The S-R Information Stream: Where's the Filter?

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Pavlovian conditioning procedures, in which events such as tastes, lights, and sounds become predictors of food, water, and shocks, have been used for studying the role of the information filter in the selection of conditioned responses. Different models posit the filter at different locations in the S-R stream, but most models suggest either a pre-encoding filter, in which much information is discarded at an early stage of processing, or a post-encoding filter, in which the information is stored but not subsequently expressed in behavior. A selective review of the literature on cue-competition effects reveals a plethora of phenomena that support a post-encoding, but not a pre-encoding filter in Pavlovian processes.

FOR A RAT PUP, LIFE can be a wonderful thing. Warm litter mates and a mother to snuggle up to, tongue baths, and the seemingly endless supply of milk. However, as the pup matures, it is quickly beset by the many horrors of the real world, such as ravenous predators, insidious traps, and competition with conspecifics over food, mates, and shelter. If the rat is not careful, it may quickly end up at the wrong side of lunch.

A creature such as a rat benefits from attending to the enormous amount of complex information streaming into its senses from its environment. However, not all stimulation from the environment is relevant to the creature's goals or needs. The animal must learn which environmental cues signal important consequences and which others are irrelevant. Furthermore, many events that coincide need not be causally connected. As scientists, we are sensitive to the notion that correlation need not infer causation. Likewise, it is adaptive for a creature to respond selectively to environmental input. One way animals such as rats and humans appear to be selective is to respond to the most likely candidate predictors or causes of important outcomes (such as the occurrence of biologically significant events), and withhold responding to less likely ones. This leads the behavioral scientist to an important question: How does an animal respond selectively to its environment? More specifically, what are the psychological processes responsible for selectivity? If we take the metaphor of a stream of information leading from stimulus input to response output, these processes may be thought to act as filters on this stream, selectively allowing some information to pass through and influence responding while holding back other information. There are many points along the Stimulus-Response (S-R) stream where such a filter may act. Stimulus processing goes through a series of loosely sequential stages, from sensation and perception (including attentional processes), to the integration and synthesis of input from multiple perceptual channels, to information storage, and finally to retrieval and response generation. Different psychological models posit the filter to act at different

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locations in the S-R stream. However, a majority of models can be sorted into two major types, *pre-encoding* and *post-encoding*. In the framework of pre-encoding models, almost all incoming information is filtered out at an early stage of processing, before it is stored in the animal's nervous system. In the framework of post-encoding models, however, quite a bit more of the incoming information is assumed to be stored in the nervous system. The stored information then competes for expression in behavior at a later processing stage, such as through retrieval, comparator, and decision processes.

In this article, I will attempt to build the case for selective processes acting late in the information stream leading from stimulus input to response output. That is, rather than acting at the time of acquisition (i.e., a pre-encoding filter), I will argue that, at least in the relatively simple situations that have been investigated in the psychologist's laboratory, response selection occurs at the time of performance (i.e., a post-encoding filter). This suggestion goes against the grain of much of contemporary learning theory which traditionally supports pre-encoding response-selection filters (e.g., the model of Rescorla & Wagner, 1972, and others derived from it). However, a growing body of evidence in support of a post-encoding filter challenges the prevailing view. In the interests of pursuing a more tractable analysis, I will restrict my focus to studies involving elementary associative processes, in particular Pavlovian conditioning. Pavlovian conditioning procedures typically involve pairing conditional stimuli (CSs) such as tastes, odors, sounds, and lights with unconditional stimuli (USs) such as food, water, and electric shocks with a forward relationship, thereby establishing a predictive relationship between CS and US. However, Pavlovian conditioning has also been posited to play an important role in other types of associative learning, such as perceptual learning and human causal judgments.

Most relevant to our interests are situations involving multiple sources of potentially redundant information, such as when multiple cues predict a single outcome (e.g., when multiple CSs are paired with the same US). A typical outcome in situations involving redundant predictive cues is that they compete for control over responding in anticipation of the outcome, a phenomenon known as cue competition. Cue-competition effects include (among others) the overshadowing effect, in which a more salient cue (A) successfully competes with a less salient cue (X; i.e., AX→US; Pavlov, 1927); blocking, in which a cue (A) that has previously acquired predictive value attenuates conditioning to a new cue (X; i.e., A→US, followed by AX→US; Kamin, 1969); the effect of relative stimulus validity, in which a more valid cue (A) attenuates responding to a less valid cue (X; e.g., AX+/BX-; Wagner, Logan Haberlandt, & Price, 1968; Wasserman, 1974); and the overexpectation effect, in which two cues (A and X) that had each been separately established as a predictor of an outcome lose some of their behavioral control through subsequent compound pairings with the outcome (i.e., A→US/X→US, followed by AX→US; Kremer, 1978; Levitan, 1975; Rescorla, 1975; Wagner, 1971).[1] Cue-competition procedures of Pavlovian conditioning are ideally suited to studying the nature of response selection processes. They have provided the battleground for testing alternative theories of conditioning that emphasize acquisition processes vs. performance processes. Most contemporary acquisition models of Pavlovian associations posit an early filter exclusively. For example, models put forth by Mackintosh (1975) and Pearce and Hall (1980) filter information at the perceptual or attentional stage. These models posit changes in the associability of a stimulus during conditioning that then affect acquisition of other stimulus-outcome relationships. Similarly, in the model of Rescorla and Wagner (1972), the information filter acts at the integrator (of information) stage in which expected outcomes lose their reinforcing properties and thus fail to enter into associations with contiguous events. Performance accounts of certain Pavlovian processes such as conditioned inhibition and cue-competition effects, however, emphasize a late filter exclusively. The comparator hypothesis (Miller & Matzel, 1988; Miller & Schachtman, 1985) and Scalar Expectancy Theory (SET; Gibbon & Balsam, 1981) are two well-known performance-based theories of Pavlovian processes.[2] While there is probably some validity to both early and late selection frameworks, for most Pavlovian paradigms, the conditions are so simple and impoverished that they probably do not come close to overtaxing an animal's capacity to process such information at an early stage. Yet, the fact that filters winnow information at later stages of processing, even under these austere conditions, suggests the importance of these late-stage filters on the selection of appropriate responses.

The Empirical Evidence for a Late-Stage Filter

Retrospective Revaluation Effects

Cue-competition effects have served as a hotbed for experiments testing acquisition and performance theories. Many cue-competition effects (such as those listed above) were initially taken as evidence supporting contemporary acquisition theories, such as the Rescorla-Wagner (1972) model. In fact, the Rescorla-Wagner model was inspired in part by Kamin's (1969) suggestion that a CS only develops an association with the US if the US was a surprising (i.e., not expected) event. If the target CS was paired with the US in the presence of another cue that had already been established as a predictor of that US, then the US on these trials is not surprising and acquisition of a target CS-US association is blocked. However, in the last two decades, a number of demonstrations have shown that cue-competition effects are not permanent. Rather, certain posttraining manipulations that do not involve any new exposure to the target CS have been shown to reverse cue-competition effects, increasing the response to the target CS and thereby uncovering the latent association between the target CS and the US. Posttraining manipulations that have been successful in reversing cue-competition effects, collectively referred to as retrospective revaluation effects, include spontaneous recovery produced by long delays between conditioning and testing, posttraining reminder treatments involving pretest exposure to an aspect of the original conditioning situation (e.g., the US, the context, and sometimes the CS itself), and extinction of the competing cue. These manipulations have been effective in attenuating the overshadowing effect (Kasprow, Cacheiro, Balaz, & Miller, 1982; Kaufman & Bolles, 1981; Kraemer, Lariviere, & Spear, 1988; Matzel, Schachtman, & Miller, 1985; Matzel, Shuster, & Miller, 1987), the blocking effect (Balaz, Gutsin, Cacheiro, & Miller, 1982; Blaisdell, Gunther, & Miller, 1999; Schachtman, Gee, Kasprow, & Miller, 1983), the US-preexposure effect (Barnet, Grahame, & Miller, 1993; Matzel, Brown, & Miller, 1987), and the overexpectation effect (Blaisdell, Denniston, & Miller, 2001).

Although retrospective revaluation effects have championed performance theories over acquisition theories of cue-competition effects, a new breed of acquisition theories have recently been developed that can account for many of the empirical demonstrations of retrospective revaluation. Van Hamme and Wasserman (1994) recently proposed a revision of the Rescorla-Wagner (1972) model, and Dickinson and Burke (1996) recently proposed a revision of Wagner's (1981) SOP model. Both of these revisions account for extinction-mediated recovery from cue-competition effects as being due to new learning to the target CS in its absence. I will not elaborate on how these models account for retro-

TABLE 1
Design Summary for Blaisdell, Bristol, Gunther, and Miller (1998) Experiment 1.

Group	LI	OV	Test	Associative Structure
LI+OV	X-	AX+	X	LI+OV: A→Con→X
OV	Y-	AX+	X	OV: A→X
LI	X-	X+	X	LI: Con→X
Acq	Y-	X+	X	

Note: LI = latent inhibition, OV = overshadowing, Acq. = acquisition control, Con = context. + and – indicate reinforcement and nonreinforcement, respectively. Strong and weak effective associative strength is represented by black and grey print, respectively. From "Overshadowing and Latent Inhibition Counteract Each Other: Support for the Comparator Hypothesis." by A. P. Blaisdell, A. S. Bristol, L. M. Gunther, & R. R. Miller, 1998, *Journal of Experimental Psychology: Animal Behavior Processes, 24*, p. 338. Copyright 1998 by the American Psychological Association. Adapted with permission.

spective revaluation effects; nevertheless, they have provided an interesting challenge to the performance models, which had previously been unique in their account of reversals of cue-competition effects.[3]

Higher-Order Comparator Effects

Partly in response to the revised acquisition models, Miller and his students have recently presented an extended comparator hypothesis that makes differential (and currently unique) predictions from the revised acquisition models (Blaisdell, Bristol, Gunther, & Miller, 1998; Denniston, Savastano, & Miller, 2001). In the framework of the comparator hypothesis, the response to a target CS is determined by a comparison of the US representation directly activated by the target CS (determined by its associative strength) and the US representation indirectly activated by other, comparator, stimuli that were present during treatment involving the target CS (determined by the CS-Comparator and Comparator-US associations). The stronger the indirect activation of the US (e.g., by a strongly excitatory comparator stimulus), the weaker the excitatory or the stronger the inhibitory response observed to the target CS. The weaker the indirect activation of the US (e.g., by a weakly excitatory comparator stimulus), the stronger the excitatory or the weaker the inhibitory response observed to the target CS. According to the *extended* comparator hypothesis, the modulatory role (on the target CS) of each comparator stimulus is affected by its own, second-order, comparator stimuli. Thus, the effectiveness of a (first-order) comparator stimulus to modulate the response to the target CS can be reduced by a strong second-order comparator stimulus. Likewise, the effectiveness of a weak first-order comparator stimulus may be increased by a weak second-order comparator stimulus. Blaisdell et al. (1998) provided the first empirical support for the extended comparator hypothesis (see left panel of Table 1) using a conditioned lick-suppression task with rats in which audiovisual CSs were paired with a footshock US. They compared the conditioned suppression to target CS X after undergoing latent inhibition treatment (i.e., X– followed by X+ treatment; Group LI), overshadowing treatment in which a more salient stimulus (A) was present during conditioning (i.e., AX+; Group OV), or both (i.e., X– followed by

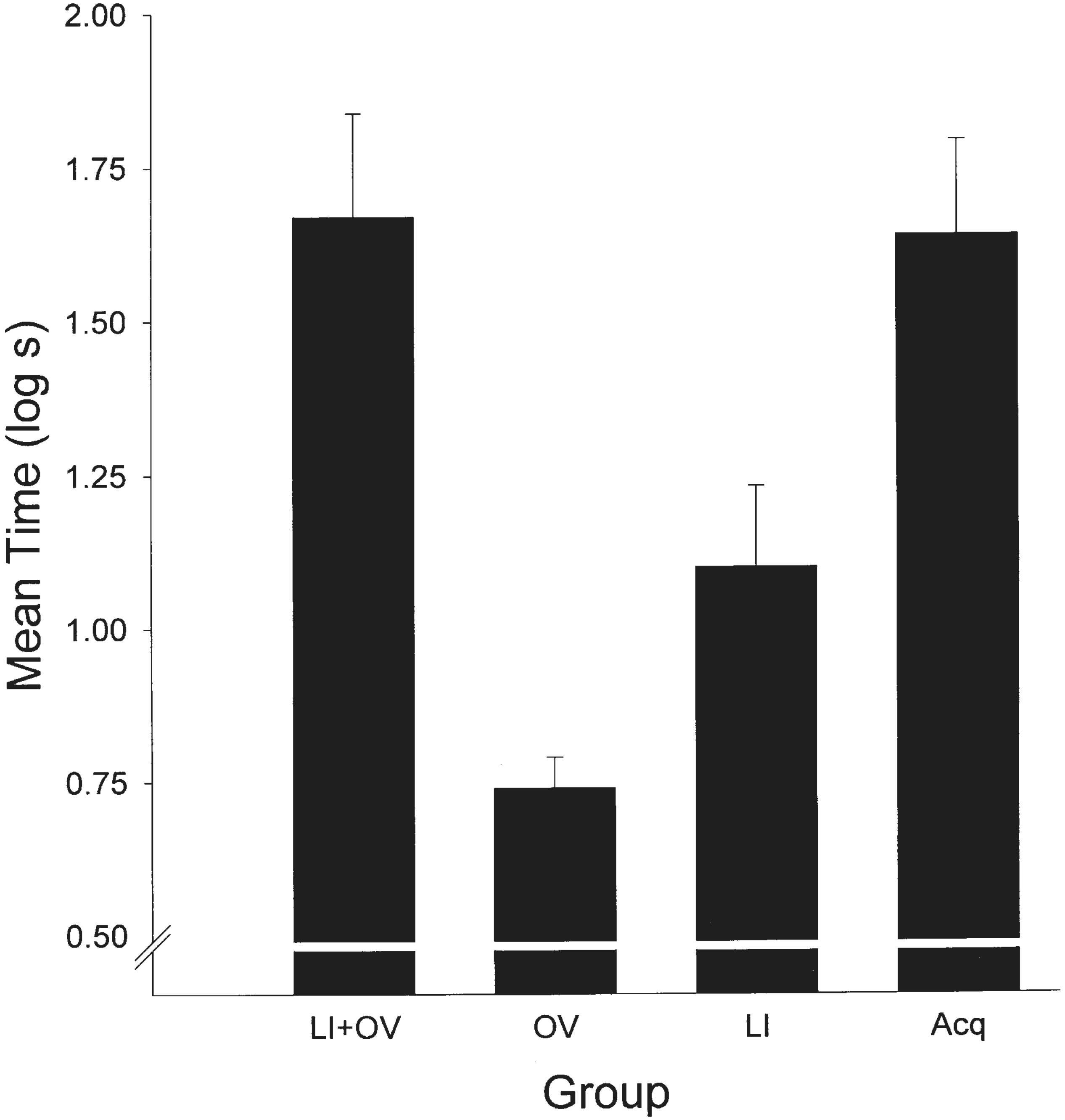


FIG. 1. Results of Blaisdell et al.'s (1998) Experiment 1. See Table 1 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Brackets represent standard errors of the mean. From "Overshadowing and Latent Inhibition Counteract Each Other: Support for the Comparator Hypothesis." by A. P. Blaisdell, A. S. Bristol, L. M. Gunther, & R. R. Miller, 1998, *Journal of Experimental Psychology: Animal Behavior Processes, 24*, p. 339. Copyright 1998 by the American Psychological Association. Adapted with permission.

AX+; Group LI+OV). Although the response to CS X in Group LI and in Group OV was predictably low (relative to Group Acq, an acquisition control group), the response to CS X in Group LI+OV was high and equivalent to the response observed in Group Acq (see Figure 1). The original comparator hypothesis attributes latent inhibition to the stronger X-Context association in Group LI than in Group Acq. Likewise, the original comparator hypothesis attributes overshadowing to CS A being a more effective comparator stimulus

TABLE 2
Design Summary for Blaisdell, Bristol, Gunther, and Miller (1998) Experiment 3.

Group	LI	OV	Inflation	Associative Structure
LI+OV(N)	X-	AX+	None	N: A→Con→X
LI+OV(A)	X-	AX+	A+	A: A→Con→X
LI+OV(Con)	X-	AX+	+	Con: A→Con→X

Note: LI = latent inhibition, OV = overshadowing. (N), (A), and (Con) = No inflation, inflation of A, or inflation of the Context, respectively. + and – indicate reinforcement and nonreinforcement, respectively. Strong and weak effective associative strength is represented by black and grey print, respectively. From "Overshadowing and Latent Inhibition Counteract Each Other: Support for the Comparator Hypothesis." by A. P. Blaisdell, A. S. Bristol, L. M. Gunther, & R. R. Miller, 1998, *Journal of Experimental Psychology: Animal Behavior Processes, 24*, p. 338. Copyright 1998 by the American Psychological Association. Adapted with permission.

for CS X in Group OV than the Context is in Group Acq. However, by taking into account the effects of second-order comparator stimuli, the extended comparator hypothesis also predicts the strong conditioned response observed to CS X in Group LI+OV. The extended comparator hypothesis does this through the following associative structure: A→Context→X, where CS A and the context are second-order and first-order comparator stimuli for CS X, respectively. Let's compare this hypothetical associative structure with that of the latent inhibition group and the overshadowing group to observe why responding is strong in Group LI+OV (right panel of Table 1). Compared to Group LI, where the Context effectively attenuates the conditioned response to CS X, second-order comparator stimulus A in Group LI+OV attenuates the modulatory role of the Context on target CS X. This alleviates latent inhibition. In Group OV, CS A serves as the first-order comparator stimulus for CS X. However, preexposure to CS X in Group LI establishes the Context as the primary first-order comparator stimulus, preventing CS A from overshadowing CS X. Support for this explanation comes from Experiment 3 of Blaisdell et al. (1998), in which either CS A or the Context was inflated (through further pairings with the US) following latent inhibition and overshadowing treatments (see left panel of Table 2). If the Context, rather than CS A, served as the first-order comparator stimulus for CS X in Group LI+OV, then inflating the associative status of the Context (Group LI+OV(Con)), but not of CS A (Group LI+OV(A)), should have attenuated conditioned responding to CS X. This was exactly what Blaisdell et al. (1998) found (Figure 2).

It is interesting to point out that, while conditioned responding to the target CS is inversely related to the associative status of its first-order comparator stimulus, responding to the target CS is *directly* related to the associative status of the second-order comparator stimulus. Denniston, Savastano, Blaisdell, & Miller (2003) provided further evidence of this relationship between the target CS and the second-order comparator stimulus by assessing the ability of an overshadowed CS X to subsequently block conditioned responding to a novel CS Y (i.e., AX+ followed by XY+). Table 3 gives the design of their experiment along with the hypothetical associative structure of Groups OV-A and OV-Cxt. Focusing on the two overshadowing groups (Groups OV-A and OV-Ctx), overshadowing treatment in Phase 1 establishes CS A as the comparator for CS X, and blocking treatment in Phase 2 establishes CS X as the comparator for CS Y. Thus, CS A serves as a second-

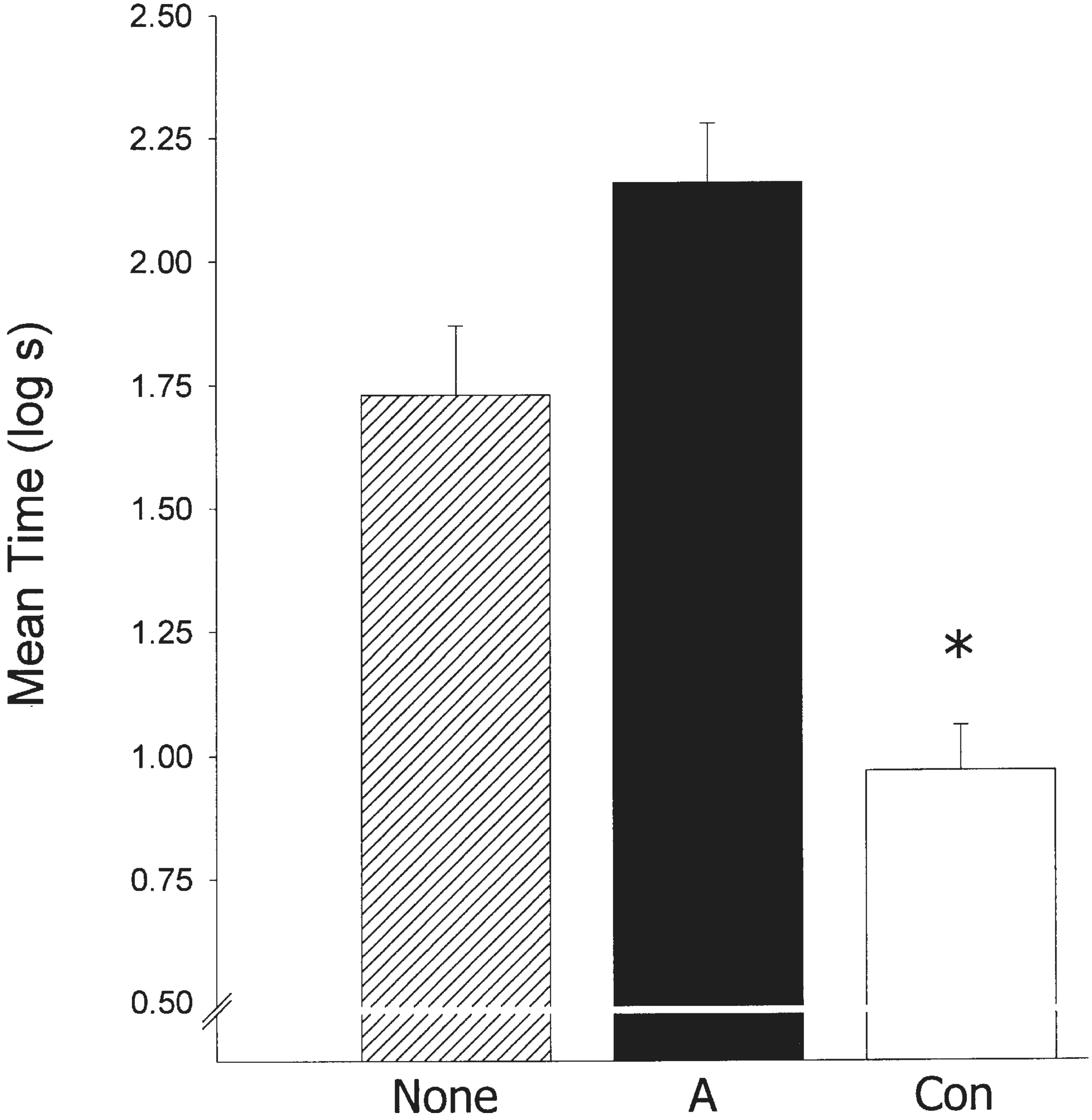


FIG. 2. Results of Blaisdell et al.'s (1998) Experiment 2. See Table 2 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Brackets represent standard errors of the mean. From "Overshadowing and Latent Inhibition Counteract Each Other: Support for the Comparator Hypothesis." by A. P. Blaisdell, A. S. Bristol, L. M. Gunther, & R. R. Miller, 1998, *Journal of Experimental Psychology: Animal Behavior Processes, 24*, p. 344. Copyright 1998 by the American Psychological Association. Adapted with permission.

order comparator for CS Y. If responding to CS Y bears a direct relationship to the associative status of CS A, then extinction of CS A (Group OV-A), but not of the Context (Group OV-Cxt), should reduce the response observed to CS Y at test (compare hypothetical associative structures of Groups OV-A and OV-Cxt in Table 3). The results of Experiment 2 of Denniston et al. support this prediction (Figure 3).

Finally, a recent experiment by De Houwer and Beckers (2002) supports the above

TABLE 3

Design Summary for Denniston, Savastano, Blaisdell, and Miller (2003) Experiment 2.

Group	Ph. 1	Ph. 2	Ph. 3	Test
OV-A	AX+	XY+	A-	Y
OV-Cxt	AX+	XY+	Context	Y
Con-A	X+	XY+	A-	Y
Con-Cxt	X+	XY+	Context	Y

Associative Structure

OV-A: A→X→Y
OV-Ctx: A→X→Y

Note: OV = overshadowing. Con = control, A = extinction of A, Cxt = extinction of Context. + and – indicate reinforcement and nonreinforcement, respectively. Strong and weak effective associative strength is represented by black and grey print, respectively. From "Cue Competition as a Retrieval Deficit." by J. D. Denniston, H. I. Savastano, A. P. Blaisdell, & R. R. Miller, 2003, *Learning and Motivation.* Copyright 2003 by the Academic Press.

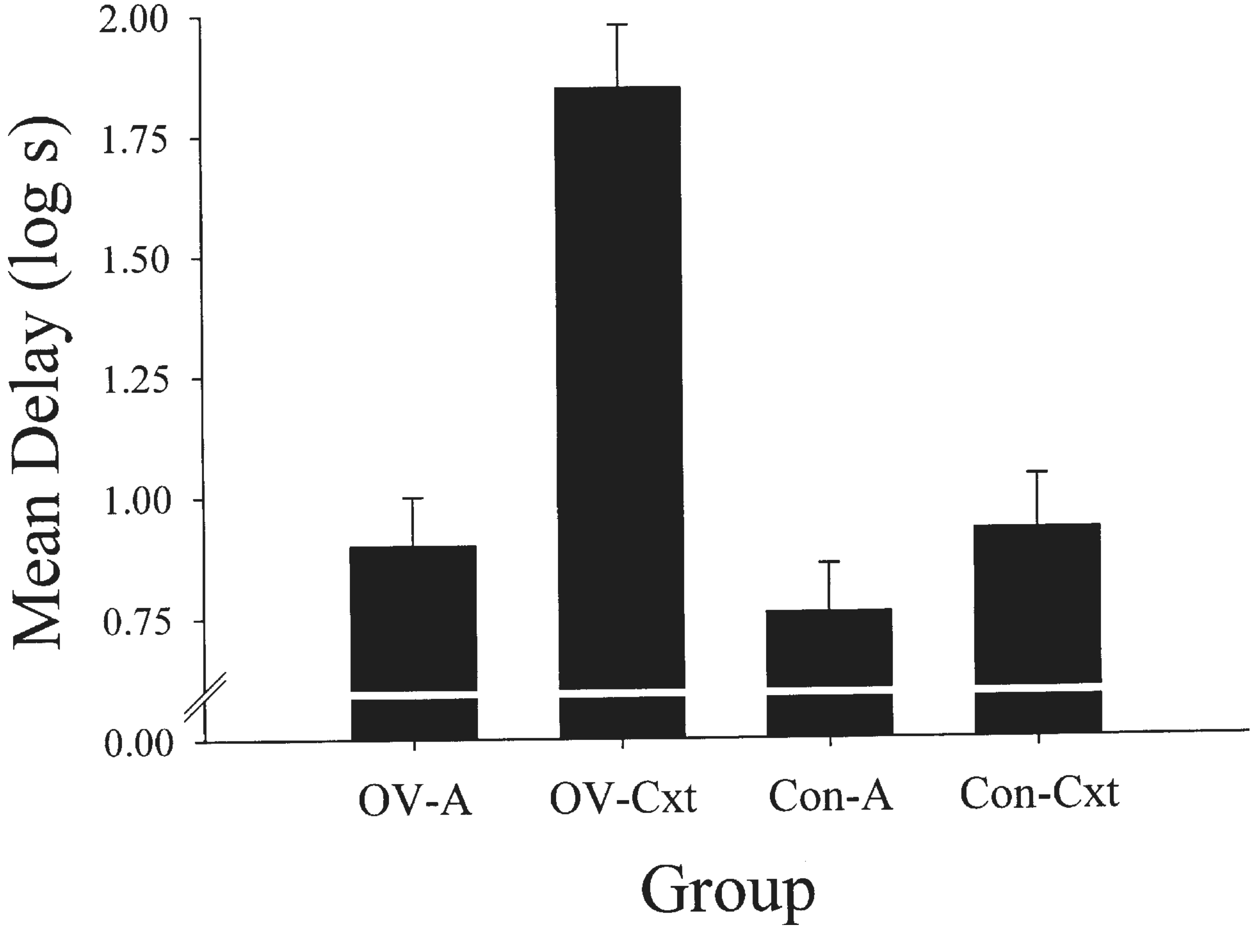
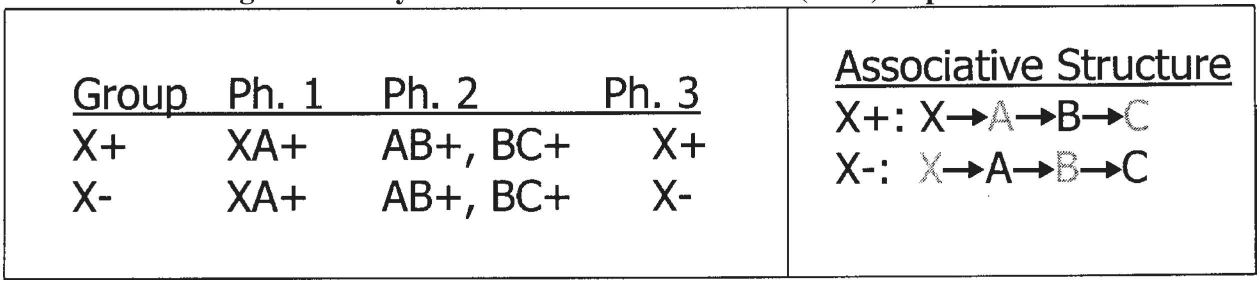


FIG. 3. Results of Denniston et al.'s (2003) Experiment 2. See Table 3 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS Y. Brackets represent standard errors of the mean. From "Cue Competition as a Retrieval Deficit." by J. D. Denniston, H. I. Savastano, A. P. Blaisdell, & R. R. Miller, 2003, *Learning and Motivation*. Copyright 2003 by the Academic Press.

TABLE 4
Design Summary for De Houwer and Beckers (2002) Experiment 2.



Group	Ph. 1	Ph. 2	Ph. 3
X+	XA+	AB+, BC+	X+
X-	XA+	AB+, BC+	X-

Associative Structure
X+: X→A→B→C
X-: X→A→B→C

Note: + and – indicate reinforcement and nonreinforcement, respectively. Strong and weak effective associative strength is represented by black and grey print, respectively.

results and, furthermore, shows that there is an inverse relationship between the response observed to the target CS and the associative status of a third-order comparator stimulus. Their procedure involved causal judgments in humans and the design and hypothetical associative structures of their Experiment 2 are presented in Table 4. In both Groups, compound cue XA is reinforced, followed by a phase in which Compounds AB and BC are separately reinforced. Finally, the associative status of third-order (with respect to Cue C) comparator stimulus X is either associatively inflated through pairings with the outcome (Group X+) or deflated through extinction treatment (Group X-). Causal ratings of each cue as a function of group are presented in Figure 4. The results clearly demonstrate that inflating the associative status of Cue X drives down ratings of Cue A, which in turn drives up ratings of Cue B, which in turn drives down ratings of Cue C. Likewise, deflation of Cue X drives up ratings of Cue A, which drives down ratings of Cue B, which drives up ratings of Cue C.

The revised acquisition models of Van Hamme and Wasserman (1994) and Dickinson and Burke (1998) predict that manipulations of the second-order comparator stimulus should either have no effect on responding to the target CS, or have an inverse relationship to responding to the target CS. Thus, the revised acquisition models fail to account for these findings, leaving the extended comparator hypothesis as the only current theory to account for them. This provides strong evidence for interpreting cue-competition effects as failures in expression of latent associations between the target CS and the US, rather than a weakened association with the US.

Posttraining Temporal Shifts in Cue Competition

We have recently published a series of experiments investigating the role of time in Pavlovian responding that favor a late-stage filter interpretation of cue-competition effects. Blaisdell, Denniston, and Miller (1998) showed that the degree of overshadowing of CS X by CS A depends on how similar the A-US temporal relationship is to the X-US temporal relationship. If the US was predicted to occur at the same point in time relative to the onsets of CS A and CS X, then a strong overshadowing effect was observed. However, overshadowing was weaker if CS A predicted the US at a different time than did CS X. More relevant to the focus of this paper, Blaisdell, Denniston, and Miller (1999) subsequently demonstrated that, even if CS A and CS X both predicted the US at the same point in time during overshadowing treatment, such that CS A overshadowed CS X, post-

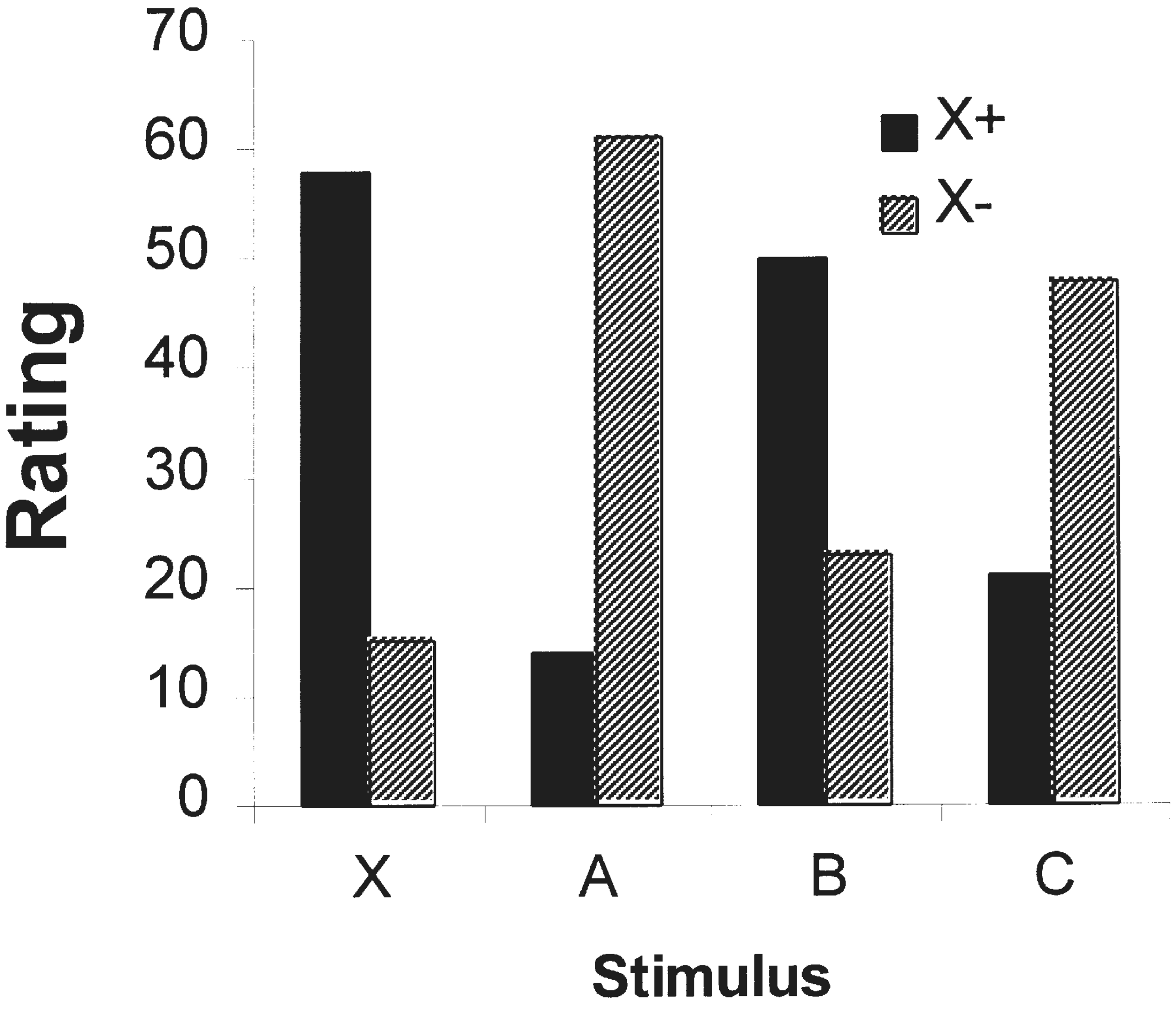
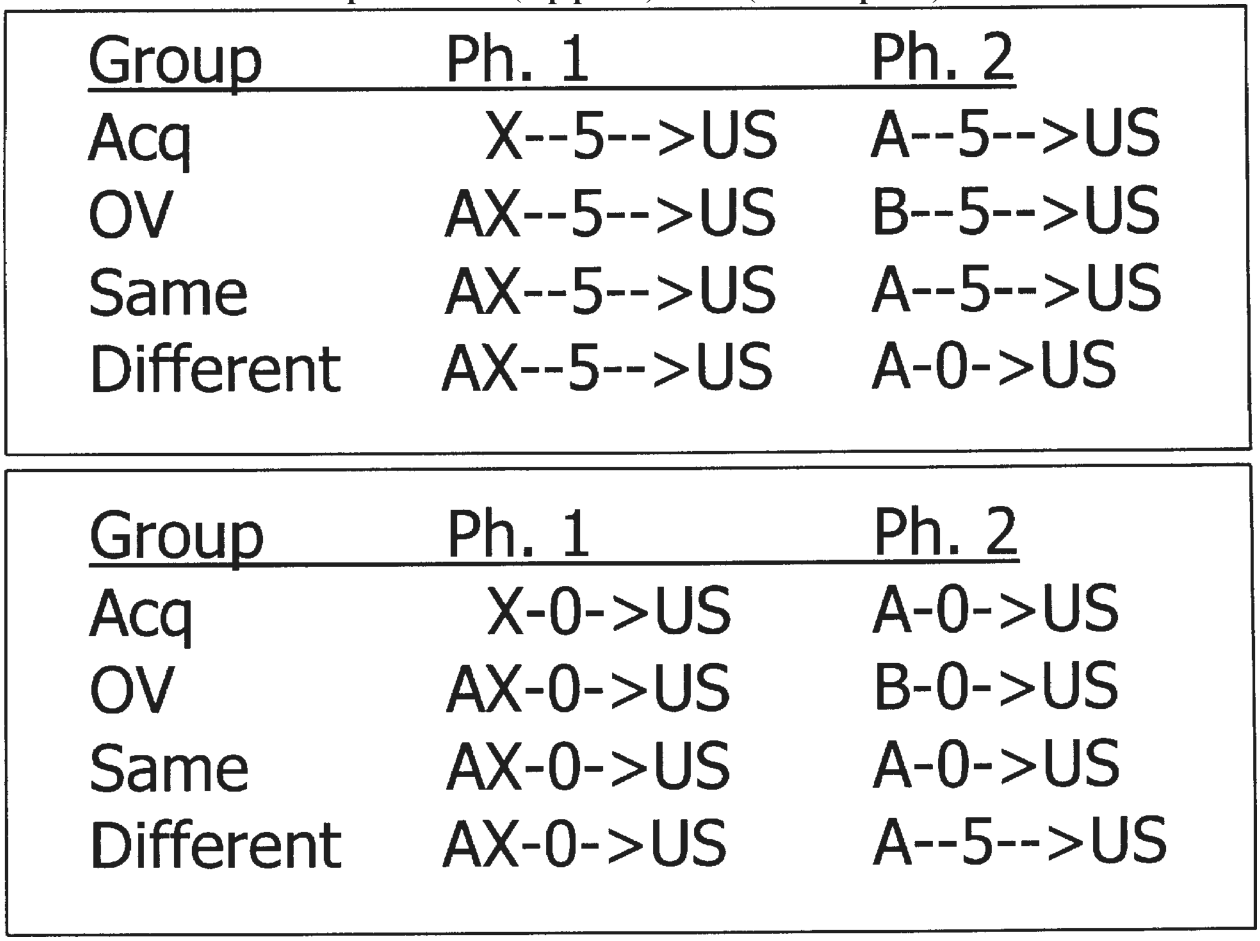


FIG. 4. Results of De Houwer and Becker's (2002) Experiment 2. See Table 4 for group treatments. Bars represent mean causal rating of each cue.

overshadowing manipulation of the A-US temporal interval attenuated the overshadowing effect. For example, in their Experiment 1 (see top panel of Table 5), Blaisdell et al. (1999) paired CS A and CS X with a footshock US with a trace relationship (i.e., a short gap separated CS termination and US onset) in Group OV. Responding to CS X was predicted to be low relative to Group Acq., an acquisition control group. However, two more overshadowing groups received further A-US pairings in a second phase of treatment. For Group Same, these pairings maintained the same trace interval as was established during overshadowing treatment in Phase 1. For Group Different, however, these pairings between CS A and the US shifted the A-US association from a trace to a delay interval. Thus, by the end of Phase 2, CS A should have predicted the US at a different point in time than CS X should have in Group Different. Because Blaisdell et al. (1998) showed that overshadowing was attenuated when CS A and CS X predicted the US at different times, we expected an attenuated overshadowing effect in Group Different, but not in Group Same. This is exactly what we found (Figure 5). Figure 6 shows the results of Experiment 2 of Blaisdell al. (1999), in which the delay relationship that was established during overshad-

TABLE 5
Design Summaries for Blaisdell, Denniston, and Miller (1999) Experiments 1 (top panel) and 2 (bottom panel).



Group	Ph. 1	Ph. 2
Acq	X--5-->US	A--5-->US
OV	AX--5-->US	B--5-->US
Same	AX--5-->US	A--5-->US
Different	AX--5-->US	A-0->US

Group	Ph. 1	Ph. 2
Acq	X-0->US	A-0->US
OV	AX-0->US	B-0->US
Same	AX-0->US	A-0->US
Different	AX-0->US	A--5-->US

Note: Acq. = acquisition, OV = overshadowing, Same = same A-US temporal relationship, Different = different A-US temporal relationship. Numbers indicate the gap (5 s= trace or 0 s = delay) between the termination of the CS and the onset of the US. Adapted from “Posttraining shifts in the overshadowing stimulus-unconditioned stimulus interval alleviates the overshadowing deficit” by A. P. Blaisdell, J. C. Denniston, & R. R. Miller, 1999, *Journal of Experimental Psychology: Animal Behavior Processes, 25*, 18–27. Copyright 1999 by the American Psychological Association. Adapted with permission.

owing treatment in Phase 1 was shifted to a trace relationship in Phase 2 for Group Different (See bottom panel of Table 5). Again, shifting the A-US temporal interval such that it was different than the X-US temporal interval alleviated the overshadowing effect.

In a more recent experiment, Blaisdell et al. (2001) extended the effect of posttraining shifting of the competing stimulus-US interval to the overexpectation effect. Table 6 shows the design of their Experiments 3 and 4. Subjects in all four groups of Experiment 3 received delay conditioning of CS A, CS X, and CS B separately in Phase 1, while subjects in all four groups of Experiment 4 received trace conditioning of CS A, CS X, and CS B separately in Phase 1. In Phase 2, AX was paired with the US with a delay (Experiment 3) or trace (Experiment 4) relationship for Groups OX.Diff, OX.Same, and OX.None. Groups Con.None received CX-US pairings in Phase 2 instead. Then in Phase 3, the A-US temporal interval was either shifted (Group OX.Diff) through further A-US pairings, remained the same (Group OX.Same) through further A-US pairings, or was left unchanged (Group

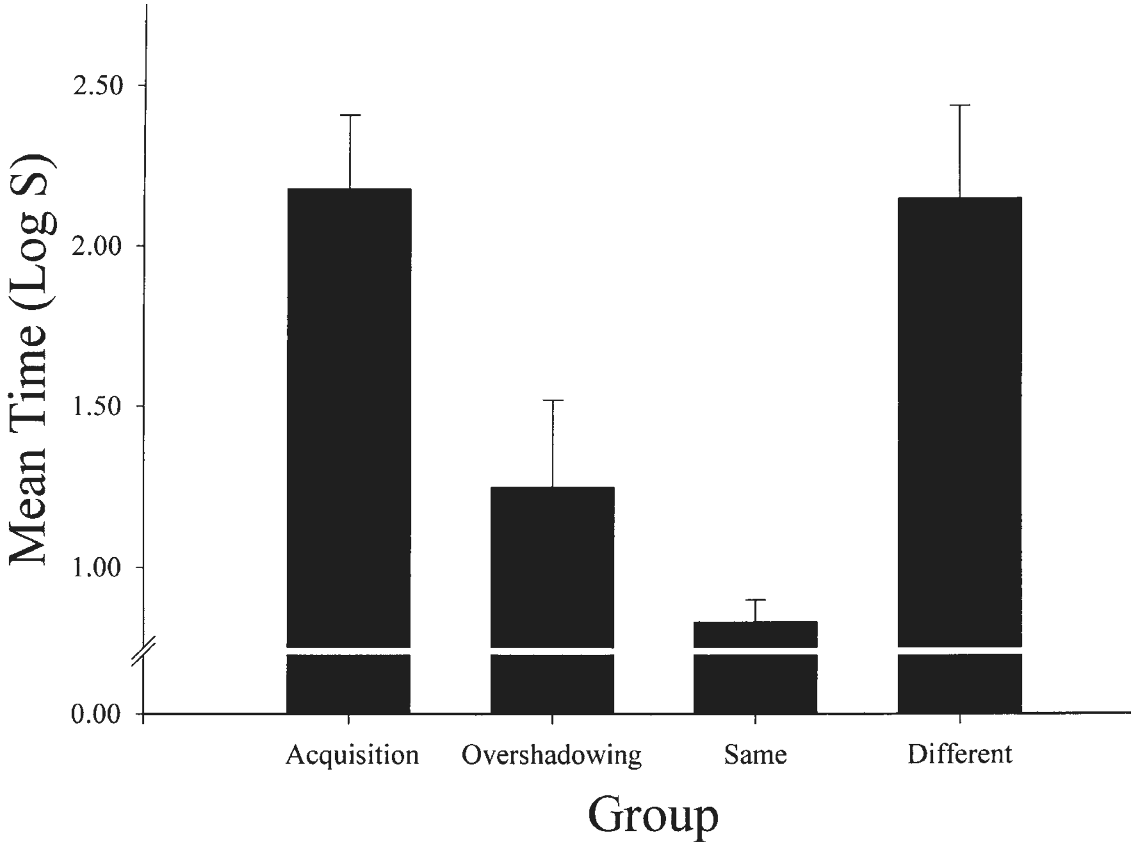


FIG. 5. Results of Blaisdell et al.'s (1999) Experiment 1. See Table 5 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Brackets represent standard errors of the mean. Adapted from "Posttraining shifts in the overshadowing stimulus-unconditioned stimulus interval alleviates the overshadowing deficit" by A.P. Blaisdell, J. C. Denniston, & R. R. Miller, 1999, *Journal of Experimental Psychology: Animal Behavior Processes, 25*, p. 22. Copyright 1999 by the American Psychological Association. Adapted with permission.

OX.None). While Groups OX.None and OX.Same demonstrated the typical overexpectation effect, only in Groups OX.Diff was the effect attenuated.

The interpretation of the posttraining temporal interval manipulations is that both the overshadowing and overexpectation effects (at least) are due not to a failure to acquire a strong X-US association (overshadowing) or the loss of a strong X-US association (overexpectation), but to the prevention of expressing those strong associations in behavior without an appropriate posttraining manipulation. The fact that the response to target CS X recovers, typically to a level that equals that of an acquisition control group, suggests that a strong but latent X-US association had been established during cue-competition treatment, and only required alleviation of the performance attenuating process in order to manifest itself in behavioral expression. Again, an early-stage filter cannot account for these results because such a filter would prevent a strong X-US association from being acquired in the first place.

Posttraining Inflation of Biological Significance on Cue Competition

The final experimental evidence I will discuss that suggests a late-stage filter being responsible for cue-competition effects comes from a recent study by Blaisdell, Denniston,

TABLE 6
Design Summary for Blaisdell, Denniston, and Miller (2001)
Experiments 3 (top panel) and 4 (bottom panel).

Group	Ph. 1	Ph. 2	Ph. 3
OX.Diff	A-0->US/X-0->US/B-0->US	AX-0->US	A-5->US
OX.Same	A-0->US/X-0->US/B-0->US	AX-0->US	A-0->US
OX.None	A-0->US/X-0->US/B-0->US	AX-0->US	B-5->US
Con.None	A-0->US/X-0->US/B-0->US	CX-0->US	A-0->US

Group	Ph. 1	Ph. 2	Ph. 3
OX.Diff	A-5->US/X-5->US/B-5->US	AX-5->US	A-0->US
OX.Same	A-5->US/X-5->US/B-5->US	AX-5->US	A-5->US
OX.None	A-5->US/X-5->US/B-5->US	AX-5->US	B-0->US
Con.None	A-5->US/X-5->US/B-5->US	CX-5->US	A-5->US

Note: OX = overexpectation, Con = control, Same = same A-US temporal relationship in Phase 3, None = no relevant (with respect to CS X) treatment in Phase 3. Numbers indicate the gap (5 s= trace or 0 s = delay) between the termination of the CS and the onset of the US. Adapted from "Recovery from the overexpectation effect: Contrasting performance-focused and acquisition-focused models of retrospective revaluation" by A. P. Blaisdell, J. C. Denniston, & R. R. Miller, 2001, *Animal Learning & Behavior, 29*, 367–380. Copyright 2001 by the Psychonomic Society. Adapted with permission.

Savastano, and Miller (2000) involving the effects of biological significance on overshadowing. Biologically significant cues are stimuli that control behavior because they have either inherent or acquired motivational value (Denniston, Miller, & Matute, 1996; Gunther, Miller, & Matute, 1997; Miller & Matute, 1996; Oberling, Bristol, Gunther, & Miller, 1999). For example, high-intensity stimuli which are inherently biologically significant have been shown to be protected from overshadowing and blocking effects compared to lower-intensity stimuli that are typically used. Similarly, Oberling et al. have shown that a cue that acquires biological (i.e., motivational) significance through pairings with saccharine prior to overshadowing (of conditioned fear) treatment are protected from the overshadowing effect. That is, stronger fear was expressed to a CS (X) that had been subject to overshadowing treatment (i.e., AX→footshock) if CS X had been previously established as a signal for saccharine (i.e., X→saccharine). Blaisdell et al. (2000) extended this finding to show that overshadowing of CS X is attenuated if CS X is established as a signal for saccharine *after* overshadowing treatment. The design of the experiment is shown in Table 7. Focusing first on Phase 2, two groups (BS and OV) received pairings between an AX compound and footshock using parameters that typically allow CS A to overshadow CS X. Two other groups (Counter and Acq) received only X-US pairings. Then in Phase 3, rats in Groups BS and Counter received pairings between CS X and a previously established signal for saccharine (B), while rats in Groups OV and Acq received pairings between CS X and a non-signal for saccharine (C). Thus, CS X is established as a second-order predictor of saccharine in Groups BS and Counter, but not in the other two groups. When Oberling et al. inflated CS X's acquired biological significance by establishing CS X as a signal for saccharine prior to overshadowing treatment, CS X was

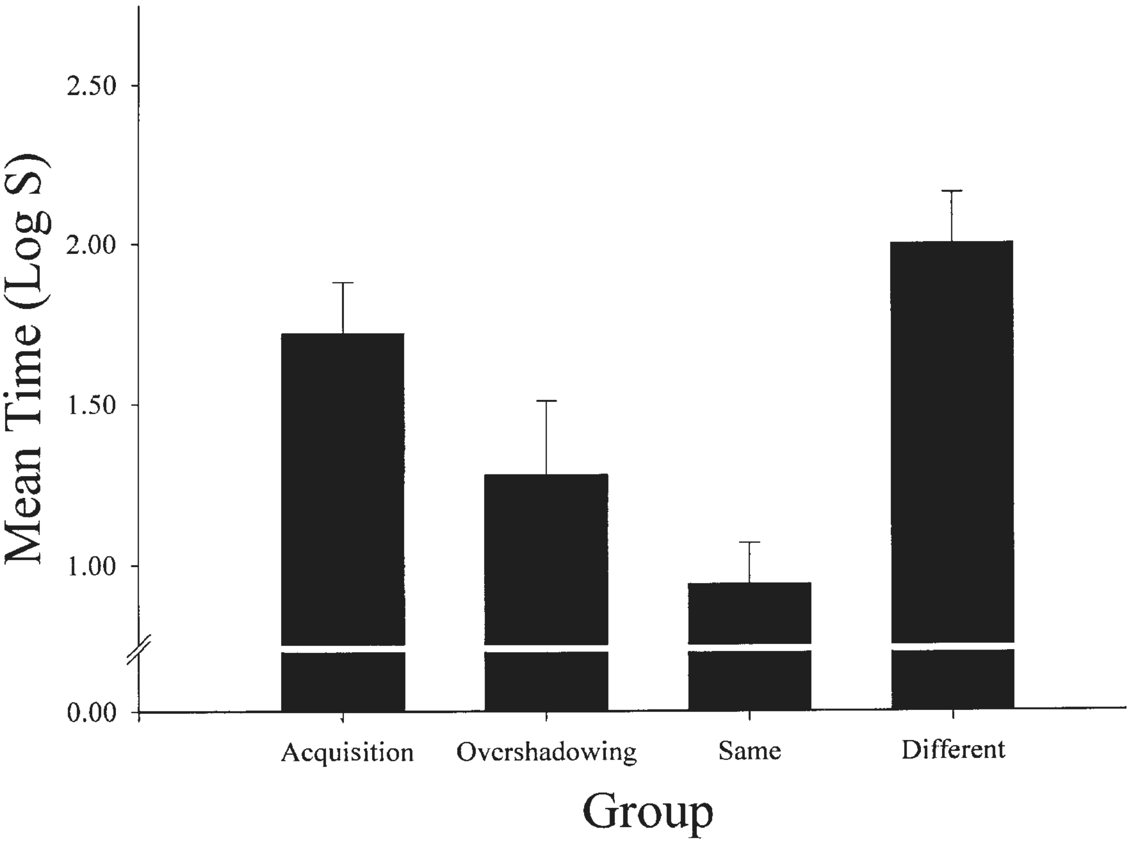


FIG. 6. Results of Blaisdell et al.'s (1999) Experiment 2. See Table 5 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Brackets represent standard errors of the mean. Adapted from "Posttraining shifts in the overshadowing stimulus-unconditioned stimulus interval alleviates the overshadowing deficit" by A.P. Blaisdell, J. C. Denniston, & R. R. Miller, 1999, *Journal of Experimental Psychology: Animal Behavior Processes, 25*, p. 24. Copyright 1999 by the American Psychological Association. Adapted with permission.

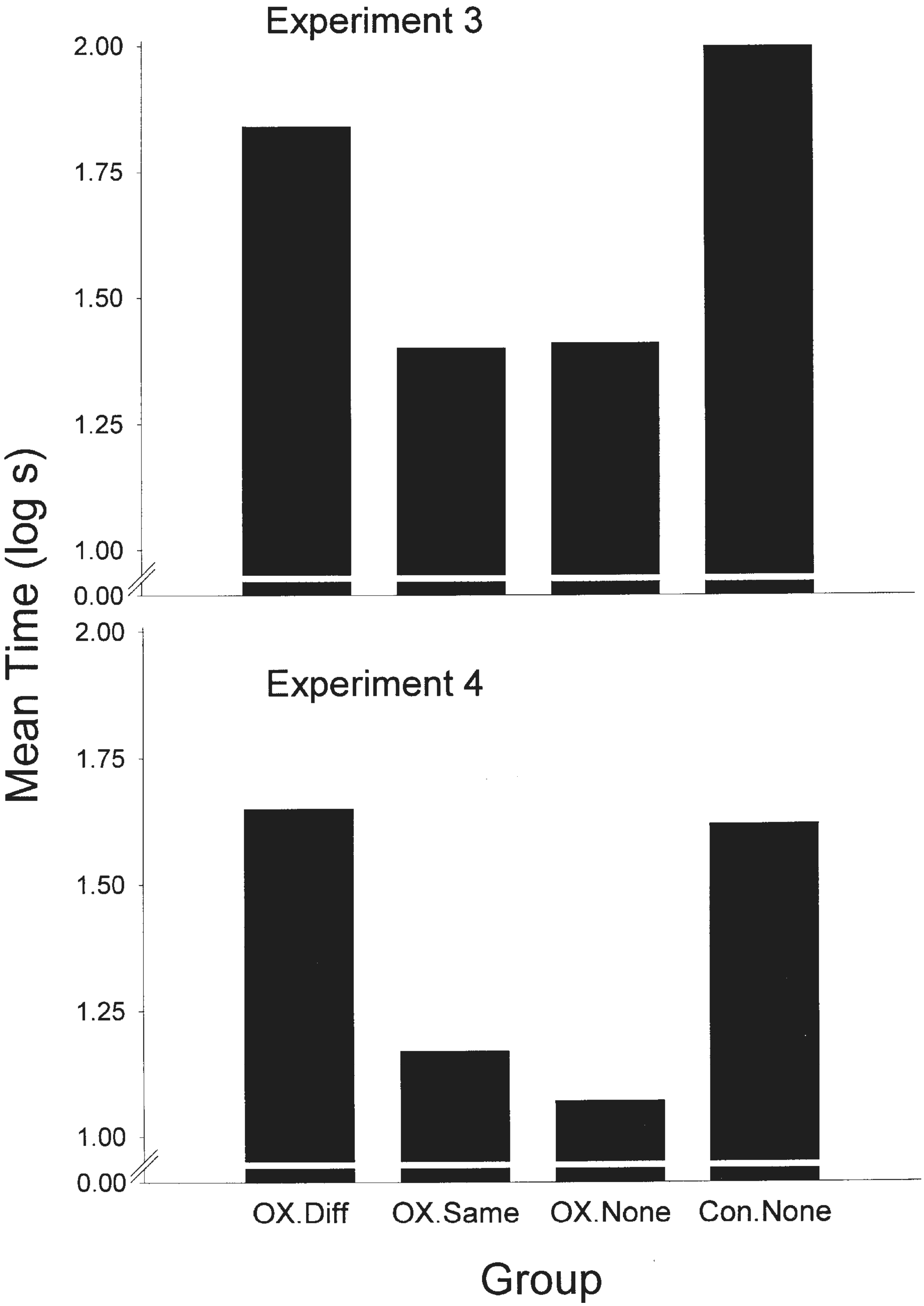
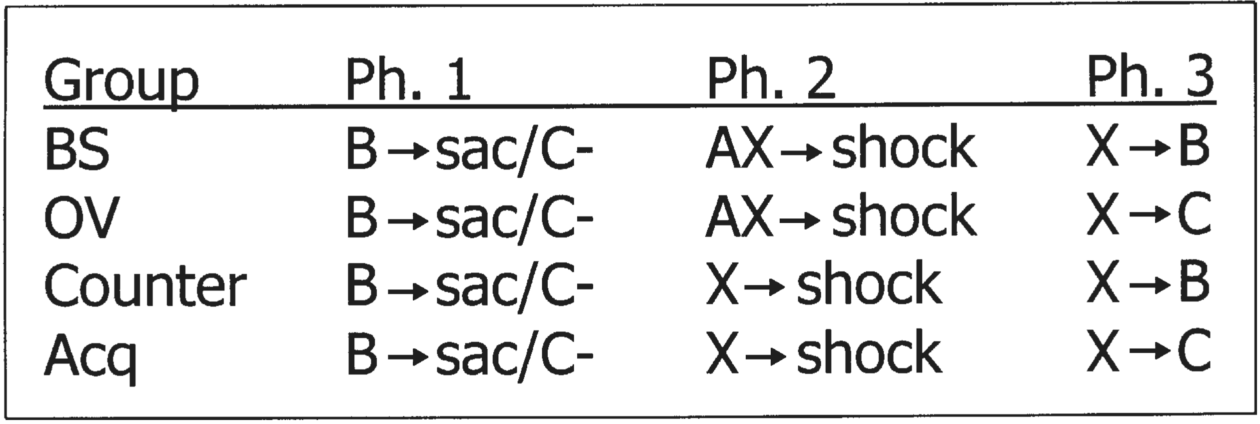


FIG. 7. Results of Blaisdell et al.'s (2001) Experiments 3 & 4. See Table 6 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Adapted from Blaisdell, Denniston, & Miller (2001), *Animal Learning & Behavior, 29*, p. 367–380. Copyright 2001 by the Psychonomic Society. Adapted with permission.

TABLE 7
Design Summary for Blaisdell, Denniston, Savastano, and Miller (2000) Experiment 1.



Group	Ph. 1	Ph. 2	Ph. 3
BS	B→sac/C-	AX→shock	X→B
OV	B→sac/C-	AX→shock	X→C
Counter	B→sac/C-	X→shock	X→B
Acq	B→sac/C-	X→shock	X→C

Note: BS = biological significance, OV = overshadowing, Counter = counterconditioning, and Acq = acquisition. sac = saccharine. Adapted from "Counterconditioning of an overshadowed cue attenuates overshadowing" by A. P. Blaisdell, J. C. Denniston, H. I. Savastano, & R. R. Miller, 2000, *Journal of Experimental Psychology: Animal Behavior Processes, 26*, p. 76. Copyright 2000 by the American Psychological Association. Adapted with permission.

protected from overshadowing of conditioned fear by CS A. Likewise, when Blaisdell et al. inflated the acquired biological significance of CS X after overshadowing treatment, CS X was protected from overshadowing (Figure 8). Comparing the groups that received overshadowing treatment in Phase 2, when CS X had been established as a signal for saccharine (Group BS), rats showed more fear to CS X (i.e., less overshadowing) than when CS X had not been established as a signal for saccharine (Group OV). The most likely interpretation of these data is that a strong X-shock association was established during overshadowing treatment, despite the presence of the more salient CS A. When a posttraining manipulation increased the motivational value of CS X (as a signal for an appetitive stimulus), the latent association to footshock (the fearful stimulus) expressed itself in behavior as well. Blaisdell et al. (2000) suggested that inflating the biological (i.e., motivational) significance of a stimulus alters the attention paid to that stimulus at test such that latent associations become more accessible. (Attention is used here to refer to post-perceptual processes that influence retrieval rather than perceptual processes that affect the associability of a stimulus [e.g., Mackintosh, 1975 and Pearce & Hall, 1981]. See Blaisdell et al., 2000, for further discussion of this issue.) Note that this idea is consistent with the notion that cues that are inherently biologically significant because of their high intensity are also presumably more salient to the subject (cf. Hull's (1949) stimulus intensity dynamism) and are protected from cue-competition effects.

Closing Remarks

The experiments reviewed above all point to the same conclusion: That deficits in conditioned responding to a target CS resulting from competition from other, more salient, predictive, or valid stimuli are best interpreted as failures to express a strongly established association between the target CS and the US, rather than the failure to establish a strong target CS-US association in the first place. This supports the view that models of cue competition would be more theoretically accurate if they posit a late-stage filter on the information stream rather than an early (e.g., pre-encoding) filter. Models such as that of

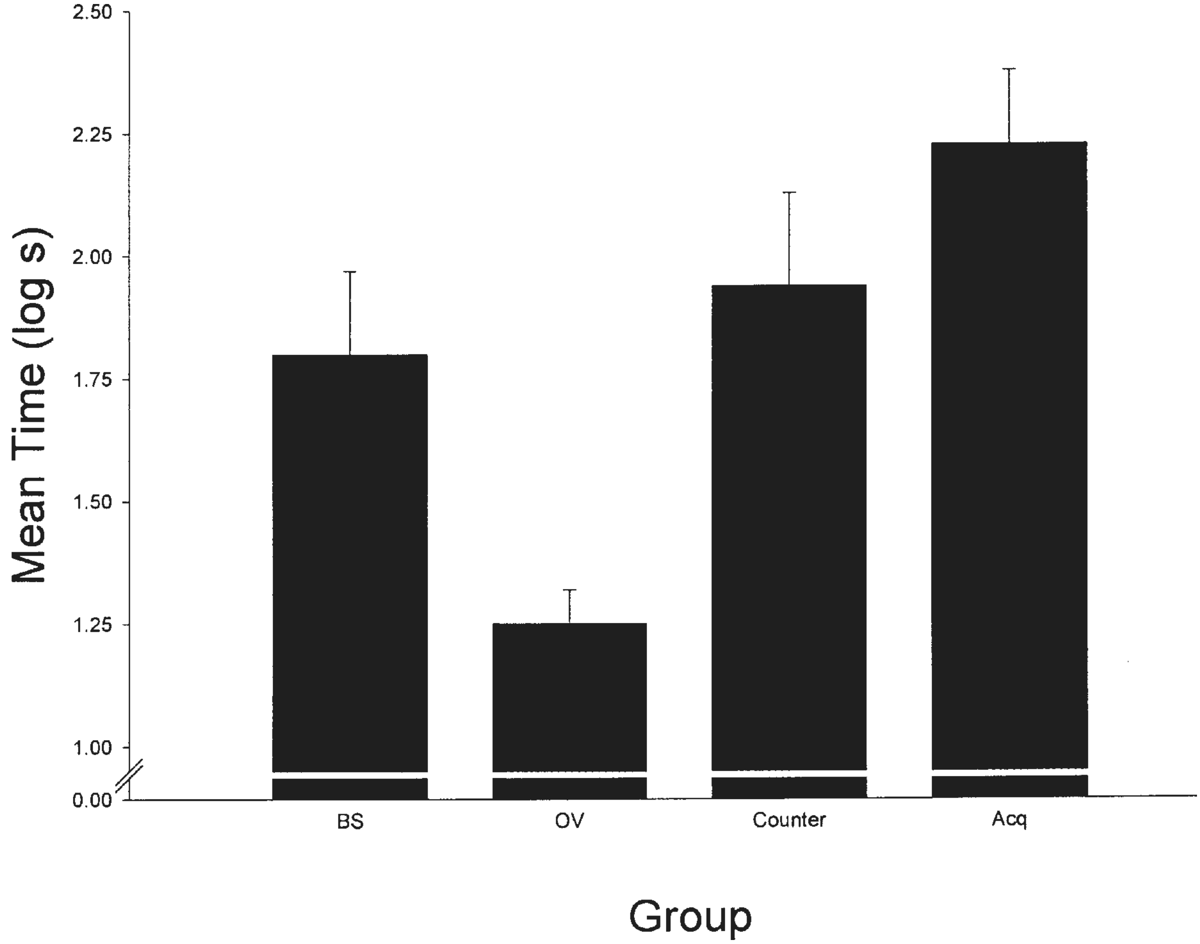


FIG. 8. Results of Blaisdell et al.'s (2000) Experiment 1. See Table 7 for group treatments. Bars represent mean times (log s) to complete 5 cumulative seconds of drinking in the presence of target CS X. Brackets represent standard errors of the mean. From "Counterconditioning of an overshadowed cue attenuates overshadowing." by A. P. Blaisdell, J. C. Denniston, H. I. Savastano, & R. R. Miller, 2000, *Journal of Experimental Psychology: Animal Behavior Processes, 26*, p. 78. Copyright 2000 by the American Psychological Association. Adapted with permission.

Rescorla and Wagner (1972) and their ilk, including the revised models of Van Hamme and Wasserman (1994) and Dickinson and Burke (1996), do not adequately describe the processes underlying Pavlovian responding. This is not to say that such models do not have their place in the investigation of learning. These acquisition-focused models have clearly driven much excellent research in the past few decades and continue to serve a heuristic role in the exploration of new psychological phenomena. However, the empirical evidence presented above clearly suggests that these models are inadequate in accounting for the richness of the psychological phenomena found in the Pavlovian laboratory, and may steer us in the wrong direction when scientists in related fields attempt to use these models to uncover their biological underpinnings. Perhaps it is time to shift our focus to investigating and modeling the processes of Pavlovian performance rather than (or in addition to) acquisition processes. The attempts that have been made so far, such as the comparator hypothesis (Blaisdell, Bristol, Gunther, & Miller, 1998; Denniston, Savastano, & Miller, 2001; Miller & Matzel, 1988; Miller & Schachtman; 1985) and Scalar Expectancy Theory (Gibbon & Balsam, 1981), have already demonstrated their successes (though they have their limitations, too). Undoubtedly, better performance models will be developed in the future. A more nuanced appreciation of the richness of the content of learning, as well as the processes responsible for that richness, will drive a greater understanding of the biological basis of both learning and performance.

Notes

1. A note about terminology. "X" will typically denote the target or test stimulus, while "A" will typically denote the competing stimulus.

"→" indicates that the stimulus or event that precedes the arrow is temporally prior to the stimulus or event that follows the arrow. Stimuli or events on either side of the

"/" were presented in separate trials within the same session(s).

'+' and '–' indicate the presence and absence of the US, respectively.

2. There are a few hybrid models that attempt to incorporate both acquisition and performance processes (e.g., Gallistel & Gibbon, 2000; Schmajuk, 1997; Wagner, 1981). However, Wagner's SOP model (see also Wagner & Brandon, 1989) and Schamjuk's neural network model are parameter dense, and are thus unable to make crisp, clear theoretical predictions. Likewise, the model of Gallistel and Gibbon relies on separate mechanisms for acquisition and retrieval with no clearly specified rule for how these two mechanisms interact. With all of these models, it is difficult to know where in the S-R stream the information filter would reside. This suggests the intriguing notion that there may be a relationship between the ability to clearly specify the location of the information filter with regards to a particular model and that model's ability to generate clearly testable predictions.

3. The revised acquisition models however, still cannot account for reversals of cue-competition effects produced by a long retention interval (i.e., spontaneous recovery) or from pre-test reminder treatments. Thus, when all instances of cue-competition reversal (i.e., retrospective revaluation effects) are taken into account, performance theories fare better than acquisition theories.

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