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Temporal Encoding as a Determinant of Overshadowing

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ABSTRACT

Three conditioned lick suppression experiments explored the effects on overshadowing of the temporal relationships of two conditioned stimuli (CSs) with an unconditioned stimulus (US). Assuming overshadowing is maximal when the potential information conveyed by two competing CSs is equivalent, the temporal coding hypothesis predicts that greater overshadowing will be observed when the CSs share the same temporal relationship with the US. Rats were exposed to an overshadowing CS that had either a forward, simultaneous, or backward relationship to the US. The relationship of the overshadowed CSs to the US was either forward (Experiment 1), simultaneous (Experiment 2), or backward (Experiment 3). The greatest amount of overshadowing was observed when both CSs had the same temporal relationship to the US. The data are discussed within the framework of the temporal coding hypothesis and of alternative models of Pavlovian conditioning based on the informational hypothesis.

ARTICLE

Cue competition refers to impaired behavioral control by a conditioned stimulus (CS) as a result of training that CS in the presence of a second CS that is more salient than (i.e., overshadowing) or is a better predictor of (i.e., blocking) the unconditioned stimulus (US). Regardless of whether one views overshadowing and blocking as arising from changes in processing of the target CS representation (e.g., Mackintosh, 1975; Pearce & Hall, 1980) or of the US representation (e.g., Rescorla & Wagner, 1972), cue competition is commonly anticipated when candidate CSs are presented together and paired with a US such that the CSs are redundant in the predictive information that they convey. Thus, an unexpected event is assumed to be necessary for learning to occur. This informational hypothesis (Cantor, 1981; Egger & Miller, 1963; Rescorla, 1972) in one or another of its variants (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972) has been widely accepted as the root explanation of cue competition (but see R. R. Miller

& Matzel, 1988; R. R. Miller & Schachtman, 1985). It also offers an explanation of why little or no conditioned responding is elicited by a CS that has been simultaneous or backward paired with a US (i.e., CS–US or US → CS, respectively) relative to a CS that has been forward paired with the US (i.e., CS → US). This view is highly congruent with a functional (i.e., evolutionary) framework in which the predictive (i.e., anticipatory) value of the CS is adaptive in permitting the organism to prepare for the impending US (i.e., a biologically significant event). Cues that signal the future occurrence of a biologically significant event allow the organism to prepare for such an event, whereas cues that correspond to the immediate presence or termination of a biologically significant event do not. In summary, the informational hypothesis posits that learning occurs only when a nonredundant predictive relationship occurs and that good temporal contiguity facilitates learning but that the CS–US temporal relationship is not part of what actually gets encoded (i.e., temporal contiguity is a catalyst for learning).

In contrast with the informational hypothesis, the temporal coding hypothesis posits that the temporal relationship between a CS and US not only facilitates learning but also is one of the attributes that is encoded as part of an association. There are four tenets of the temporal coding hypothesis that together explain many phenomena reported in the conditioning literature (see also Gallistel, 1990; Gibbon & Balsam, 1981; and Honig, 1981, for other models that assume temporal relationships are encoded). They are as follows: (a) Contiguity is sufficient for the formation of an association. The degree of spatial and temporal proximity between two events (stimuli or responses) determines the extent to which they are associated. (b) The temporal relationship between the associates is automatically encoded as part of the association and the association is bidirectional. (c) This temporal information plays a critical role in the nature and magnitude of the associatively based response emitted when one of the associates is subsequently presented. (d) The temporal relationships between multiple cues (including those trained at different times) can be integrated (i.e., superpositioning of temporal maps) to determine the nature and magnitude of responding.

There appear to be two situations that encourage memory integration: presentation of cues from unrelated training experiences being presented together and presentation of a cue that activates independent memories of two or more training experiences that share a common element. An example of the first situation is stimulus summation tests, which are often used to assess associative summation or conditioned inhibition. In this situation, each cue presumably has been encoded with its own temporal relationship with the US, and at test both CS–US temporal associations are primed to produce either convergent or competing expectancies of the US. Consistent with this model, conditioned inhibitors have been observed to be most effective when the inhibitory CS representation shares the same temporal relationship with the no-US representation as the excitatory CS shares with the US representation (e.g., Barnett & Miller, 1996).

The second situation in which memory integration is anticipated is exemplified by second-order conditioning, in which the integration takes place either in Phase 2 (during second-order training) or at test. During second-order training (i.e., second-order stimulus [CS2] → first-order stimulus [CS1]), the first-order stimulus, which has previously been paired with the US, is thought to prime the representation (and thus expectation) of the US (e.g., Wagner, 1981), thereby evoking representations of the first-order stimulus and the US (replete with temporal information) that are

active at the time that the second-order stimulus is presented. Evidence for temporal learning in second-order relationships has been observed in many situations (e.g., Barnet, Arnold, & Miller, 1991; Cole, Barnet, & Miller, 1995; Matzel, Held, & Miller, 1988). The present research focuses on this second type of memory integration.

Assuming that cue competition is maximal when the competing cues convey the same information, the temporal coding hypothesis makes different predictions regarding cue competition than does the informational hypothesis. The temporal coding hypothesis posits that the temporal relationship between a CS and a US constitutes one of the attributes encoded in an association. Consequently, it predicts less cue competition between two CSs with different temporal relationships to the US than between two CSs with the same temporal relationship to the US. In contrast, the conventional formulations of the informational hypothesis do not anticipate associations encoding temporal relationships. Therefore, in the informational framework cue competition is based on competing associative strengths alone rather than requiring similarity of temporal relationships to the US.

Several specific contrasting predictions emerge from these views. For example, the temporal coding hypothesis predicts that a CS simultaneously paired with the US will better overshadow or block another simultaneous CS than overshadow or block a CS that is forward paired with the US. (Special techniques are necessary to assess simultaneous associations; see Matzel et al., 1988.) However, the assumption of the informational hypothesis that forward associations are more readily formed than simultaneous associations leads to the same prediction, provided simultaneous pairings yield sufficient behavioral control to detect overshadowing. Other predictions of the temporal coding hypothesis are free of this ambiguity. For example, a forward CS would be expected to better compete with another forward CS than with a CS that is simultaneous with the US. This prediction is contrary to conventional formulations of the informational hypothesis, which regard simultaneous associations as being merely weaker versions of the same basic associations that result from forward pairings, which are therefore presumably easier to block or overshadow.

Barnet, Grahame, and Miller (1993) examined the role of temporal encoding in blocking by using the second-order conditioning technique of Barnet et al. (1991), which facilitates assessment of simultaneous and backward associations. They found that a CS forward paired with the US in Phase 1 blocked responding to a novel forward-paired CS in Phase 2 more completely than did a CS simultaneously paired with the US in Phase 1. Similarly, a CS that was simultaneously paired with the US in Phase 1 blocked responding to a simultaneous-paired CS in Phase 2 more completely than did a CS forward paired with the US in Phase 1. Thus, blocking was found to be greatest when the blocking and blocked CSs shared the same temporal relationship with the US.

In the present research, we performed a series of overshadowing experiments to further test the predictions of the temporal coding hypothesis and to ascertain if the influence of the CS–US interval on cue competition is unique to blocking. To minimize confounding of stimulus elements (i.e., of the overshadowing and overshadowed CSs) during training as well as within-compound associations between the competing CSs, one CS was a flashing light of moderate intensity, and the other CS was a moderately weak, complex tone. We had already established that, in our

situation, such a flashing light overshadows the tone when both cues are forward paired with the US and are coterminous (R. R. Miller, Esposito, & Grahame, 1992). Because simultaneous-paired (i.e., CS–US) and backward-paired (i.e., US → CS) first-order CSs do not elicit robust conditioned lick suppression, second-order conditioning (with a click train as a forward second-order CS [i.e., CS2 → CS1]) was used to assess the associative status of all potentially overshadowed (i.e., target) CSs, including, for the sake of equivalence between experiments, forward-paired target CSs. However, suppression elicited by the first-order target CSs themselves was also examined following assessment of the second-order CS.

Experiment 1

Experiment 1 tested the prediction made by the temporal coding hypothesis that a low-salience CS (moderate intensity tone) that is forward paired with the US (footshock) will be maximally overshadowed by a high-salience CS (bright flashing light) that is also forward paired with the US relative to otherwise equivalent flashing-light CSs that are either simultaneous or backward paired with the US. Excitatory conditioning was assessed by using a second-order stimulus (click train) to equate all procedures, except the temporal relationship of the overshadowing CS and the US, in this and the following two experiments (in which the target CS was either simultaneous or backward paired with the US). Poor conditioned responding is often elicited by such first-order CSs, but otherwise latent CS–US associations can be revealed through the use of a second-order CS. Thus, for consistency between experiments, conditioned responding to second-order CSs was the primary dependent variable in all of the following experiments.

Method

Animals

Thirty male (weight range = 225–370 g) and 30 female (weight range = 185–285 g) experimentally naive Sprague-Dawley-descended rats (*Rattus norvegicus*), which were bred in our colony from Holtzman stock (Madison, WI), served in Experiment 1. Rats were randomly assigned to one of five groups ($ns = 12$), which were counterbalanced for sex. Rats were individually housed in wire-mesh cages in a vivarium maintained on a 16:8-hr light–dark cycle. Experimental manipulations occurred approximately midway through the light portion of the cycle. A progressive water deprivation schedule was imposed over the week prior to the beginning of the experiment, until water availability was limited to 30 min per day at the beginning of the study. All rats were handled three times per week for 30 s from weaning until the beginning of the study.

Apparatus

Twelve identical clear Plexiglas chambers, each measuring 12.0 × 24.0 × 20.0 cm (l × w × h), were individually housed in 30.0 × 25.0 × 32.0-cm (l × w × h) environmental isolation chests. The floor of each chamber was constructed of 0.5-cm diameter rods, 2.0 cm center-to-center, connected by NE-2 neon bulbs that allowed a 0.5-mA constant-current footshock to be delivered

by means of a high voltage AC circuit in series with a 1.0-M Ω resistor. The interior of each environmental isolation chest was dimly illuminated by a #1820 incandescent houselight mounted on the ceiling of the experimental chamber. Each chamber was equipped with a water-filled lick tube (opening = 0.3 cm in diameter) that extended about 1.0 cm from the rear of a cylindrical niche, 4.5 cm in diameter. The lick tube was left–right centered on one wall and centered 4.0 cm above the grid floor. An infrared photobeam was projected horizontally across the niche 0.5 cm in front of the lick tube. To drink from the tube, rats had to insert their heads into the niche, thereby breaking the photobeam. Thus, we could monitor exactly when the rats were accessing the lick tube. A 45- Ω speaker mounted on the interior wall of each environmental chamber could deliver a complex high-frequency tone (3000 and 3200 Hz) 6 dB(C) above background. A second 45- Ω speaker mounted on the ceiling of each experimental chamber was used to deliver a click stimulus (clicks [6/s] produced by a homemade click generator) 6 dB(C) above background. Ventilation fans in each enclosure provided a constant 76-dB(C) background noise. A 75-W (nominal at 120 VAC but driven at 90 VAC) incandescent light, which could flash at 0.25 s on/0.25 s off, was mounted at the center of the back wall of each environmental chest. Given the close proximity of this light to rats in the experimental chambers (approximately 30.0 cm), the light was a highly salient stimulus. The houselight was turned off when the light stimulus was being flashed. All stimuli, including the footshock, were 5 s in duration.

Procedure

The critical aspects of the training procedure are summarized in Table 1. All training and testing occurred in the same chamber for any given rat.

Table 1
Design of Experiment 1

Group	Phase 1: Overshadowing	Phase 2: SOC	Test 1	Test 2
F	LT \rightarrow +	C \rightarrow T	C	T
B	T \rightarrow + \rightarrow L	C \rightarrow T	C	T
S	T \rightarrow +L	C \rightarrow T	C	T
OSC	T \rightarrow +, L	C \rightarrow T	C	T
GDC	T \rightarrow +	C \rightarrow TL	C	TL

Note. SOC = second-order conditioning; F = forward paired; B = backward paired; S = simultaneous paired; OSC = overshadowing control; GDC = generalization decrement control; L = flashing light (the overshadowing stimulus); T = tone (the first-order overshadowed stimulus); + = footshock (the US); C = clicks (the second-order stimulus). Adjacent symbols (e.g., LT) were coterminous. LT \rightarrow + indicates that the coterminous light and tone were immediately followed by the US. A comma separates events that were explicitly unpaired.

Design of Experiment 1

Acclimation

On Days 1 and 2, all rats were acclimated to the experimental chambers with the lick tubes in place. During each 60-min session, rats received one nonreinforced presentation each of the tone (T) and flashing light (L) separated by 20 min. This was intended to eliminate through habituation any unconditioned responding to these stimuli.

Overshadowing training

On Days 3–8, rats received four reinforced (i.e., footshock) trials per day for a total of 24 reinforced trials. During each 60-min session, these trials were pseudorandomly distributed with a mean intertrial interval of 12 min. Specifically, the forward-paired group (Group F) received the tone and flashing light coterminously followed immediately by the footshock (+; LT → +); the backward-paired group (Group B) received the tone followed immediately by footshock, which in turn was followed immediately by the light (T → + → L); the simultaneous-paired group (Group S) received the tone followed immediately by the footshock and light, which had a common onset and termination (T → +L); the overshadowing control and generalization decrement control groups (Groups OSC and GDC, respectively) received the tone followed immediately by the footshock (T → +). Group OSC also received four nonreinforced exposures to the light each day, which were pseudorandomly distributed but never less than 4 min before or after the tone. Thus, in Experiment 1, the potentially overshadowed stimulus (tone) was always forward paired with the US, whereas the temporal relationship of the light differed between groups. Lick tubes were not present during these sessions.

Second-order conditioning

On Day 9, rats in Groups F, B, S, and OSC received four presentations of the clicks (C) followed immediately by the tone (C → T), whereas Group GDC received four presentations of the clicks followed immediately by the tone–light simultaneous compound (C → TL). These trials were pseudorandomly distributed over the 60-min session with a 12-min mean intertrial interval. Lick tubes were not present.

Reacclimation

On Days 10 and 11, rats were allowed to access the lick tubes during each daily 60-min session to reestablish baseline levels of drinking. During these sessions, there were no nominal stimulus presentations.

Testing

The test of central interest occurred on Day 12. To assess overshadowing of the first-order CS, behavioral control by the second-order CS was measured because in Experiments 2 and 3 the first-order CS lacked a predictive relationship to the US and consequently was not expected to control behavior even in the absence of overshadowing. Rats in each group were tested for conditioned lick suppression to the click stimulus (the second-order CS) by presenting the stimulus on completion of 5 cumulative s of drinking (as measured by the total amount of time the infrared photobeam was disrupted). Thus, all rats were drinking at the time of CS onset. Times to complete this initial 5 cumulative s of licking and times to complete an additional 5

cumulative s of licking in the presence of the CS were recorded. For the purpose of equating treatment across rats so as not to affect performance on the subsequent test, the click stimulus remained on for a consistent duration of 10 min regardless of the rat's behavior.

On Day 13, all rats were tested for conditioned suppression to the tone (the first-order putative overshadowed stimulus), except for the rats in Group GDC, which were tested with a simultaneous compound of the tone–light. Testing was conducted and times were recorded as in the Day 12 test.

In all of the experiments reported, suppression data were transformed to log (base 10) scores to facilitate the use of parametric statistics, which are much more sensitive than nonparametric statistics. Raw times have a strong positive skew that is largely eliminated by a log transformation, thereby making the within-group distribution more normal. (In neither this nor in the following experiments was the ordinal relationship of group means altered by the data transformation.) An alpha level of .05 (two-tailed) was adopted for all tests of statistical significance. Data from 5 rats (1 from each group) were lost because of an equipment failure. Two other rats (1 from Group S and 1 from Group OSC) died before the completion of the experiment. Additionally, following the convention of our laboratory, rats that took over 60 s to complete their first 5 cumulative s of licking (i.e., prior to CS onset) were eliminated from the study on the grounds of their showing unusually great fear of the test context. In preliminary research, we have found that such animals tend to be outliers in their groups. Two rats, 1 from Group B and 1 from Group S, were eliminated from the study on the basis of this criterion.

Results and Discussion

The central observation from Experiment 1 was that overshadowing, as assessed through the responding to the second-order stimulus (clicks), was observed in Group F. In this group alone, the overshadowing and the overshadowed cues shared the same forward temporal relationship with the US. Overshadowing was not observed in Groups B and S, which did not differ from Groups OSC or GDC. These outcomes are illustrated in Figure 1.

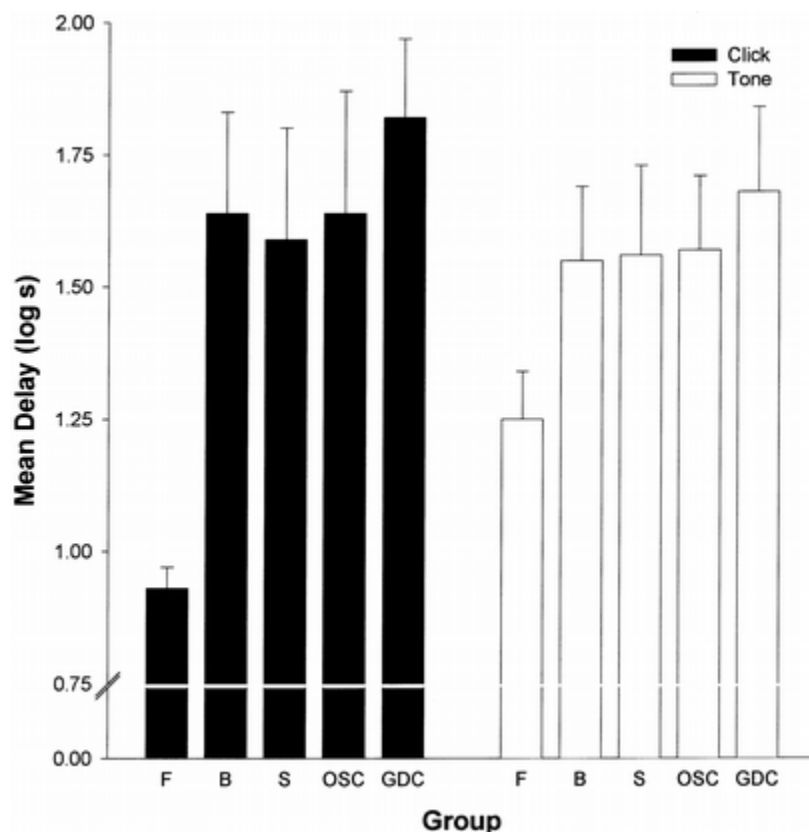


Figure 1. Experiment 1. Mean times (log s) to lick for 5 cumulative s in the presence of the second-order conditioned stimulus (clicks) and the first-order overshadowed stimulus (tone). Error bars represent standard errors of means. First- and second-order stimuli were not counterbalanced. Furthermore, the second-order stimulus (moderate clicks) was more salient than the first-order stimulus (soft tone). This accounts for less suppression that was observed in response to the tone relative to the clicks. F = forward; B = backward; S = simultaneous; OSC = overshadowing control; GDC = generalization decrement control

Second-Order CS Data

A one-way analysis of variance (ANOVA) conducted on times to complete the first 5 cumulative s of licking (i.e., prior to CS onset) on Day 12 found no significant group differences in baseline drinking behavior on either test day in this experiment or on any test day in the subsequently described experiments, $F < 1.0$. A one-way ANOVA conducted on suppression scores during the second-order CS (clicks) revealed a treatment effect, $F(4, 46) = 3.95$. Planned comparisons were conducted by using the overall error term from the latter ANOVA. Group F suppressed less to the clicks than did Group OSC, $F(1, 46) = 8.21$. However, Groups B and S did not differ from Group OSC, both F s < 1.0 . Thus, as assessed through the responding to the second-order CS, overshadowing only occurred when both first-order CSs (the tone and light) were presented simultaneously with each other, which in this case was with a common forward temporal relationship with the US.

First-Order CS Data

A one-way ANOVA conducted on the suppression scores during the first-order CS (tone) failed to reveal a treatment effect, $F(4, 46) = 1.75$. Planned comparisons failed to reveal differences in suppression to the tone in Groups B, S, or GDC relative to Group OSC, all $F_s(1, 46) < 1.0$. There was a nonsignificant tendency for Group F to suppress less to the tone than did Group OSC, $F(1, 46) = 3.25, p = .08$, indicating a tendency toward overshadowing as assessed by responding in the presence of the first-order stimulus. The absence of significant overshadowing as seen in the first-order CS was unexpected given the presence of overshadowing as seen in the second-order CS. However, a direct comparison of first- and second-order CSs would be inappropriate because it would confound the physical stimuli serving as the first- and second-order CSs as well as confound the order of testing (the second-order CS was always tested first, and in unpublished past research we have commonly found that group differences are reduced by repeated testing even across different test stimuli).

Stimulus generalization decrement provides an alternative to cue competition mechanisms as an explanation of most overshadowing studies. Specifically, if the overshadowing CS and overshadowed CS are configured during training, it is reasonable to expect responding to the overshadowed CS to be attenuated (relative to a control group trained with the overshadowed CS alone) in direct proportion to the dissimilarity between the configured compound stimulus and the overshadowed CS alone. The case for a generalization decrement interpretation of overshadowing has perhaps been made most compellingly by [Pearce \(1987\)](#). In the framework of Pearce's configural hypothesis, the effects of training with X and testing with AX should produce an amount of generalization decrement equal to that of training with AX and testing with X (i.e., overshadowing). The symmetry between these generalization decrement effects is built into Pearce's equation for the similarity between training and test stimuli, which is the basis of generalization decrement in Pearce's model.

$${}_A S_{A'} = \frac{P_{com}}{P_{\Sigma A}} \cdot \frac{P_{com}}{P_{\Sigma A'}} \quad (1)$$

In this equation, ${}_A S_{A'}$ is the similarity between A and A' and is equal to the similarity between A' and A. (P_{com} is determined by the perceived intensity of the common stimulus elements on all trials, and $P_{\Sigma A}$ and $P_{\Sigma A'}$ are determined by the perceived intensities of the A and A' stimuli on A and A'-alone trials, respectively.) Thus, if overshadowing in our experiment had been a result of generalization decrement, there should have been an equal deficit in responding in Group GDC, which received training with X and testing with AX. Notably, the strong tendency toward overshadowing seen in Group F, relative to Group OSC, was not observed in Group GDC. Moreover, Figure 1 illustrates that Group GDC suppressed as much as Group OSC, thereby indicating an absence of any appreciable amount of generalization decrement in responding. However, a generalization decrement interpretation of this and all overshadowing studies can be salvaged through the following argument. Perhaps pairing the tone alone with the shock increases attention to the tone. When the light is then added to the tone, rats may now pay little

attention to the light, and any generalization decrement when testing with the tone alone will be modest. However, our control group did include a control for generalization decrement as defined by Pearce's formal model of generalization decrement. There are other forms of generalization decrement that could explain our data, but none have to date been proposed as part of a formal model. Consequently, the overshadowing observed in Group F may reasonably be attributed to the more salient A stimulus (light) outcompeting the X stimulus (tone) in acquiring effective behavioral control on the basis of pairings with the US. Thus, on the basis of the second-order CS data, we successfully demonstrated that, as predicted by the temporal coding hypothesis, overshadowing is greatest when the overshadowing and the overshadowed stimuli share the same forward temporal relationship with the US.

The outcome of Experiment 1 is not surprising given that the overshadowing stimulus (light) probably acquired stronger behavioral control in Group F than in Groups S or B; this greater behavioral control should have translated into stronger overshadowing according to almost all contemporary models of learning. Much more interesting are the predictions of the temporal coding hypothesis regarding cue competition when the potentially overshadowed CS is simultaneously or backward paired with the US. According to models of learning that are based on the informational hypothesis, an overshadowing CS that is forward paired with the US should still be the most effective overshadowing stimulus relative to simultaneous- or backward-paired overshadowing stimuli. In contrast, the temporal coding hypothesis predicts that the most effective overshadowing CS will be the overshadowing cue that has the same temporal relationship to the US as the potentially overshadowed stimulus has. However, assessment of the associative status of simultaneous or backward CSs is difficult. In these cases, responding to a first-order CS is often weak or nonexistent. The informational hypothesis attributes this to a failure to acquire a CS–US association because simultaneous and backward CSs are not positioned to provide predictive information. In contrast, the temporal coding hypothesis states that associations between all contiguous events are learned. Thus, when two cues are presented in compound, simultaneous or backward with the US, there is the potential for one cue to overshadow the other cue in controlling conditioned responding. The following experiments address this prediction that overshadowing can be demonstrated with both simultaneous (Experiment 2) and backward (Experiment 3) conditioning.

Experiment 2

Experiment 2 assessed overshadowing of a low-salience CS (tone), simultaneously paired with a US (footshock), by a high-salience CS (flashing light) that was either forward, simultaneous, or backward paired with the US. On the basis of the temporal coding hypothesis, greatest overshadowing of the tone was expected in the simultaneous condition, in which both cues shared the same temporal relationship with the US. Excitatory conditioning was assessed by using a second-order stimulus (clicks) to circumvent the problem of poor conditioned responding to first-order CSs that were simultaneously paired with the US.

Method

Animals and Apparatus

The animals were 30 male (weight range = 330–200 g) and 30 female (weight range = 240–185 g), naive Sprague-Dawley-descended rats (*Rattus norvegicus*), which were bred in our colony from Holtzman stock (Madison, WI). Rats were randomly assigned to one of five groups ($ns = 12$), which were counterbalanced for sex. The rats were housed and maintained as in Experiment 1. The apparatus and stimuli were identical to those used in Experiment 1.

Procedure

On Days 1 and 2, all rats received acclimation to the experimental chambers as in Experiment 1. On Days 3–8, rats received overshadowing training as in Experiment 1, except that the overshadowed stimulus (tone) was simultaneously paired (coterminous) with the US (see Table 2). On Days 9–13, rats received second-order conditioning, reacclimation, and testing as in Experiment 1. Data from 3 rats were lost because of an equipment failure (1 from Group F, 2 from Group B). No rats took more than 60 s to complete their first 5 cumulative s of licking (i.e., prior to CS onset).

Table 2
Design of Experiment 2

Group	Phase 1: Overshadowing	Phase 2: SOC	Test 1	Test 2
F	L → T+	C → T	C	T
B	T+ → L	C → T	C	T
S	TL+	C → T	C	T
OSC	T+, L	C → T	C	T
GDC	T+	C → TL	C	TL

Note. SOC = second-order conditioning; F = forward paired; B = backward paired; S = simultaneous paired; OSC = overshadowing control; GDC = generalization decrement control; L = flashing light (the overshadowing stimulus); T = tone (the first-order overshadowed stimulus); + = footshock (the US); C = clicks (the second-order stimulus). Adjacent symbols (e.g., LT) were coterminous. A comma separates events that were explicitly unpaired.

Design of Experiment 2

Results and Discussion

The central observation from Experiment 2 was that overshadowing, as assessed through the responding to the second-order stimulus (click train), was observed in Group S, in which the overshadowing and the overshadowed cues shared the same simultaneous temporal relationship

with the US. Overshadowing was not observed in Groups F and B, which did not differ from Groups OSC or GDC. These outcomes are illustrated in Figure 2.

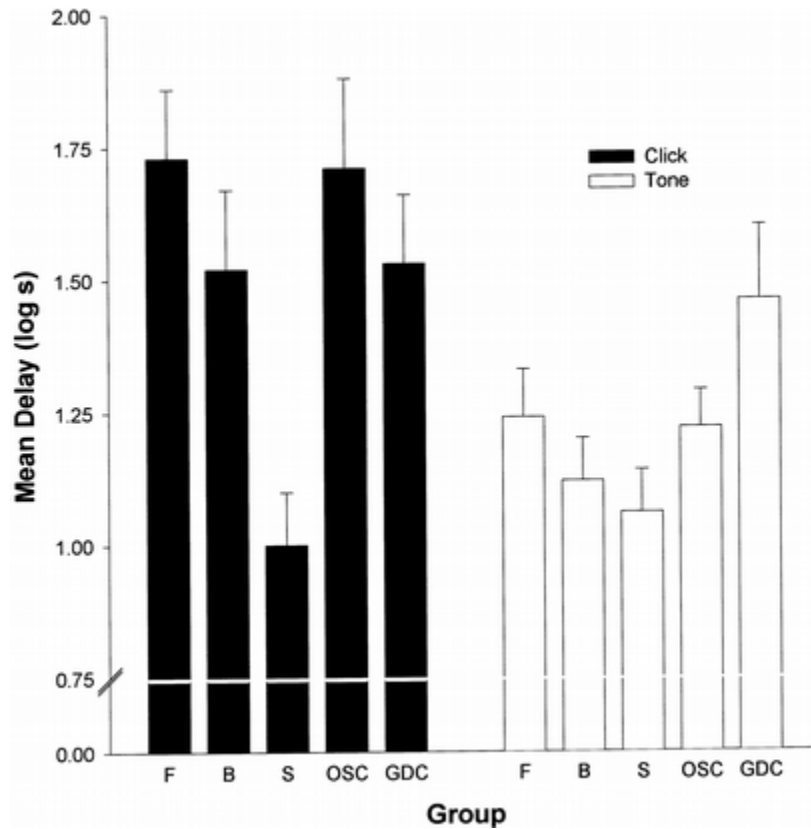


Figure 2. Experiment 2. Mean times (log s) to lick for 5 cumulative s in the presence of the second-order conditioned stimulus (clicks) and the first-order overshadowed stimulus (tone). Error bars represent standard errors of means. First- and second-order stimuli were not counterbalanced. Furthermore, the second-order stimulus (moderate clicks) was more salient than the first-order stimulus (soft tone). This accounts for less suppression that was observed in response to the tone relative to the clicks. F = forward; B = backward; S = simultaneous; OSC = overshadowing control; GDC = generalization decrement control

Second-Order CS Data

A one-way ANOVA conducted on suppression scores from the second-order CS (clicks) test revealed a treatment effect, $F(4, 52) = 4.31$. Planned comparisons were conducted by using the overall error term. Group S suppressed less to the clicks than did Group OSC, $F(1, 52) = 13.32$, whereas Groups F and B did not differ from Group OSC, all $F_s < 1.0$. Thus, overshadowing was observed only when the presentation of the first-order stimuli (tone and light) was simultaneous, which, in this experiment, was also simultaneous with the US. There was no difference in suppression observed between Group OSC, which was trained and tested with the tone alone, and Group GDC, which was trained with the tone alone but tested in the presence of both the

tone and light, $F(1, 52) = 7.43$, indicating that the low responding observed in Group S is not attributable to generalization decrement.

First-Order CS Data

A one-way ANOVA conducted on the suppression scores from the first-order CS (tone) test revealed a treatment effect that just reached significance, $F(4, 52) = 2.61$. Planned comparisons failed to reveal differences in suppression to the tone in Groups F, B, and S relative to Group OSC, all $F_s(1, 52) < 3.40$. This failure to observe overshadowing in responding to the first-order stimulus presumably arises from the weak responding seen in Group OSC, which is not surprising because the first-order CS was simultaneously paired with the US, and simultaneous-paired CSs are well-known to acquire little behavioral control (unless a small number of trials, e.g., 1, are administered; e.g., Heth, 1976; see also Burkhardt & Ayres, 1978; and Mahoney & Ayres, 1976).

Experiment 3

Experiment 3 assessed overshadowing of a low-salience CS (tone) that was backward paired with a US (footshock) by a high-salience CS (flashing light) that was either forward, simultaneous, or backward paired with the US. The temporal coding hypothesis predicts that the greatest overshadowing of the tone should occur in the backward condition, in which both CSs shared the same backward temporal relationship with the US. Excitatory conditioning was assessed by using a second-order stimulus (clicks) because of the expected weak conditioned responding to first-order CSs that are backward paired with the US. Group GDC 1 received the same treatment as did Group GDC in Experiments 1 and 2 (i.e., tone–shock pairings in Phase 1, clicks–tone/light pairings in Phase 2, and testing on the tone–light compound). However, a second control group (GDC 2) was added to assess the possibility that, in this and in the prior two studies, responding to the second-order CS (clicks) by Group GDC was due not to second-order conditioning but to the click–light pairings with the light serving as a US. Group GDC 2 received footshock followed by the tone in Phase 1 and clicks followed by the flashing light (but no tone) in Phase 2 (see Table 3). Subsequently, these rats were tested on the clicks on the first test day and on the tone on the second test day. We did not expect the flashing light to be able to support conditioned responding on its own; thus, we anticipated little conditioned responding to the second-order stimulus (clicks).

Table 3
Design of Experiment 3

Group	Phase 1: Overshadowing	Phase 2: SOC	Test 1	Test 2
F	L → + → T	C → T	C	T
B	+ → TL	C → T	C	T
S	L+ → T	C → T	C	T
OSC	+ → T, L	C → T	C	T
GDC 1	+ → T	C → TL	C	TL
GDC 2	+ → T	C → L	C	T

Note. SOC = second-order conditioning; F = forward paired; B = backward paired; S = simultaneous paired; OSC = overshadowing control; GDC = generalization decrement control; L = flashing light (the overshadowing stimulus); T = tone (the first-order overshadowed stimulus); + = footshock (the US); C = clicks (the second-order stimulus). Adjacent symbols (e.g., LT) were coterminous. + → LT indicates that the US was immediately followed by the coterminous light and tone.

Design of Experiment 3

Method

Animals and Apparatus

The animals were 36 male (weight range = 180–300 g) and 36 female (weight range = 175–215 g) naive Sprague-Dawley-descended rats (*Rattus norvegicus*), which were bred in our colony from Holtzman stock (Madison, WI). Rats were randomly assigned to one of six groups ($n_s = 12$), which were counterbalanced for sex. The rats were housed and maintained as in Experiments 1 and 2. The apparatus and stimuli were identical to those used in Experiments 1 and 2.

Procedure

On Days 1 and 2, all rats received acclimation to the experimental chambers as in Experiments 1 and 2. On Days 3–8, rats received overshadowing training as in Experiments 1 and 2, except that for all rats the overshadowed stimulus (tone) was backward paired with the US (see Table 3). Additionally, for Groups GDC 1 and 2, the 5-s footshock was terminated simultaneously with the onset of the tone on each trial. Thus, all groups received the tone immediately after the footshock. On Days 9–13, all rats in Groups F, B, S, OSC, and GDC 1 received second-order conditioning, reacclimation, and testing as in Experiments 1 and 2. Group GDC 2 received second-order conditioning consisting of the clicks terminating simultaneously with the onset of the light. This group was then tested for suppression to the clicks on the first test day and to the tone on the second test day. Two rats, 1 each from Groups GDC 1 and GDC 2, were eliminated from the study prior to testing because of illness. Additionally, 1 rat from Group B and 2 rats

from Group S were eliminated from the study for taking over 60 s to complete their first 5 cumulative s of licking (i.e., prior to CS onset).

Results and Discussion

The central observation from Experiment 3 was that overshadowing, as assessed through responding to the second-order stimulus (clicks), was observed in Group B, in which the overshadowing and the overshadowed cues shared the same backward temporal relationship with the US. Overshadowing was not observed in Groups F and S, which did not differ from Groups OSC or GDC 1. These outcomes are illustrated in Figure 3.

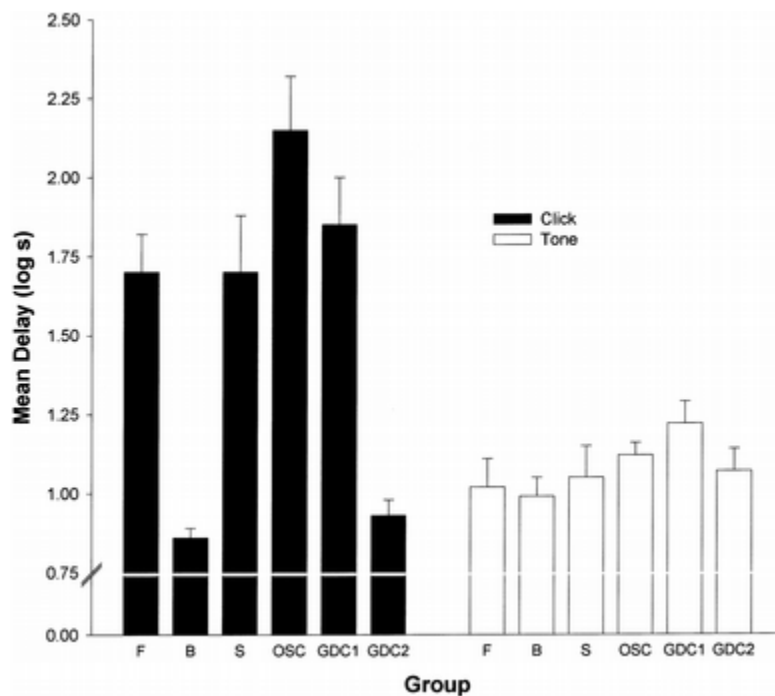


Figure 3. Experiment 3. Mean times (log s) to lick for 5 cumulative s in the presence of the second-order conditioned stimulus (clicks) and the first-order overshadowed stimulus (tone). Error bars represent standard errors of means. First- and second-order stimuli were not counterbalanced. Furthermore, the second-order stimulus (moderate clicks) was more salient than the first-order stimulus (soft tone). This accounts for less suppression that was observed in response to the tone relative to the clicks. F = forward; B = backward; S = simultaneous; OSC = overshadowing control; GDC 1 = generalization decrement control 1; GDC 2 = generalization decrement control 2

Second-Order CS Data

A one-way ANOVA conducted on suppression scores from the second-order CS (clicks) tests revealed a treatment effect, $F(5, 61) = 15.73$. Planned comparisons were conducted by using the overall error term. Group B suppressed drinking less to the clicks than did Group OSC, $F(1, 61)$

= 49.22. Additionally, Groups F and S suppressed less to the clicks than did Group OSC, $F_s(1, 61) = 6.34$ and 5.69 , respectively, illustrating a small serial overshadowing effect in which the light either preceding or co-occurring with the US appears to have weakly overshadowed the tone, which followed the US. Examination of Figure 3 indicates that the magnitude of this serial overshadowing effect in Groups F and S was much less than that of the overshadowing effect seen in Group B, in which the overshadowing CS and overshadowed CS had the same temporal relationship with the US. Thus, a strong overshadowing effect was observed only when the first-order stimuli (tone and light) were presented simultaneously, which in this case had a backward temporal relationship to the US. Conditioned responding in Group GDC 1 was greater than that in Group B, $F(1, 61) = 27.67$, indicating that the low responding observed in Group B is not attributable to generalization decrement. Group GDC 2, which received training with the tone in Phase 1 and second-order training that consisted of tone–light pairings in Phase 2, failed to suppress to the light, $F(1, 61) = 44.14$, indicating that rats were not responding unconditionally to the light or conditionally to the clicks on the basis of the light possibly serving as a US. Thus, the responding to the clicks in Group GDC 1 here and in the GDC groups of Experiments 1 and 2 stands as evidence that overshadowing in this series of experiments was due to cue competition rather than to stimulus generalization decrement.

First-Order CS Data

A one-way ANOVA conducted on the suppression scores during the first-order CS (tone) failed to reveal a treatment effect, $F(5, 61) = 1.18$. This demonstrates a failure to observe overshadowing in responding to the first-order stimulus; it also reveals no appreciable generalization decrement in responding on the basis of differences in the cues present during training relative to the cues present during testing. This outcome was expected because of the fact that the tone was backward paired with the US in all groups, and backward-paired CSs are known to exhibit little behavioral control (Heth, 1976). The second-order CS data indicate that overshadowing occurred but was masked by a floor effect arising from the lack of predictive value of the first-order association with respect to the US.

General Discussion

The present series of experiments investigated the prediction made by the temporal coding hypothesis that overshadowing (a form of cue competition) will be greatest when the overshadowing and overshadowed CSs share the same temporal relationship with the US. The central outcomes of these experiments support this prediction. Overshadowing of a CS with a forward (Experiment 1), simultaneous (Experiment 2), or backward (Experiment 3) relationship with the US was greatest when the overshadowing CS also had a forward, simultaneous, or backward relationship with the US, respectively (see Table 4). Notably, the temporal coding hypothesis does not offer an explanation of cue competition. For this, one must turn to models of acquisition (e.g., Rescorla & Wagner, 1972) or to models of conditioned responding (e.g., Miller & Matzel, 1988). However, both of these approaches to cue competition anticipate maximal overshadowing when the two competing cues have the same associative attributes. The temporal coding hypothesis asserts that temporal relationships are an inevitable attribute of any

association. Thus, less overshadowing should be expected when the overshadowing and overshadowed CSs have different temporal relationships with the US. The present data are entirely consistent with this expectation.

Table 4
Mean Delay (log s) to Second-Order Conditioned Stimuli (CSs) in Experiments 1, 2, and 3

Overshadowing CS-US relationship	Overshadowed CS-US relationship		
	Forward (Experiment 1)	Simultaneous (Experiment 2)	Backward (Experiment 3)
Forward	0.92	1.73	1.70
Simultaneous	1.59	1.00	1.70
Backward	1.70	1.52	0.86
Control	1.64	1.71	2.15

Note. US = unconditioned stimulus.

Mean Delay (log s) to Second-Order Conditioned Stimuli (CSs) in Experiments 1, 2, and 3

These results extend to overshadowing the finding of Barnet et al. (1993) that cue competition between CSs was greatest when the CSs shared the same temporal relationship with the US in both phases of the blocking treatment that they used (also see Schreurs & Westbrook, 1982; but see Kohler & Ayres, 1979; Maleske & Frey, 1979). A potential problem with our interpretation that cue competition will be maximal when the competing CS has the same temporal relationship with the US as does the target CS is that, in our experiments, the CSs with the same temporal relationship with the US were presented simultaneously as opposed to sequentially. Thus, one CS might perceptually mask the other CS rather than engage in postperceptual associative competition. This alternative interpretation is also applicable to Barnet et al.'s (1993) blocking study. However, in blocking, as opposed to overshadowing, the use of two phases of treatment allows differentiation of these two interpretations. Barnet et al. (1993) explicitly examined the possibility that the important factor in determining a CS's ability to block another stimulus was not that both stimuli share the same temporal relationship with the US but that both stimuli are presented simultaneously. They included groups in which the blocking stimulus was either forward or simultaneously paired with the US in Phase 1 and was subsequently simultaneously or forward paired with the US, respectively, in compound with the putative blocked CS, which was also forward or simultaneous paired with the US in Phase 2. If simultaneity of the blocking CS with the blocked CS is what produces the greatest blocking, then we would expect to see strong blocking of the putative blocked CS. However, if a common relationship of the blocking CS to the US (established in Phase 1) and of the blocked CS to the US (established in Phase 2) were critical, little blocking would be expected in these two cases. In fact, strong responding to the putative blocked CSs was observed, indicating that simultaneity of blocking and blocked CSs alone was insufficient in producing blocking. Rather, the critical factor was the similarity of the established temporal relationship between the blocking cue and the US (Phase 1) with the presented temporal relationship between the blocked cue and the US (Phase 2). In light of the data of Barnet et al. (1993), it seems implausible that stimulus simultaneity rather than a common CS-US temporal relationship was the critical factor in the present research.

Prior research has also demonstrated the validity of predictions made by the temporal coding hypothesis concerning timing of the presence (e.g., Barnet et al., 1991; Cole et al., 1995; Matzel et al., 1988) and absence of the US (e.g., conditioned inhibition; Barnet & Miller, 1996; Denniston, Cole, & Miller, 1996). In combination with Barnet et al.'s (1993) data, the present results extend the scope of the temporal coding hypothesis's predictions to include multiple forms of cue competition effects.

The four tenets of the temporal coding hypothesis—(a) association by contiguity, (b) automatic encoding of temporal attributes, (c) response generation based on temporal attributes, and (d) integration of temporal maps based on different training experiences—can explain all of these phenomena. However, the informational hypothesis requires a cue to be both anticipatory and nonredundant for it to enter into an association with the US. The present data indicate that stimuli paired with a US in a nonanticipatory fashion (i.e., Experiments 2 and 3) can compete for associative status as effectively as stimuli paired with a US in an anticipatory manner. This finding is contrary to the central premise of the informational hypothesis that to enter into associations, a potential CS must have an anticipatory relationship to the US. Other research has demonstrated that redundant cues can enter into associations, but such associations are ordinarily latent unless special steps are taken to reveal them (e.g., recovery from overshadowing through reminder treatments [Kaspro, Cacheiro, Balaz, & Miller, 1982]; extinction of the overshadowing stimulus [Kaufman Bolles, 1982; Matzel, Schachtman, & Miller, 1985]; and spontaneous recovery [Kraemer, Lariviere & Spear, 1988; J. S. Miller, McKinzie, Kraebel, & Spear, 1993]). Thus, both tenets of the informational hypothesis are challenged. That is, associative acquisition appears to require neither an anticipatory relationship between associates nor a relationship that is not redundant with that between an accompanying second signal and the outcome. Possibly, the informational hypothesis could be salvaged by positing that different parts of the US each have their own reinforcement values. For example, with our procedure, the onset of the 5-s shock may have been best associated with stimuli that preceded the shock, the middle of the shock may have been best associated with stimuli that accompanied the shock, and the end of the shock may have been a good reinforcer for stimuli that followed the shock. Thus, the best way to overshadow learning about the tone and the middle of the shock would be to present it simultaneously with a more salient stimulus such as the light. A similar argument could be made when the tone is presented after the shock. However, this view is a distinct departure from the original informational hypothesis because in the backward case the tone is surely not a predictor of anything having to do with the shock.

Clearly, both second-order conditioning (and sensory preconditioning) effects and posttraining recovery manipulations (e.g., extinction, reminder treatments, and lengthened retention intervals) have yielded data detrimental to each of these two assumptions of the informational hypothesis as they pertain to the acquisition of associations. However, the hypothesis may still be a viable explanation for the expression of acquired information. These phenomena support the temporal coding hypothesis as a guiding principle for the acquisition of associations. This rule is, simply, that associations (which will always encode temporal relationships) will be formed between events that are presented to the animal with good contiguity during the training trial. Thus, cues that are redundant in the information they provide regarding the US (e.g., overshadowed or blocked cues) will nevertheless form an association with the US. Whether this association will be readily expressed in the animal's behavior appears to depend largely on the saliency and prior

history (validity) of other cues that were present during training with the target CS. However, this rule for the expression of associations with respect to cue competition is basic to the comparator hypothesis (R. R. Miller & Matzel, 1988; see also R. R. Miller & Schachtman, 1985). The temporal coding hypothesis per se provides both a simple rule for acquisition (i.e., contiguity) and one of the several rules that jointly apply to associative expression (i.e., an anticipatory relationship to the US). Thus, the temporal coding hypothesis is able to explain why second-order conditioning is effective in assessing simultaneous and backward first-order associations, as well as why CSs with different temporal relationships to a common US compete less than do CSs with a common temporal relationship to the US. However, the comparator hypothesis (or some other rule for the expression of associations) is required to explain cue competition. Therefore, the temporal coding hypothesis and the comparator hypothesis complement each other in providing a complete explanation of the present data.

The attractiveness of the informational hypothesis is its functional value, that is, its ability to explain why organisms make preparatory responses in anticipation of biologically significant events. However, the informational hypothesis explains the anticipatory nature of acquired behavior through processes that modulate acquisition (e.g., Rescorla & Wagner, 1972). An alternative to this approach, provided by the temporal coding hypothesis, is to explain the anticipatory nature of acquired behavior through processes that act at the level of retrieval or response generation. Moreover, perhaps it is actually adaptive to form associations between events on the basis of contiguity alone. Conceivably, situations often arise in which an organism encounters a biologically significant event simultaneously with or immediately followed by an initially neutral (first-order) stimulus event. Then, at some point in the future, the organism may encounter a second neutral stimulus followed immediately by the first-order stimulus. Thus, the second-order stimulus may well accrue the potential to act indirectly as a signal for the impending biologically significant event. The organism would be well served to prepare for the biologically significant event when it later encounters the second-order stimulus. However, the organism should make a preparatory (adaptive) response to the second stimulus only if (a) a forward association was formed between the second-order stimulus and the first-order stimulus, and (b) an association was formed between the first-order stimulus and the biologically significant event. According to the temporal coding hypothesis, only one of these two associations need be predictive for the second-order stimulus to have a predictive relationship to the biologically significant event when the two memories are integrated (either at the time of second-order training or at test). (In the present research, it was the second-order CS that consistently provided an anticipatory relationship to the US.)

In contrast, the informational hypothesis predicts the formation of an association between the second-order stimulus and the first-order stimulus because of the predictive relationship of one cue for the other, but it does not predict the formation of an association between a simultaneous or backward first-order stimulus and a US because of the absence of a predictive relationship between that cue and the US. Thus, organisms that are not able to encode anticipatory and nonanticipatory temporal relationships may have a lower fitness relative to organisms that are sensitive to both types of temporal relationships. The latter organisms should be able to make adaptive responses on the basis of integrated information from first- and second-order associations that jointly allow second-order CSs to convey information about biologically significant events. Thus, a logically compelling argument can be made for the functional value of

learning by contiguity, which is a simple mechanism for the formation of associations that has historical roots dating back to Aristotle's time, and which was revitalized by Locke, Hume, J. S. Mill, and other British empiricists. The temporal coding hypothesis is a modern-day version of this position, which makes unique predictions regarding the acquisition, expression, and interactive effects of multiple cues (CSs) that become associated with a biologically significant event.

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