initial trials of the over-expected elements. In similar appetitive scenarios involving negative prediction error, Norris, Acosta, Ortega, and Papini (2009) observed a reduced tendency for naloxone-injected subjects to abandon lever pressing for food following extinction when compared to saline-injected animals. The role of opioid receptors in reward loss situations at the very least suggests that a frustration or emotional reaction may induce the paradoxical effect. It is not clear whether the supposed manifestation of this frustration-induced rejection of conditioned responding would support a successive unlearning as described by the RW-Model however, generalized changes in emotional reactions would not necessarily equate to timed response decrements. Future neurobiological work will reveal more about what specific brain regions modulate this generalized readjustment of responding. A large majority of neurobiology and the OXE has focused on fear conditioning (e.g., McNally, Pigg, & Weideman, 2004; Garfield & McNally, 2009, however animal indices of fear (e.g., freezing) easily masks more subtle elements of timing that are more dynamic and sensitive in appetitive conditioning.

Adding a timing component to a special instance of cue-competition allowed a glimpse into the possible temporal properties of the OXE. The timed decrements that followed our OX manipulations indicated that the OX induced response decrement to X appeared to be exaggerated based on specific temporal information the subjects encoded in past phases. The

ability for animals to encode time as a factor, and integrate associative information across time further extends predictions derived from the temporal coding hypothesis to new domains of conditioning. Overexpectation, a member of the cue-competition family, continues to be a reliable, yet perplexing phenomenon in Pavlovian conditioning.

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[2]* Ruprecht, C.M., & Leising, K.J. (*in prep*). "Hierarchical control of spatial relations in pigeons and humans. *Psychomonic Bulletin & Review*
[3] Wolf, J.W., Ruprecht, C.M., & Leising, K.J. (*in press*). "Visual Discrimination Learning with an i-Pad equipped apparatus". *Behavioral Processes.*

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ABSTRACT

EXPLORING TEMPORAL PROPERTIES OF THE OVEREXPECTATION EFFECT

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The overexpectation effect (OXE) is the finding that following compound training with two asymptotic elements, X and A, animals respond less during tests of X or A alone compared to animals that did not receive such a compound treatment. During Pavlovian conditioning, the temporal relationship between a conditioned stimulus (CS) and an unconditioned stimulus (US) modulates both the nature (e.g., timing) and magnitude of the conditioned response (Catania, 1970; Roberts 1981). In three experiments, we used a conditioned magazine approach paradigm to evaluate the role of timing in the OXE. We hypothesized that the response decrement seen following overexpectation would manifest as temporally specific drops in magazine approach behavior during tests of X. In Phase 1, rats were given separate trials in which X (40 s in duration) and A (10 s in duration) signaled the arrival of a common US (e.g., sucrose). The delivery the US, moreover, occurred either 30s (Experiment 1), 15 s (Experiment 2) or 5 s (Experiment 3) after the onset of X. In Phase 2, we embedded A into X such that both elements signaled the same sucrose delivery, and consequently, the rats expected twice the sucrose. Tests of X revealed that rats responded less during the time periods in which sucrose was previously overexpected, as compared to rats that received only training trials of X alone in Phase 2 (Experiment 1 and 3) or trials with a novel element, C, embedded in X (Experiment 2). These are the first studies demonstrating a temporally specific OXE.