Primacy and recency effects in extinction and latent inhibition: A selective review with implications for models of learning

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Abstract

In the framework of animal conditioning and human associative learning, primacy and recency effects on acquired stimulus control of behavior refer to the superior influence of first-learned and last-learned associations, respectively. Most contemporary associative models of learning anticipate unwavering recency effects and claim support from numerous published studies. But, for pragmatic reasons, almost all of these studies were conducted under select conditions that favored recency effects. When these conditions are not met, recency effects are far from ubiquitous. We review the literature on primacy and recency effects regarding extinction and latent inhibition (i.e., interference between outcomes), with special emphasis on the impact of certain post-training manipulations and test conditions on conditioned responding. Evidence for recency-to-primacy shifts and for memory integration is examined in light of contemporary models of learning.
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1. Introduction: interference between outcomes

The extensive research of Pavlov (1927) and his colleagues publicized the existence of conditioned reflexes, that is, responses to an initially irrelevant stimulus (i.e., a conditioned stimulus [CS], such as a dim light or a soft tone) based on its repeated pairings with a stimulus that elicited a response upon first en-

counter (i.e., an unconditioned stimulus [US], such as food or a footshock). Pavlov not only investigated the conditions necessary for the formation of conditioned responses to CSs, but also some experimental treatments that produced a weakening of a previously established conditioned response by subsequently pairing the CS with an outcome other than the target US. These effects are now sometimes referred to collectively as *retroactive interference between outcomes* (Bouton, 1993). Moreover, Pavlov observed that some of these response-weakening effects could be attenuated by select manipulations performed after the target and interfering treatment phases. Hereafter we will

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refer to these manipulations as *post-training manipulations*.[1]

1.1. Attenuation of interference between outcomes achieved by post-training manipulations

Pavlov (1927) primarily studied two types of retroactive interference between outcomes: extinction and counterconditioning. Regarding experimental extinction, he observed that the conditioned response previously established based on CS–US pairings decreased if the CS was presented without the US (i.e., CS-alone presentations, which might be viewed as CS–noUS presentations). However, Pavlov observed that after a sufficient passage of time following the extinction treatment the extinguished CS came to again elicit a conditioned response, albeit weaker than initially, despite no further pairings of it with the US, an effect that he named *spontaneous recovery*. Spontaneous recovery of extinguished responding has attracted much attention in the literature, and has been replicated in many different species and conditioning preparations (e.g., Brooks, 2000; Brooks and Bouton, 1993; Brooks et al., 1999; Rescorla, 1996, 1997; Robbins, 1990; Rosas and Bouton, 1996, 1998; see also Rosas et al., 2001, for evidence with humans). Although less extensively studied, spontaneous recovery of responding has also been found after a counterconditioning treatment (e.g., Bouton and Peck, 1992). In a counterconditioning treatment, the conditioned response elicited by the CS following CS–US pairings is weakened by pairings of the CS with another US, usually a US related to an opposing motivational system relative to the initial US (e.g., CS–food pairings followed by CS–shock pairings). Interposing a retention interval between counterconditioning treatment and testing also results in a partial recovery of the conditioned response appropriate to the initial CS–US pairings.

The interpolation of a retention interval between outcome interference treatments such as extinction or counterconditioning and testing with the CS is not the only post-training manipulation that can recover the initially acquired response. The response elicited by a CS can also be recovered following retroactive interference between outcomes by testing the CS in a context different from that in which outcome interference treatment was performed (i.e., *renewal of responding*, e.g., Bouton and Bolles, 1979a; Bouton and King, 1983; Bouton and Peck, 1989; Bouton and Ricker, 1994; Brooks and Bouton, 1994; Gunther et al., 1998; Harris et al., 2000; Rosas and Bouton, 1997, 1998; also see Paredes-Olay and Rosas, 1999; Pineño and Miller, 2004; Rosas et al., 2001, for demonstrations with humans). Another treatment that recovers responding after outcome interference consists of presenting the target US alone before testing (i.e., in the case of counterconditioning, the US initially paired with the CS), an effect known as *reinstatement* (e.g., Bouton, 1984; Bouton and Bolles, 1979b; Bouton and King, 1983; Brooks et al., 1995; Rescorla and Heth, 1975; see García-Gutiérrez and Rosas, 2003a,b; Vila and Rosas, 2001, for demonstrations with humans). Finally, although infrequently studied, presenting intense extraneous stimuli (i.e., stimuli different from the CSs and the USs) immediately before testing can also recover responding following retroactive outcome interference (i.e., *disinhibition*, e.g., Hunter, 1935; Pavlov, 1927; Rexroad, 1937).

Given the broad variety of post-training manipulations that are known to produce a recovery from extinction or counterconditioning, resulting in responding appropriate to the initially trained CS–US association, one might ask what, if anything, these manipulations have in common. One possible answer to this question is that provided by Bouton's (1993) retrieval model, according to which these manipulations are all assumed to produce a change in either the physical or the temporal context of testing relative to that of the interfering treatment. In the framework of this model, responding recovers because retroactive interference between outcomes, such as that seen in extinction and counterconditioning, do not involve unlearning of the original excitatory CS–US association as proposed by Rescorla and Wagner (1972). Instead, retroactive interference appears to be due to the formation of an inhibitory CS–US association (Pavlov, 1927; Konorski, 1948) or a CS–noUS association (Konorski, 1967) in the case of extinction and the formation of a CS–newUS

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[1] Some post-training manipulations of contemporary interest involve presentations of a non-target CS previously associated with the target CS, either alone or paired with the US. However, throughout this paper, by post-training manipulations, we will be referring exclusively to manipulations that involve no direct learning experience with any CS present during target training (e.g., interposing retention intervals and changing contexts).

association in the case of counterconditioning. According to this proposal, retrieval of the inhibitory CS–US association depends upon its being primed at the time of test by its training context (a priming stimulus here refers to a stimulus that sets the occasion for retrieval of a specific US representation by a CS). But, why do inhibitory associations depend upon their priming by the training context while excitatory associations are relatively free of this constraint? To answer this question, Bouton (1994) suggested that organisms have evolved or developed so that learning mechanisms favor the contextual dependency of inhibitory associations relative to excitatory associations probably due to intrinsic differences in the very nature of these associations (e.g., inhibitory associations are usually less important for survival relative to excitatory associations). Thus, the deleterious impact of the interfering (inhibitory) treatment on the target (excitatory) behavior is expected to be maximal when testing occurs in a spatiotemporal context similar to that of interference treatment (i.e., in a physically similar context with a short retention interval) and hence, when the inhibitory association is strongly primed by the test context. Testing in an altered temporal context (such as that produced by interposing a long retention interval between the end of treatment and testing) or physical context (i.e., renewal) from that of the interfering treatment should result in the interfering association being difficult to retrieve, with the result that it no longer interferes with retrieval of the excitatory CS–US association. In other words, testing outside of the context in which the interfering association was trained directly impairs retrieval of this association and, indirectly, releases the excitatory association from interference. As a consequence, the excitatory target CS–US association is strongly retrieved and thus, expressed in behavior.

1.2. Enhancement of interference between outcomes achieved by post-training manipulations

Although Bouton's (1993) retrieval theory provided a reasonable account for the existing evidence at the time that the model was developed, the model was soon challenged by later findings, mostly involving latent inhibition. In a typical latent inhibition (i.e., CS-pre-exposure) experiment, CS-alone presentations prior to reinforced presentations impair responding to the CS during subsequent CS–US pairings (Lubow, 1973;

Lubow and Moore, 1959); hence, latent inhibition is a type of proactive interference between outcomes. Note that latent inhibition basically involves the same experience with the CS and the US as experimental extinction, but in reverse order. Latent inhibition, when observed, is expressed as retarded acquisition of stimulus control and usually found on the first few pairings of the CS with the US. That is, given sufficiently many CS–US pairings, latent inhibition eventually dissipates. One of the first problematic findings that Bouton's (1993) theory encountered was that retrieval of an excitatory CS–US association (i.e., as opposed to retrieval of the inhibitory CS–US association, as proposed by the theory) was context specific in a latent inhibition treatment, in which CS-alone treatment precedes CS–US pairings (Swartentruber and Bouton, 1992). That is, in a latent inhibition treatment the CS–US association proved at least as context dependent as the CS–noUS association in an extinction treatment. Another set of findings problematic for Bouton's (1993) model was the so-called super-latent inhibition effect (De la Casa and Lubow, 2000, 2002; Lubow and De la Casa, 2002; Wheeler et al., 2004; and for an example with humans, see Stout et al., in press). De la Casa and Lubow (2000, 2002) found that, when CS pre-exposure and the CS–US pairings were followed by a long retention interval before testing, a strong reduction occurred in the conditioned response elicited by the CS relative to a group lacking the CS-alone exposures, a result that can be interpreted as due to improved retrieval of the CS-alone memory. Alternatively stated, the interpolation of a long retention interval after latent inhibition treatment yielded an effect contrary to the one that usually occurs after extinction, a response attenuation rather than a response recovery.[2]

The super-latent inhibition effect was problematic for Bouton's (1993) model because, if the CS–noUS association that is presumed to underlie latent inhibition in this theory was context specific, passage of time should attenuate, rather than enhance, latent inhibition. That is, as occurs in extinction, testing the CS after a retention interval (i.e., in a different *tem-*

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[2] There are also a few reports of the opposite effect, that is, a long retention interval attenuating latent inhibition (e.g., Aguado et al., 1994). But most of these studies had the subjects spend the retention interval in the training context, which allowed extinction of the training context, a complicating factor.

poral context, in Bouton's terminology) should result in impaired retrieval of the interfering memory (i.e., CS-alone), thereby releasing the CS–US association from latent inhibition. The resolution to this conflict was already on hand, provided by Bouton's (1997) revision of his original model, in which second-learned associations (instead of inhibitory associations based on non-reinforcement) depend on the context for retrieval. Bouton's (1997) model was motivated at the theoretical level by the view that initial training (i.e., the first-learned association) is ordinarily unambiguous, but later training (i.e., the second-learned association, e.g., the inhibitory CS–US association in extinction or counterconditioning) makes the CS ambiguous. According to Bouton's (1997) model, this ambiguity in the meaning of the CS can be resolved by using information provided by the context. When a second association is learned involving the CS and, hence, the CS becomes ambiguous by acquiring a second meaning, the organism begins to pay attention to contextual stimuli in an attempt to determine what might have caused this change in the CS–US relationship. In words of Bouton and Nelson (1998), the context becomes an occasion setter for the second-learned association and, therefore, its presence strongly determines retrieval of this association. In this new framework, following extinction treatment responding elicited by the CS recovers when testing occurs in a different context (either physical or temporal) because the CS–US association (learned in the first place) is released from interference caused by the CS–noUS association (learned in the second place). Consistent with this, after latent inhibition treatment, responding decreases because retrieval of the CS–noUS association (learned in the first place) is no longer impaired by the CS–US association (learned in the second place).

2. Primacy and recency effects in interference between outcomes

As previously discussed, Bouton's (1993) model emphasized the *nature of associations* in relation to the impact of post-training manipulations on responding to the CS after interference between outcomes (i.e., retrieval of *inhibitory* associations wanes as the contexts of outcome interference training and testing increasingly differ). In contrast, Bouton's (1997) model em-

phasized the *order in which associations are learned* (i.e., retrieval of *second-learned* associations wanes and consequently retrieval of first-learned associations increases as the contexts of outcome interference training and testing increasingly differ).

Bouton's (1997) model of outcome interference, which emphasizes the temporal sequence of CS–US training and CS–noUS (or CS–newUS) training, strongly relies on the classic distinction between proactive and retroactive interference (e.g., Slamecka and Ceraso, 1960). In *proactive interference* the first-learned association interferes with the retrieval or expression of the second-learned association. Conversely, in *retroactive interference*, the second-learned association interferes with the first-learned association. The emphasis of Bouton's (1997) theory on the role of trial order in interference phenomena (i.e., first-learned versus second-learned associations) certainly limits the importance of the nature of the associations (i.e., excitatory versus inhibitory associations) on interference phenomena. That is, in Bouton's newer model, the inhibitory association is not necessarily viewed as the context-dependent association. However, it is important to note here that, in common practice, the nature of associations determines the identity of the associations as either the target or the interfering association. In principle, one might correctly assume that, as the CS–noUS association can interfere with the expression of the CS–US association, so too can the CS–US association interfere with the expression of the CS–noUS association. However, in the conditioning literature, responding based on CS–US pairings (i.e., the excitatory association) is usually treated as a first-order phenomenon and interference with this responding (i.e., the inhibitory association) is viewed as the manipulation superimposed upon responding. That is, the CS–US association is usually the target association in conditioning experiments merely because its existence can be directly assessed (by the production and strength of a conditioned response), whereas the CS–noUS association can only be indirectly assessed (Rescorla, 1969). This can explain why latent inhibition and extinction are often viewed as instances of proactive and retroactive interference, respectively. In both of these instances, the competing association (CS–noUS) is viewed as interfering with the excitatory association (CS–US).

Bouton's (1997) view of trial order as a determining factor of which association, if any, becomes con-

text dependent was additionally supported by studies showing that Pavlovian conditioned inhibition (i.e., inhibitory behavioral control elicited by a CS, X, due to training with alternated A-US and AX-noUS trials) is not necessarily context dependent (Bouton and Nelson, 1994; Nelson and Bouton, 1997). If, as predicted by Bouton's (1993) theory, the inhibitory CS–US association depended upon context merely due to its inhibitory nature, a Pavlovian conditioned inhibitory association should *always* be strongly affected by contextual manipulations performed prior to test. However, research has shown that a conditioned inhibitor, X, becomes context dependent only when the inhibitory X-US association (or X-noUS association) is learned in second place, after learning of the excitatory X-US association. When the inhibitory X-US association is the one learned in first place, no such contextual dependency is found (Nelson, 2002). Whether conditioned excitation or conditioned inhibition is context dependent depends on which relationship is trained second (i.e., excitation training following inhibition training or vice versa; Nelson, 2002). Further support for this view came from a study showing that partial reinforcement is not subject to the renewal effect (Bouton and Sunsay, 2001). In partial reinforcement, CS–US and CS–noUS trials are presented during training in an interspersed fashion and, hence, contrary to what happens in extinction and latent inhibition, the two presumed associations are not learned in a specific order. Because both an excitatory and an inhibitory association are assumed to be learned in this procedure, Bouton's (1993) theory would predict that partial reinforcement should be sensitive to several types of post-training manipulations. However, according to Bouton's (1997) theory, neither association should become relatively more strongly attached to the training context. That is, both excitatory and inhibitory associations might become either strongly or weakly dependent on the context, but one association should not show a stronger contextual dependency for its retrieval relative to the other.

It seems, therefore, that the order in which the target and interfering associations are acquired plays a critical role in determining the recoverability of responding to the CS (e.g., extinction) and responding appropriate to the interference treatment (e.g., latent inhibition) following a post-training manipulation. The relevance of trial order in determining the specific nature of interference between outcomes should not surprise the reader. Since Ebbinghaus, in 1885, performed his original studies on memory (see Ebbinghaus, 1913), it has been well known that the items learned early and late in a list are better recalled than the middle items. This superior list recall by humans of first-learned and last-learned items, which is generally known as *primacy* and *recency* effects, respectively, certainly applies to other species (e.g., Wright and Roediger, 2003; Wright et al., 1984) and other types of learning in humans, such as contingency learning (e.g., Chapman, 1991; Dennis and Ahn, 2001; López et al., 1998; Yates and Curley, 1986) and memory for items in a list (e.g., Knoedler et al., 1999).

In outcome interference phenomena within conditioning preparations, primacy or recency effects are usually observed when the same CS is paired with different outcomes (e.g., US and noUS) in separate phases. In such situations, recency and primacy effects are in opposition to one another (in contrast to, say, list learning in which both can be observed at the same time). Whereas recency effects can be directly observed in outcome interference, primacy effects can ordinarily only be indirectly inferred. To clarify this point, consider an extinction procedure (i.e., CS–US pairings followed by CS-alone presentations). In this procedure, recency would be suggested by a reduction in responding elicited by the CS over an extensive series of non-reinforced presentations of the US (i.e., extinction of responding). Analogously, one might also claim that primacy (i.e., of the CS–US pairings) would be suggested by resistance to extinction during the initial CS–noUS trials relative to subjects lacking the prior CS–US pairings (e.g., Nevin, 1988). However, we have to take into account that during the *initial* non-reinforced training trials with the CS, the CS–US association is not only the first-trained association (primacy), but also the last-trained association (recency), thereby clouding the distinction between primacy and recency. Moreover, resistance to extinction could also reflect the impact of the larger number of reinforced trials relative to the number of non-reinforced trials early in extinction, a factor that requires no need to appeal to trial–order effects. The same logic applies to the latent inhibition procedure (i.e. CS-alone presentations followed by CS–US pairings). Here, a recency effect is suggested when the CS elicits strong responding soon after several reinforced presentations. However, the impaired responding elicited by the CS during the initial

CS–US pairings could be viewed as arising from either a primacy or recency effect because the CS–noUS memory is not only the first-learned association, but also the most recently learned association; thus, the distinction between primacy and recency effects is again unclear. However, the view of latent inhibition as due to the recency of CS-alone presentations is consistent with evidence showing slow reacquisition of responding to an extensively extinguished CS (e.g., Bouton, 1986; Bouton and Swartzentruber, 1989; Calton et al., 1996; Hart et al., 1995). During the initial CS–US pairings in the reacquisition phase, the CS–noUS memory can benefit from recency but not from primacy and, still, as in latent inhibition, the CS-noUS association strongly impairs responding elicited by the CS. An unexploited means of directly assessing primacy effects in Pavlovian preparations might be to phasically train three different USs, each with its own unique conditioned response. Waning recency might be expected to facilitate expression of the first- and second-learned associations, whereas a shift to primacy would favor the first-learned association over the second-learned association.

The question then is how can primacy effects be observed with two-phase procedures? Primacy effects would be suggested by a strong resistance to a change in responding to the CS despite extensive training of the second-learned association relative to an appropriate control condition. For example, primacy might be assumed to prevail if following CS–US pairings responding to the CS did not extinguish after extensive non-reinforced training or, inversely, if following CS-alone exposure responding to the CS did not increase after extensive reinforced training. But this is not usually the case in conditioning experiments; responding to a CS usually rapidly adapts to the most recent contingency (which is particularly true in the case of reinforcement). Primacy effects, however, can be observed indirectly, by performing certain post-training manipulations between training of the second-learned association and testing with the CS. We elaborate upon this in the next section.

2.1. Recency-to-primacy shift versus memory integration in interference between outcomes

Summarizing our previous discussion, different manipulations (e.g., long retention intervals or contextual changes), when performed after training of the target and interfering associations, can attenuate the recency effect in interference between outcomes. That is, the subjects' behavior at test typically no longer shows a strong dependency on the most recent training experience. Instead it reflects an increasing influence of the original learning experience. However, the process leading to this attenuation of second-learned behavior is not entirely clear. At least two different mechanisms are plausible. The first is *a shift from recency-to-primacy,* and the second is *memory integration*. Simply put, the recency-to-primacy shift account is based on the notion that, after a post-training manipulation, the first-learned association again prevails over the second-learned association with respect to responding elicited by the CS. In contrast, the memory integration account proposes that, after a post-training manipulation, the recency effect fades and responding elicited by the CS is based on the CS's total associative history, with little impact of trial order (i.e., with minimal or no primacy nor recency effects). According to both accounts, as a result of the post-training manipulation, the last-trained association no longer prevails in memory (i.e., the recency effect is partially or completely abolished).

The difference between these two accounts is subtle and, in many cases, they predict a similar impact of the post-training manipulations following outcome interference treatment. For example, when a retention interval is interpolated between extinction treatments and testing, both accounts predict that responding will recover. That is, spontaneous recovery of responding can be viewed as due to either the CS–US and CS–noUS associations both having an impact on performance (memory integration) or the CS–US association again having the larger impact on performance (recency-to-primacy shift). The two accounts both rely on the recency effect waning as time elapses after the last phase of training. The recency-to-primacy shift view predicts that responding at test will resemble responding at the end of training of the first-learned association. According to this view, after a post-training manipulation strong responding should be observed in the case of an extinction procedure (i.e., because the CS–US association is again expressed), whereas weak responding should occur in the case of a latent inhibition procedure (i.e., because the CS–noUS association is again expressed). In contrast, the memory integration view merely states that all previously learned associations

will simultaneously affect responding to the CS during testing. Hence, the putative integrative response would appear as a partial recovery of the CS–US memory following extinction treatment or as a partial recovery of the CS-pre-exposure memory after latent inhibition and reinforced training treatments. Importantly, within the memory integration view no privileged retrieval of the first-learned association is essential for this change in performance. This integration could occur prior to any retrieval or, alternatively, following retrieval of the two associations into working memory.

It is important to note that based on theoretical arguments, some post-training manipulations might be expected to produce a direct shift from a recency effect to a primacy effect because the manipulation includes presentation of a discriminative stimulus for initial training. An example of this is the ABA renewal design (e.g., Bouton and King, 1983), in which conditioning and extinction take place in contexts A and B, respectively, with the CS then being tested in context A. In this design, at test the presence of contextual cues that accompanied the CS–US pairings presumably primes retrieval of the US representation when the CS is presented, resulting in strong responding to the CS, which is consistent with a recency-to-primacy shift. However, what is usually observed is a partial recovery of responding (i.e., renewal, like spontaneous recovery, is rarely complete), which could as readily reflect memory integration as an incomplete recency-to-primacy shift. Only if responding is greater than a control group that received the same numbers of CS–US and CS–noUS trials, interspersed but in their respective contexts, would there be unambiguous evidence for a recency-to-primacy shift as opposed to discriminative learning independent of trial order. In contrast to ABA renewal, the expectation of a recency-to-primacy shift based on the context serving as a discriminative stimulus does not exist in the case of other renewal designs, such as the ABC design (i.e., conditioning, extinction, and testing each in a different context, e.g., Bouton and Bolles, 1979a) or the AAB design (i.e., conditioning and extinction in a single context, different from that of testing, Bouton and Ricker, 1994) because testing does not occur in the context of reinforced training. Possibly a stronger recency-to-primacy shift in the ABA renewal design is responsible for the generally observed larger efficacy of the ABA renewal design in producing a response recovery after extinction, relative

to the ABC and AAB renewal designs (for discussion, see Bouton and Ricker, 1994). Similarly, other post-training manipulations, such as long retention intervals or presentations of intense extraneous stimuli, may not produce unimpeded retrieval of the first-learned association, but a mere attenuation of the impact of the most recently acquired association because there is nothing within these treatments to prime the first-learned association. However, it is ultimately an empirical question as to whether contextual changes that would not be expected to facilitate retrieval of the first-learned association, such as ABC and AAB renewal treatments and long retention intervals, produce a shift from a recency effect to a primacy effect or a shift from recency to memory integration.

Although most evidence in the literature could be viewed as consistent with both the recency-to-primacy shift and memory integration views, some studies have yielded exclusive support for one of these positions. The recency-to-primacy shift view was strongly supported by a study recently performed in our laboratory with rats (Wheeler et al., 2004), in which the impact of a retention interval interpolated between training and testing was examined in both extinction and latent inhibition paradigms. Initially animals received either reinforced trials followed by non-reinforced trials (extinction treatment) or non-reinforced trials followed by reinforced trials (latent inhibition treatment). When animals were tested with the CS after a short delay, responding to the CS was subject to a recency effect. That is, strong responding was observed in the latent inhibition condition (i.e., reflecting recent training of the CS–US association) and weak responding was found in the extinction condition (i.e., reflecting recent CS-alone presentations). However, when testing was delayed by a 27-day retention interval, the pattern of responding was completely reversed, showing stronger responding in the extinction condition than in the latent inhibition condition despite identical numbers of reinforced and non-reinforced trials in the two conditions. Convergence of the two training conditions at the long retention interval would have been ambiguous because it could have reflected either memory integration or an incomplete recency-to-primacy shift. But Wheeler et al. saw a crossover between these two training conditions as a function of retention interval, which is consistent only with a recency-to-primacy shift.

Comparable data from human participants were observed in a contingency learning situation by Stout et al. (in press). Moreover, Stout et al. included a control condition in which the cue–Outcome and cue–noOutcome trials were interspersed (i.e., partial reinforcement training). With a short retention interval (7 s), not surprisingly the extinction group reported a weak cue–outcome contingency (relative to the partially reinforced group) soon after receiving many nonreinforced trials and the latent inhibition group reported a strong contingency (relative to the partially reinforced group) soon after receiving many reinforced trials. However, with a long retention interval (48 h), spontaneous recovery increased the contingency reported by the extinction group to a level greater than the partially reinforced group and super-latent inhibition decreased the contingency reported by the latent inhibition group to a level lower than the partially reinforced group. Memory integration would have resulted in convergence of the extinction and latent inhibition groups at the long retention interval to the level of the partially reinforced groups (which did not differ as a function of the retention interval). Only the recency-to-primacy shift account fits this crossover effect. It is not clear, however, which mechanism underlies this shift from recency-to-primacy. Mere passage of time could be the cause of the prevailing status of the first-learned association when testing occurred after the long retention interval. Alternatively, it is also possible that, in the long interval condition, cues associated with reseating the participants upon their returning to be tested could have directly primed the first-learned association at test. That is, cues associated with the participants' arrival in the laboratory at the start of the experiment could become retrieval cues for the cue–outcome relation learned in first place. Research with non-human animals indicates that explicit discrimination training may be necessary in order for different types of cues, such as contextual cues (Thomas and Empedocles, 1992) or handling cues (Thomas and Sherman, 1986), to gain retrieval value. However, this possibility cannot be categorically rejected in regard to Stout et al.'s study until further research is performed.

In contrast, the integrative response view received apparent support from a human contingency learning study by Matute et al. (2002). These authors observed that, in the absence of any post-training manipulation prior to testing with the target cue, the ratings of this cue were strongly affected by recency (i.e., extinction treatment in their experiments). But the ratings of the cue tested after interpolation of a post-training manipulation (e.g., presenting a screen with instructions between training and testing) closely represented the overall cue–outcome contingency during training, with no apparent primacy or recency effect. Therefore, evidence concerning the impact of post-training manipulations performed following training and interference treatment might be viewed as mixed. However, the logic of the two positions makes it harder to refute the recency-to-primacy shift framework than the memory integration framework. Results showing a clear shift from recency-to-primacy are problematic from the memory integration viewpoint, whereas any finding that is claimed to demonstrate memory integration could be alternatively viewed as due to an incomplete shift from recency-to-primacy. This difficulty in refuting the recency-to-primacy account is a weakness of the position, but is not as problematic as the above-cited clear failures of the memory integration viewpoint.

It is worth noting that memory integration might be viewed as a more normative strategy than a shift from recency-to-primacy. That is, with short retention intervals, prior experience with stability of environmental contingencies makes it reasonable to expect environmental contingencies to stay as they most recently were. But with a longer retention interval or a change in context, consistency with the last experienced contingency is less likely and it becomes more reasonable to base one's expectation on all relevant prior experience. However, it should not be forgotten that much behavior is suboptimal (e.g., Gould and Lewontin, 1979), so a strategy being normative provides little support for that strategy actually being used by organisms.

2.2. Recency-to-primacy shift and memory integration in models of learning

The various contemporary models of associative learning make different predictions regarding how primacy and recency effects on conditioned responding following outcome interference might arise from post-training manipulations. According to traditional acquisition-focused models of learning (e.g., Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972; Wagner, 1981), the more recently trained relationships will tend to dominate responding

to the CS at test. That is, these models anticipate recency effects will be impervious to post-training manipulations that do not involve any of the training stimuli. Thus, neither recency-to-primacy shifts nor memory integration are predicted. Consider extinction for example. Some of these models (Mackintosh, 1975; Rescorla and Wagner, 1972) anticipate that extinction will result in the unlearning of the target association. That is, CS-alone trials following CS–US pairings presumably result in a weakening of the previously formed CS–US association. Hence, by the end of extinction training, the target association is assumed to be *erased* from the subject's memory. The implication of the account that these models offer for outcome interference is that post-training manipulations involving no further training of the CS (e.g., retention intervals and context shifts) should have no impact at all on responding to the target CS. Other models (e.g., Pearce and Hall, 1980; Wagner, 1981) view extinction treatment as resulting in the formation of an inhibitory association. However, this formulation also fails to anticipate effects of the post-training manipulations discussed here. It is possible to integrate this viewpoint with successful interference theories such as that of Bouton (1997). But then the explanatory burden with respect to these post-training manipulations would fall squarely on the interference theory rather than on the learning theory.

Another group of learning models also rejects the view that retroactive outcome interference is due to unlearning. Instead, these models focus on performance deficits to account for these effects. This is the case of statistical models of learning (e.g., Allan, 1980; Cheng and Novick, 1992), as well as at least one associative model of learning (Miller and Matzel, 1988; see also Denniston et al., 2001). These models reject the view that outcome interference results from the deletion of the target memory; thus, they might initially be thought to better account for spontaneous recovery and renewal. However, these models are unable to account for trial–order effects because they all assume that the different learning experiences are encoded and equally stored in the subject's memory, and that responding to the target CS depends on the interaction among different stored experiences at the time of testing. Consequently, they can explain neither primacy nor recency effects. Memory integration is assumed to occur by default. Moreover, these models lack a mechanism by which the specific post-training manipulations

discussed above might influence responding to the target CS at test. Thus, despite the different learning experiences (e.g., reinforcement and non-reinforcement) not competing for associative status in this framework, these models fail to explain effects such as spontaneous recovery or renewal of responding following outcome interference. One non-associative model, Gallistel and Gibbon (2000), posits that subjects retain knowledge of all prior experiences along with the order in which they occurred. This allows the model to anticipate recency effects. However, the model has no mechanism to account for the effects of post-training manipulations such as long retention intervals or changes in contexts.

Importantly, however, performance-focused models of learning such as Allan (1980) and Cheng and Novick (1992) lend themselves to the incorporation of certain modifications that would allow them to explain primacy and recency effects, as well as the impact of some post-training manipulations. For example, these models could incorporate some primacy and recency effects, such as serial position effects (e.g., Kanak and Stevens, 1992), by assuming that the impact on responding of the different trial types in the 2×2 contingency matrix (i.e., cue–outcome, cue alone, outcome alone, and no cue or outcome) is weighted, with the weight of first and last training trials being larger than the weight of trials in the middle of the training experience. Likewise, these models could be also adapted to account for the impact of post-training manipulations such as long retention intervals and context shifts which tend to reveal primacy shifts. For example, the impact of recently experienced trial types on responding could be assumed to wane with time (spontaneous recovery) or to be weaker in a different context (renewal). However, it should be noted that these modifications are post hoc.

Some recent models, such as the one proposed by Bouton in 1997, are better able to explain the effects of these post-training manipulations. According to this model, after interference between outcomes the most recent association is better retrieved from memory and hence interferes with retrieval of the previously trained association. Moreover, post-training manipulations performed after outcome interference treatment can impair retrieval of the second-learned association, thereby releasing the first-learned association from outcome interference. This account of the recency-to-primacy shift can readily explain a large

amount of the evidence in the literature concerning retention intervals and context shifts.

Additionally, there is another less developed account that speaks to the effects of these post-training manipulations, at least as applied to human contingency learning. Catena et al. (1998), Hogarth and Einhorn (1992) and Pennington and Hastie (1992) have suggested various belief revision models. According to this approach, all information is processed and stored as a function of the frequency of judgment in force during training, which is established by the experimental demands regarding the participant's production of a response. A response may be required on a trial-by-trial basis, after a block of trials, or only at the end of all training. Specifically, in Catena et al.'s model a cue's rating is determined conjointly by its previous rating and, with greater weight, by information that the participant received about that cue since the last rating was produced. This model can explain why, in Matute et al.'s (2002) experiments, a cue that underwent extinction treatment was given higher ratings when a rating was required of the participants only at the end of all training trials than when participants were required to give a rating on each trial. Importantly, if it is also assumed that post-training manipulations, such as contextual changes and long retention intervals, have the same effect on responding to an extinguished cue as shifting the participant into a judgment frequency mode that favors equally weighting all prior experience, Catena et al.'s model can also explain the impact of these manipulations. The underlying assumption here is that memory integration is fundamental and other judgment frequency modes are context specific. In this view, post-training manipulations performed after outcome interference treatments would encourage memory integration. As the context changes from that of training, a memory integration strategy is revealed. However, like all memory integration arguments, any supporting data can be viewed as an incomplete shift from recency-to-primacy.

In a similar vein, some models developed outside the area of stimulus-stimulus learning (e.g., classical conditioning and human contingency learning) could be adapted to explain the impact of post-training manipulations after outcome interference. Such is the case of the cumulative-effect model (Davis et al., 1993), which was developed to account for choice behavior in the operant conditioning tradition (see,

e.g., Herrnstein, 1961). Like traditional associative models (e.g., Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972; Wagner, 1981), the cumulative-effects model is sensitive to trial order. However, in contrast to traditional associative models, which can only explain recency effects, its sensitiveness to trial order allows the cumulative-effects model to account for both primacy and recency effects. Even more important, contrary to traditional associative models, the cumulative-effects model is able to retain the complete training experience (i.e., it is an integrative model or, in the authors' words, a non-local model). Therefore, unlike traditional associative models, the cumulative-effects model does not postulate the destruction of first-learned information due to subsequent, more recent learning. Although this model speaks of competition between response tendencies (choice behavior), it could be adapted to explain interference between outcomes (J.A. Nevin, personal communication) in the classical conditioning paradigm by assuming that competition takes places between response tendencies appropriate to the excitatory versus inhibitory associations, instead of between two excitatory and incompatible response tendencies (e.g., tendencies to respond to the right versus left keys, the procedure typically used in the choice behavior paradigm). It must be noted, however, that this model does not incorporate any process by which post-training manipulations such as context changes or retention intervals could affect responding at test. But, since the cumulative-effects model retains the complete memory of the training experience, post hoc adaptations similar to those that could be made in statistical models are also possible here (e.g., the impact of excitatory versus inhibitory response tendencies could be weighted in the response rule).

3. Concluding comments

In this article, we have discussed outcome interference effects in relation to the impact of post-training manipulations, including long retention intervals and changes in context. We have suggested that these manipulations, which have often been viewed as producing a shift from recency-to-primacy (e.g., Bouton, 1997), can be alternatively viewed as producing an integration of memory. The memory integration ac-

count has the virtue that it is seemingly normative, but the drawback is that any supporting data could simply reflect an incomplete shift from recency-to-primacy. Moreover, memory integration was directly challenged, at least in a few specific situations, by the results of Stout et al.'s (in press) and Wheeler et al.'s (2004) experiments, which showed clear evidence of a recency-to-primacy shift following outcome interference (see Section 2.1). The clearest test of recency and primacy effects comes from studies that include a partially reinforced control group with the same total number of reinforced and non-reinforced presentations of the target CS as the interference groups. This provides a guide for future experimental design.

We have also briefly discussed the predictions of different models of learning regarding recency and primacy effects, as well as the impact of post-training manipulations on these effects. Traditional models of learning (e.g., Rescorla and Wagner, 1972) are readily able to explain recency effects. However, in these models outcome interference effects are accounted for as learning deficits and, hence, most of them are ill-equipped to account for changes observed following post-training manipulations, such as long retention intervals and context shifts, on responding to CSs that previously underwent outcome interference. In contrast, statistical models of learning (e.g., Allan, 1980) and some associative models (e.g., Miller and Matzel, 1988) assume that outcome interference is not due to unlearning, but to a performance deficit. However, without additional assumptions these models cannot account for primacy and recency effects nor the impact of post-training manipulations.

Seemingly, the model that fares best without additional assumptions is Bouton's (1997) retrieval model, which explains the influence of these post-training manipulations as resulting from a change in context between training and testing. This change presumably prevents the test context from facilitating retrieval of the most recently acquired association, thereby allowing expressing of initially acquired associations (i.e., a shift from recency-to-primacy). The privileged status of the initial memory arises from its being unambiguous when it was acquired. Although the preponderance of existing data is easier to reconcile with a recency-to-primacy viewpoint than a memory integration account, the normative nature of memory integration calls for researchers to develop tests for it that would preclude an account based on an incomplete shift from recency-to-primacy.

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