

# Inter-stage context and time as determinants of latent inhibition

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## Introduction: effects of time and context on latent inhibition

Despite its apparent simplicity, the phenomenon of latent inhibition (LI) represents one of the most sophisticated and flexible mechanisms that organisms with complex nervous systems have developed through evolution to ensure efficient interaction with the environment. Because the environment is constantly changing, mechanisms that determine the processing of a neutral stimulus depend on a large range of different circumstances. In this chapter we will focus on the role played by two factors, namely, time and context, that seemingly affect LI separately, as well as in combination. The impact of these factors (both apart and conjointly) on LI is still one of the greatest challenges to associative theories of learning.

In any learning process there is a series of elements that determine the intensity and type of association that is formed. In the case of classical conditioning, some of the parameters on which Pavlov (1927) concentrated in his original studies were related to the temporal contiguity between stimuli (e.g., whether the stimuli involved in the pairings were presented simultaneously or sequentially, or the order in their presentation when presented sequentially), as well as to the excitatory vs. inhibitory nature of the association acquired under different treatments. Some other elements that have subsequently demonstrated their relevance to associative learning were also pointed out by Pavlov, although sometimes in a quite intuitive manner. For example, he mentioned that conditioned reflexes could be affected by the surrounding stimuli during conditioning in the animal's environment. Thus, for instance:

The environment of the animal, even when shut up by itself in a room, is perpetually changing. Footfalls of a passer-by, chance conversations in neighbouring rooms, slamming of a door or vibration from a passing van, street-cries, even shadows cast through the windows into the room, any of these casual uncontrolled stimuli falling upon the receptors of the dog set up a disturbance in the cerebral hemispheres and vitiate the experiments [...]

(Pavlov, 1927, *Lecture II*)

The role of context for conditioning and associative learning has, since then, always been recognized and accompanied by extensive research (see, e.g., Balsam & Tomie, 1985). In particular, the essential role played by context in the modulation of LI has received extensive empirical and theoretical analysis in recent years (e.g., Hall & Channell, 1985, 1986; Lovibond, Preston, & Mackintosh, 1984; Westbrook, Jones, Bailey, & Harris, 2000). More specifically, using two-stage experimental procedures to induce the LI effect (i.e., preexposure stage with the to-be-conditioned stimulus without consequences, followed by a conditioning stage), it has been clearly established that the change of context between the two stages results in the weakening or even the abolition of the LI effect. More recently, these effects have been explored with three-stage procedures (i.e., preexposure, conditioning, and testing), which allow for a greater number of possible context switches (AAA, ABA, and AAB designs, with each letter representing the context at preexposure, conditioning, and testing stages, respectively). Specifically, Westbrook *et al.* (2000) demonstrated that conducting preexposure in a context different from that of conditioning and testing (i.e., ABB) increased the conditioned response at test (i.e., attenuation of LI), relative to a condition given no context change throughout training (i.e., AAA). Moreover, if the change of context was limited to the conditioning stage (i.e., ABA) the LI effect was enhanced.

The second factor on which we shall focus in this chapter, the effect of the passage of time on previously established associations, was a subject also covered by Pavlov (1927) when he analyzed, for instance, spontaneous recovery, the recovery of conditioned responding to an extinguished CS when testing was delayed. However, after Pavlov's studies, the interest of researchers of associative learning mainly centered on factors determining the *acquisition* of associations, effectively sidelining the study of the effects of time on the expression of previously acquired associations. This may explain why the study of the effect of passage of time on learning has usually been linked more strongly to the field of memory than to the study of associative learning (with some exceptions, such as the above-mentioned case of spontaneous recovery or the analysis of the fear-incubation effect, e.g., Eysenck, 1968). As for the effect of the passage of time on LI, empirical findings have been contradictory. The first studies evaluating the role of this variable on LI were conducted in the 1970s and revealed that passage of time by itself did not affect LI (for a review see Lubow, 1989, pp. 67–69). In the 1980s, a series of conditioned taste aversion studies, using a three-stage procedure for inducing LI, showed that the introduction of time intervals between conditioning and test stages attenuated LI (e.g., Kraemer & Ossenkopp, 1986; Kraemer & Roberts, 1984). Although these studies did not allow definitive conclusions to be drawn because they presented different tastes across experimental stages, they were soon followed by others which did use the same stimuli throughout the experiment. Under such circumstances, a lengthening of the retention interval resulted in a recovery of the conditioned aversion response. For example, Aguado, Symonds, and Hall (1994) found that when testing was performed 14 days after

conditioning LI was weaker than when the test was performed 48 hours after conditioning. This result has also been obtained with other experimental procedures, such as conditioned freezing (e.g., Killcross, Kiernan, Dwyer, & Westbrook, 1998). The recovery of the conditioned response (reduction of LI) with an increase in time between conditioning and test stages has been repeatedly cited as evidence that LI is the result of a failure in information retrieval (e.g., Bouton, 1993; Miller & Matzel, 1988), an account that directly challenged the traditional view whereby LI is the result of a failure in the acquisition of the conditioning association (e.g., Lubow, 1989; see Section 2 for a discussion).

The first interpretation of the effect of delayed testing on LI was proposed by Kraemer and Roberts (1984), who considered that passage of time has a differential effect on each of the two associations formed during the preexposure and conditioning stages (CS–nothing and CS–US, respectively). The first, relatively less important association, would tend to lose impact on behavior over time, while the second, relatively more important due to its biological significance, would tend to increase its capacity to control behavior as time elapsed.

A different interpretation of the attenuation of LI after the introduction of a delay between conditioning and testing stems from the view that the passage of time acts like a context change (e.g., Bouton, 1993). According to this premise, passage of time would lead to an attenuation of LI similar to that observed when the physical context is changed between conditioning and testing stages (e.g., Lovibond *et al.*, 1984; Westbrook *et al.*, 2000). Despite the success of this view in explaining the reported data, other studies using similar procedures soon showed that this manipulation did not always produce the attenuation of LI. On some occasions, the LI effect remained intact despite the introduction of the delay (e.g., Alvarez & Lopez, 1995). Even more critically, the opposite effect was found: *super*-LI was observed when a long time-interval (21 days) was introduced between conditioning and testing (e.g., De la Casa & Lubow, 2000, 2002, 2005; Lubow & De la Casa, 2002). For example, De la Casa and Lubow (2000) found a decrease in aversive responding elicited by the conditioned taste (i.e., an increase in LI) when the test was delayed by 21 days compared to a group in which the test was delayed by only one day. Similar results have been obtained in other studies using conditioned taste aversion (e.g., De la Casa & Lubow, 2000, 2002, 2005), as well as with conditioned suppression procedures (e.g., Wheeler, Stout, & Miller, 2004), and with humans using a contingency learning task (Stout, Amundson, & Miller, 2005).

In a recent example from our laboratory (De la Casa, unpublished results), we used an eyeblink conditioning procedure with human participants to ascertain the effect of interposing a retention interval (7 days) between conditioning and testing stages in a three-stage LI treatment. All participants were instructed to watch a silent movie, during which time the stimulus preexposed group (PE,  $n = 20$ ) was presented with an auditory stimulus (i.e., either a tone or a white noise, counterbalanced). The non-preexposed group (NPE,  $n = 20$ ) was exposed to the same experimental situation, but

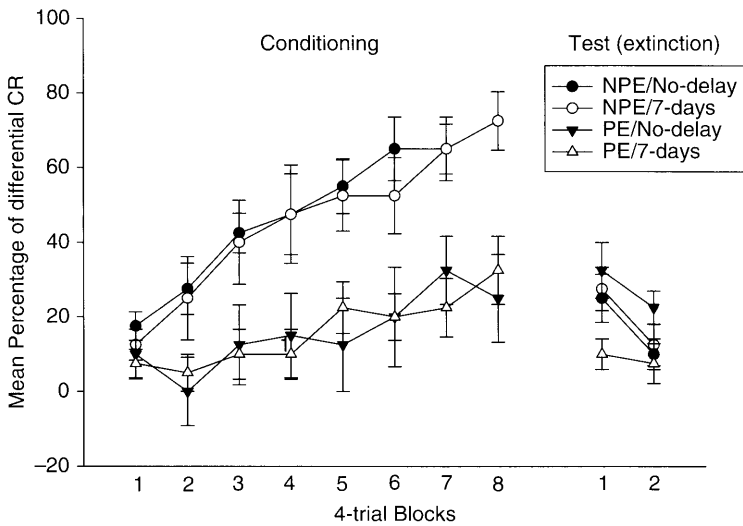


Figure 3.1. Mean percentage of differential CR (i.e., % CR to the CS+ – % CR to the CS–) in 4-trial blocks in each of four experimental conditions during Conditioning (left panel) and Test (right panel) stages. PE, preexposed; NPE, non-preexposed.

without receiving any nominal auditory stimuli. Subsequently, one of the stimuli (either tone or white noise, counterbalanced) was paired 32 times with the air-puff US (CS+ condition); the second stimulus was also presented 32 times, but without the US (CS–). The test stage was conducted either 3 s (no-delay) or 7 days after conditioning. The test stage consisted of eight presentations each of CS+ and CS–. The four experimental groups resulting from combining the Preexposure and Delay factors were: NPE/No-delay, PE/No-delay, NPE/7-days, PE/7-days. Figure 3.1 depicts the mean differential conditioned responses (the percentage of conditioned responses to CS+ minus the percentage of conditioned responses to CS–) for conditioning and testing stages as a function of groups. As can be seen, the expected LI effect emerged across conditioning trials, yielding a lower rate of responding for the PE groups than for the NPE groups. As expected (see below), the Preexposure  $\times$  Delay interaction at testing stage was significant,  $F(1, 36) = 4.17$ ,  $P < 0.05$ , due to differential CRs in the test stage being significantly lower for the PE/7-days group than for the PE/No-delay group, thus revealing that the retention interval induced an *increase* of the LI effect.

An analysis of the experiments that have studied the effect of passage of time on LI reveals procedural differences related to intensity of the stimuli, temporal parameters, number of preexposures and conditioning trials, and length of the retention interval. However, one factor is consistently associated with the direction of the time-induced LI effect, attenuated or potentiated: the context in which the retention interval is spent. Specifically, in cases where the attenuation of LI is observed the retention interval is spent in the *same* context as that of the other experimental stages

(typically the home cage). In those experiments reporting enhanced LI, the delay occurred in a context that was *different* from the contexts of the preexposure, conditioning, and testing stages. Lubow and De la Casa (2005) proposed that the retention interval context was fundamental for determining the effect of the passage of time on LI (see section *Explaining time–context interactions*).

### **Theoretical implications**

Despite the broad variety of phenomena studied in the associative learning literature, it would be fair to say that a small collection of effects have been the primary target of most research, thereby critically guiding theoretical advance. A classic example is the case of the blocking effect (Kamin, 1969), which encouraged the development of the Rescorla and Wagner (1972) model. Similarly, it could be claimed that the need for a comprehensive explanation of LI encouraged the development of a whole family of learning theories, both general and specific to LI (e.g., Bouton, 1997; Lubow, Weiner, & Schnur, 1981; Mackintosh, 1975; McLaren & Mackintosh, 2000; Miller & Matzel, 1988; Pearce & Hall, 1980; Schmajuk, 2002; Wagner, 1981). In the present section we will discuss these models in regard to LI and, specifically, in relation to their account for the impact of contextual and/or temporal manipulations on LI (for detailed discussions of other aspects of some of these models, see Westbrook & Bouton and Escobar & Miller, in the present volume).

### ***Acquisition-deficit models***

A common distinction of associative models has to do with their explanations of stimulus competition phenomena (e.g., overshadowing and blocking) and interference effects (e.g., extinction and LI) as either acquisition or performance deficits. Briefly, according to acquisition-deficit models, LI consists of the *impaired acquisition* of the target CS–US association due to the prior exposure of the CS in the absence of the US. By contrast, performance-deficit models propose that LI consists of the *impaired conditioned response* elicited by the CS due to CS-preexposure. In other words, according to performance-deficit models CS-alone exposures hinder conditioned responding to the CS, but do not interfere with the acquisition of the CS–US association. In the present section, we will discuss the acquisition-deficit account of LI, represented by attentional models of learning (e.g., Lubow *et al.*, 1981; Mackintosh, 1975; Pearce & Hall, 1980) as well as by Wagner’s (1981) SOP model. (Performance-deficit accounts of LI will be discussed in the next section.)

### ***Attentional models***

Attentional models of learning have provided the most popular explanation of LI, perhaps because it best fits with the common view of stimulus competition and

interference phenomena as reflecting the organism's limited information processing resources. Simply put, since it would be practically impossible for an organism to attend to the immense array of stimuli in its environment, much of this information must be ignored. Although some stimuli will "demand" processing merely based on their inherent physical properties (e.g., high salience), other stimuli will "deserve" this processing based on their acquired *informative value*, a value that is determined by their reliability as signals for the occurrence of relevant events (i.e., stimuli of biological significance, such as food, water, or pain). Within this framework, models agree that, in an LI treatment, exposure to the CS in the absence of the US will result in a progressive loss of attention to the CS. In turn, because attention to the CS determines, at least in part, its ability to acquire associative strength, the effectiveness of subsequent CS-US pairings will be diminished relative to a condition with no CS-preexposure. As we will see, attentional models diverge, however, in the specific mechanisms leading the decline of attention, as well as in their views of the very nature of attention.

Soon after the publication of the model by Rescorla and Wagner (1972), its inability to explain LI became apparent. According to their model, the repeated presentation of the CS in the absence of the US during preexposure has no effect upon the CS's ability to subsequently acquire associative strength. Mackintosh (1975) was quick in realizing that the Rescorla-Wagner model could be revised in order to extend its explanatory power, thereby allowing it to account for several additional phenomena, including LI. Mackintosh added to the Rescorla-Wagner model a rule by which the associability of the CS (i.e.,  $\alpha_{CS}$ , which corresponds to the CS salience in the Rescorla-Wagner model) could change its value according to experience with the CS. Specifically, according to Mackintosh, on each presentation of the CS the value of  $\alpha_{CS}$  is updated based on a comparison between the CS's associative strength and the associative strength of all other CSs present on that trial. When the associative strength of the target CS is greater than the associative strength of the other CSs,  $\alpha_{CS}$  increases. Conversely, when the associative strength of the target CS is smaller than (or equal to) the associative strength of the other CSs,  $\alpha_{CS}$  declines. Because the CS's associability, or  $\alpha_{CS}$ , corresponds to the attentional processing received by the CS, this rule in Mackintosh's model could be restated as follows: attention to the target CS directly correlates with its relative ability to predict the US. As the CS becomes a better predictor of the US, it receives more attention; conversely, as the CS loses predictive value, it also loses attention. Interestingly, in Mackintosh's (1975) model, attention to the CS (or associability, or  $\alpha_{CS}$ ) is considered to be an attribute of the CS, whose value is initially (when the CS is novel) determined by its physical properties (e.g., salience) and then (when the CS is familiar) by its prior associative history. Therefore, a reciprocal relation between attention and learning was proposed: not only attention to the CS determined its subsequent ability to acquire associative strength, but also the CS's associative strength determined its subsequent attentional processing. Mackintosh's attentional

model explained LI by assuming that the associability of the CS ( $\alpha_{CS}$ ) declines during its preexposure, a decline that is due to the CS having an identical associative strength (i.e., zero strength) to that of the rest of the CSs or contextual cues<sup>1</sup>. As a consequence, during the CS–US pairings, the CS will acquire a weak (or no) association with the US due to the low value of  $\alpha_{CS}$ . In psychological terms, during CS-alone presentations the animal first learns that the CS is not a reliable predictor of the US and, thus, withdraws its attention from the CS. Because attention allocated to the CS during the subsequent CS–US pairings is reduced, the acquisition of the CS–US association is impaired.

Another attentional model, this one proposed by Pearce and Hall (1980), shares Mackintosh's (1975) view that the attentional processing received by the CS is represented by CS associability ( $\alpha_{CS}$ ). In the Pearce–Hall model, the value of  $\alpha_{CS}$  also changes according to the CS's associative history. However, this model diverges from that of Mackintosh in regard to the rules determining the change of  $\alpha_{CS}$ . Whereas, according to Mackintosh,  $\alpha_{CS}$  directly correlates with the associative strength of the CS (i.e., the CS receives more attention as it better predicts the US), in the Pearce–Hall model the value of  $\alpha_{CS}$  *decreases* as the CS becomes a more reliable predictor of the outcome, regardless of whether this outcome consists of the occurrence of the US or the absence of the US (i.e., “no US”; Konorski, 1967). Thus, in the Pearce–Hall model, both CS–US pairings and CS-alone presentations will have an identical detrimental impact on the value of  $\alpha_{CS}$ : as the animal learns to predict the outcome of the CS, less attentional processing will be devoted to the CS (i.e., the value of  $\alpha_{CS}$  will decrease). In this view, once the “meaning” of the CS has been already learned, the CS will not demand further attentional effort and, therefore, these resources can be devoted to those CSs the animal still needs to learn about. In this model, it is precisely when the outcome of the CS is not completely predictable that attention will be paid to the CS (i.e.,  $\alpha_{CS}$  will maintain a high value). In the Pearce–Hall model, as in Mackintosh's model, LI is due to the low value of  $\alpha_{CS}$  following CS preexposure, which results in the impaired acquisition of associative strength during the subsequent CS–US pairings. However, contrary to Mackintosh's model, which claims that the low value of  $\alpha_{CS}$  following CS-alone trials is due to the CS being a poor predictor of the US, in the Pearce–Hall model the low value of  $\alpha_{CS}$  following CS-alone trials is due to the CS being a reliable predictor of the absence of the US (i.e., the CS fully predicts the occurrence of the “no US”).

Despite their multiple merits, the attentional models of Mackintosh (1975) and Pearce–Hall (1980) are unable to explain the effects of contextual or temporal manipulations on LI. Because, according to these models, the value of  $\alpha_{CS}$  depends on the CS's reliability as a predictor of the occurrence of the US (as well as of the

<sup>1</sup> The decrease in the value of  $\alpha_{CS}$  when the CS is a worse predictor of the US than the other stimuli can be perfectly justified. However, the same cannot be said about the decrease in the value of  $\alpha_{CS}$  when the CS and the other stimuli are equally reliable predictors of the US. In fact, there is no reason why this latter scenario should not produce an increase, rather than a decrease in the value of  $\alpha_{CS}$ . Alternatively, the model could assume no variation in the value of  $\alpha_{CS}$  under these conditions.

"no US", in the Pearce–Hall model), experimental manipulations that cause no change in the associative strength of the CS are of no consequence on the CS's associability ( $\alpha_{CS}$ ) and, hence, on the acquisition of the CS–US association following CS-preexposure. However, these models could easily account for the impact of certain contextual/temporal manipulations on LI by merely assuming that the reduced CS associability could be directly restored after these manipulations: if, after a context change or a retention interval,  $\alpha_{CS}$  was reset to its original value, LI would be attenuated (i.e., because the CS can now readily enter into an association with the US during CS–US pairings). This would allow the models of Mackintosh and Pearce–Hall to account for attenuation of LI when the preexposure and conditioning phases (i.e., in a two-stage design for LI) are separated by a retention interval (e.g., Hall & Minor, 1984; Pineño, De la Casa, Lubow, & Miller, 2006; Rosas & Bouton, 1997; Wagner, 1979; Westbrook, Bond, & Feyer, 1981), a context change (e.g., Hall & Channell, 1985, 1986; Lovibond *et al.*, 1984; Westbrook *et al.*, 2000), or the presentation of novel stimulation (e.g., Escobar, Arcediano, & Miller, 2005; Lantz, 1973; Pineño *et al.*, 2006; Rudy, Rosenberg, & Sandell, 1977). However, even if this assumption (i.e.,  $\alpha_{CS}$  reset to its original value after a context switch or a time break) was adopted, these models would still be unable to explain the impact of such manipulations when they are performed between conditioning and test stages of a three-phase LI procedure. In this latter case, because the CS associability ( $\alpha_{CS}$ ) exclusively determines the CS's ability to enter into an association with the US (i.e., it has no influence on the expression of a previously acquired association), any putative variation in the value of  $\alpha_{CS}$  should have a negligible impact on responding to the CS at test. Thus, even if these models adopted an *attentional restoration* process (i.e., reset in the value of  $\alpha_{CS}$ ), they would still be unable to explain the results from studies showing that, when a retention interval is interpolated between conditioning and testing, LI can be either attenuated (e.g., Aguado *et al.*, 1994; Bakner, Strohen, Nordeen, & Riccio, 1991; De la Casa & Lubow, 1995; Kraemer & Ossenkopp, 1986; Kraemer, Randall, & Carbary, 1991; Kraemer & Roberts, 1984; Kraemer & Spear, 1992; Westbrook *et al.*, 2000) or enhanced (i.e., the so-called super-LI effect; De la Casa & Lubow, 2000, 2002; Lubow & De la Casa, 2002; Wheeler *et al.*, 2004; for evidence of enhanced LI with a contextual switch between conditioning and test, see Swartzentruber & Bouton, 1992; Westbrook *et al.*, 2000).

An alternative attentional model, Lubow *et al.*'s (1981) Conditioned Attention Theory (CAT), proposed a view of attention as a response, instead of as an attribute of the CS. According to CAT, any novel CS initially elicits an attentional response (e.g., an orienting response), which is necessary in order to learn other responses to the CS. This attentional response decreases as a function of the number of CS presentations, regardless of whether the CS is presented alone or with a US (although the decay in the strength of the attentional response presumably follows different patterns in each case, with this rate being faster during CS-preexposure than during conditioning). That is, CAT, as in the Pearce–Hall model, states that LI is not an

exclusive product of CS preexposure, but of any treatment in which the CS becomes a perfect predictor of a given outcome, including the US (e.g., Hall & Pearce, 1979). Of critical importance for CAT, the attentional response behaves according to the laws of any other conditioned response and, thus, its decline during CS-preexposure can be viewed as a parallel of the decline typically observed during the extinction of Pavlovian conditioned responses. This view of CAT also implies that any experimental manipulation that would affect the acquisition and/or expression of a conditioned response (e.g., a contextual switch or a retention interval) should also affect the attentional response and, thus, have an impact on LI. More specifically, CAT predicts a recovery of the attentional response and, hence, attenuation of LI, when the preexposure and conditioning phases are conducted in different contexts (i.e., attentional recovery akin to a renewal of responding; Bouton & Bolles, 1979), or when they are separated by a retention interval (i.e., attentional recovery akin to spontaneous recovery of responding; Pavlov, 1927). In other words, CAT explains those results in the literature that were not accounted for by Mackintosh and Pearce–Hall, unless they adopted the attentional restoration construct. However, CAT cannot explain LI effects resulting from contextual and temporal manipulations that are conducted between conditioning and test stages. The reason is the same as that previously pointed out in regard to the Mackintosh and Pearce–Hall models. Specifically, because in CAT the attentional response elicited by the CS modulates the acquisition, but not the expression, of a CS–US association, any change in attention elicited by the CS at test *after* the CS–US pairings should not affect responding to the CS.

### *Memory priming*

Wagner's (1981) SOP model also accounts for LI as an acquisition failure, in this case due to the CS being rehearsed or primed in short-term memory by the context during the CS–US pairings. In the framework of the SOP model, the elements of a stimulus representation in memory (i.e., a node) can be in one of three activation states: inactive (I); a primary activation state (i.e., A1), in which the stimulus is in the attentional focus; and a secondary activation state (i.e., A2), in which the stimulus is in the attentional periphery. Briefly, the learning rules of the SOP model state that an excitatory CS–US association is formed when the elements in the nodes of the CS and the US are simultaneously activated in the A1 state. By contrast, when the elements of the CS and US nodes are simultaneously activated into A1 and A2, respectively, an inhibitory CS–US association is formed. According to this model, no association is formed when the CS node is activated in the A2 state, regardless of the activation state of the US node (but see Dickinson and Burke's [1996] revision of Wagner's [1981] SOP model). In the SOP model, the elements of a stimulus node can reach the A2 state through either a decay from the A1 state (i.e., according to its rules of temporal dynamics) or the associative activation of the stimulus-node by another

stimulus: when stimuli X and Y maintain an excitatory association, the presentation of stimulus X can activate (prime) the node of stimulus Y in short-term memory, specifically into the A2 state. Of importance, when a stimulus is associatively activated into A2, it will be poorly activated into A1, even if it is subsequently presented, because its nodal elements, already activated into A2, cannot be immediately recruited for the A1 activation state.

Based on the previous summary of selected features of the SOP model, its explanation of LI becomes straightforward. First, during CS-preexposure, the CS forms a bidirectional association with the context. Based on this association, the context is able to strongly activate (prime) the CS-node into A2, thereby preventing the activation of most of the nodal elements of the CS into A1. As a consequence, during the subsequent conditioning phase, a weak CS-US association is formed. From this explanation, it directly follows that LI should be attenuated when preexposure and conditioning treatments are conducted in different contexts: because the conditioning context maintains no association with the CS, the CS is not activated into the A2 state during the initial CS-US pairings and, thus, it uneventfully enters into an association with the US. However, the SOP model faces difficulties in explaining attenuation of LI when a retention interval is interposed between preexposure and conditioning. SOP can only explain such data when the retention interval is spent in the context in which CS-preexposure took place, thereby allowing the context-CS association to undergo extinction (i.e., because the animal is exposed to the context in the absence of the CS), thereby subsequently reducing the A2 activation of the CS by the context during the conditioning stage. Notably, although some studies have reported attenuation of LI when the retention interval was spent in the context of preexposure (e.g., Escobar, Arcediano, & Miller, 2003; Hall & Minor, 1984; Wagner, 1979; Westbrook *et al.*, 1981), attenuation of LI has also been reported when the retention interval was spent in a different context (e.g., Rosas & Bouton, 1997). Finally, the SOP model predicts no effect of a context change or a retention interval when such manipulations are performed between conditioning and testing in a three-stage design of LI. The model predicts that these manipulations would allow the CS to be more strongly activated into A1 at test (i.e., because of the weaker A2 activation caused by the test context), but this treatment should have no detectable impact on responding elicited by the CS because of the previous failure to acquire the CS-US association.

### *Performance-deficit models*

In the framework of performance-deficit models, interference effects (e.g., extinction and LI) and cue competition phenomena (e.g., blocking and overshadowing) are not due to a failure in the acquisition of the target CS-US association, but to a failure in the "translation" of an acquired CS-US association into a conditioning response.

Specifically, interference and cue competition effects can be viewed as a failure to either retrieve (Bouton, 1993, 1997) or express (Miller & Matzel, 1988) the target CS-US association. In the present section we will discuss these two models in relation to their explanation of LI, with emphasis on their accounts of the effects of contextual changes and passage of time.

*Retrieval-deficit: Bouton's (1993, 1997) retrieval failure model*

From early on, the Rescorla-Wagner (1972) model has faced problems with its explanation of interference between outcomes. Not only was the model unable, as previously mentioned, to offer an account for LI, but it also provided an explanation of extinction that had already proven problematic. Although the Rescorla-Wagner model could simulate neat acquisition and extinction curves, its explanation of extinction relied on the assumption that the CS-US association, previously acquired during the conditioning phase, was erased during the subsequent CS-alone trials (i.e., catastrophic interference; McCloskey & Cohen, 1989). However, since Pavlov's (1927) early studies, it was well known that extinction did not consist of the removal of the CS-US memory: the weak conditioned response elicited by the CS following extinction treatment recovered after a lapse of time (i.e., spontaneous recovery). This problem for the Rescorla-Wagner model soon became more evident when Bouton and his collaborators (e.g., Bouton & Bolles, 1979; Bouton & King, 1983; Bouton & Ricker, 1994) found that conditioned responding could also recover by a context change following extinction – an effect that they named *renewal* of responding.

Both spontaneous recovery and renewal effects strongly indicated that extinction could not be accounted for in terms of erasure of the original CS-US memory. Rather, it seemed that extinction consisted of the acquisition of a second memory, which somehow interfered with the memory of the excitatory CS-US association. This idea was elegantly developed by Bouton (1993), who proposed that the extinction memory (i.e., an inhibitory CS-US association) interfered with the *retrieval* of the conditioning memory (i.e., the excitatory CS-US association). That is, the excitatory CS-US memory remained intact during the subsequent CS-alone trials, but became poorly retrievable due to the interference caused by the more recently acquired and, hence, more strongly retrieved inhibitory CS-US memory. In addition, this model posited an important asymmetry between the excitatory and inhibitory CS-US associations: the inhibitory association, but not the excitatory association, was encoded as context-specific and, thus, depended upon its training context for retrieval. Thus, when the CS was presented outside the extinction context, the inhibitory association could no longer be retrieved and the excitatory association was thereby released from the interference otherwise caused by the inhibitory association. This allowed the excitatory association to be again retrieved from memory and, thus, expressed in conditioned responding. Spontaneous recovery was analogously explained by Bouton's retrieval-failure model. Because the model views passage of

time as an instance of a contextual change (i.e., in this case, it is the temporal context, rather than the physical context, that is changed), spontaneous recovery and renewal were explained by the same principle, as a failure of the memory of extinction to be retrieved at the time of test, indirectly resulting in the effective retrieval of the memory of conditioning.

The explanation of LI according to Bouton's (1993) model was very similar to that of extinction. In the case of LI, however, interference was presumed to occur proactively (i.e., the first-learned memory interferes with the second-learned memory), rather than retroactively (i.e., the second-learned memory interferes with the first-learned memory). Explaining LI required just a small adjustment to the theory. Because during CS-preexposure the animal has not yet experienced the US, the inhibitory CS-US association cannot be acquired. Consequently, Bouton proposed, in line with Konorski (1967; also see Pearce & Hall, 1980), that during CS-preexposure the animal learns a CS-no-US association, better viewed as a CS-nothing association (i.e., the animal learns that the CS is followed by no event). This CS-nothing association then interferes with the retrieval of the CS-US association during the conditioning stage, resulting in the LI effect. Bouton's (1993) retrieval model provides a straightforward account for attenuation of LI by the interpolation of either a contextual switch or a retention interval between preexposure and conditioning stages. Because the CS-nothing association will be poorly retrieved by the new context in which CS-US pairings are given, the excitatory CS-US association will be strongly retrieved and, thus, the CS will be able to elicit strong responding (i.e., attenuated LI). Interestingly, the same prediction, attenuation of LI, is made by this model when these contextual/temporal manipulations are performed after conditioning and prior to testing (e.g., Aguado *et al.*, 1994; Westbrook *et al.*, 2000). Assuming that the retrieval of the excitatory CS-US association during the conditioning stage was still incomplete, changing the context (physical or temporal) between conditioning and testing could further impair retrieval of the CS-nothing association, thereby allowing for a better recovery of the excitatory CS-US association at test (i.e., attenuated LI). This prediction provides Bouton's (1993) model with an advantage over the previously described acquisition-focused models, which predict that LI should not be affected by manipulations conducted after the conditioning stage.

In spite of its merits, Bouton's (1993) model fails to explain the enhancement of LI that results from interpolating a retention interval in a different context (i.e., super-LI; e.g., De la Casa & Lubow, 2000), or from switching the context (e.g., Westbrook *et al.*, 2000) between conditioning and test. A revision of this model (Bouton, 1997), however, does account for enhancement of LI after these contextual/temporal manipulations. According to Bouton (1997), it is not the nature of the associations (i.e., excitatory vs. inhibitory), but the order in which they are learned, that determines which association becomes context-dependent for retrieval. Specifically, it is not the inhibitory CS-US association (or the CS-no-US association), but

the association learned in second place, that depends on the context for its retrieval. The second-learned association becomes context-dependent because it is when this association is learned when the CS acquires a second “meaning” and, thus, becomes ambiguous. When the CS is followed by a second outcome, the animal presumably pays attention to contextual cues in an attempt to disambiguate its new meaning. Although this newer version of Bouton’s retrieval failure model does not make any differential prediction regarding extinction (i.e., because in this case the inhibitory association is also the second-learned association and, thus, it is expected to depend on the context for retrieval), its predictions regarding LI are diametrically different from those of his 1993 model: in an LI experiment, the excitatory CS–US association is second-learned and, hence, it is the association that is context-dependent. Therefore, the CS–no-US (or CS–nothing) association should be relatively context-independent and, thus, highly retrievable in a new context. In other words, stronger LI should be observed when the CS is tested in a context (physical or temporal) different from the conditioning context. Contrary to his original model, Bouton’s (1997) revised model can readily explain enhancement of LI when the conditioning and test phase are separated by a retention interval (e.g., De la Casa & Lubow, 2000), as well as when these phases take place in different contexts (e.g., Westbrook *et al.*, 2000). Interestingly, as opposed to the earlier version, the newer model (Bouton, 1997) cannot explain attenuation of LI when these contextual/temporal manipulations are performed either between the preexposure and conditioning stages, or between the conditioning and test stages. In sum, although Bouton’s retrieval failure model provides a relatively comprehensive explanation of a variety of LI effects, it is still unclear how it can be revised in order to embrace the aforementioned contrary effects of context/time upon LI.

*Expression-deficit: Miller and Matzel’s (1988) comparator hypothesis*

Another performance-deficit account of LI is provided by Miller and Matzel’s (1988) comparator hypothesis (also see Denniston, Savastano, & Miller, 2001). According to this model, cue competition phenomena (e.g., blocking and overshadowing) are due to the poor expression of the target CS–US association. In this model, cues do not compete for the acquisition of associative strength, nor do their associations with the US compete for retrieval (but see Denniston, Savastano, Blaisdell, & Miller, 2003). Instead, cues compete for the behavioral expression of their associative strength. Briefly, the model posits that on pairings of the target CS (X) with the US, CS X acquires an association with the US, as well as with other stimuli (CSs or contextual cues, Y) that are presented in compound with CS X (i.e., the so-called X’s comparator stimuli). When CS X is later presented at test, it consequently retrieves the memory of the US both directly (i.e., based on the X–US association) and indirectly (i.e., based on the conjoint action of the X–Y and Y–US associations). The response elicited by CS X at test is assumed to be the result of a comparison

between the direct and the indirect activation of the US-representation. CS X produces a detectable conditioned response only when the direct US-representation is stronger than the indirect US-representation, with the strength of this response being a function of the balance between the direct and the indirect activation of the US-representation.

The comparator hypothesis explains LI based on the same processes posited in its explanation of other cue competition phenomena. First, during CS-preexposure, the CS acquires an association with the context. During the subsequent CS-US pairings, both the CS and the context enter into an association with the US. When the CS is then presented at test, its direct activation of the US-representation (i.e., based on the CS-US association) will not be fully expressed into responding due to the strong retrieval of the memory of the context (i.e., based on the strong CS-context association acquired during preexposure), which, in turn, activates the US (i.e., based on the context-US representation), thereby resulting in a strong indirect activation of the US-representation. Therefore, the comparator hypothesis explains LI as an instance of overshadowing, only with the context, instead of a punctate cue or CS, overshadowing the target CS. Notably, this account of LI yields many unique predictions, many of which have received empirical support (for a review, see Escobar & Miller, this volume).

The comparator hypothesis, however, has difficulties in explaining the impact of contextual/temporal manipulations on LI. According to the comparator hypothesis, contextual manipulations can only affect responding to the target CS in an LI treatment to the extent that these manipulations affect the strength of the CS-context association, the context-US association, or both (because only these manipulations can modify the indirect activation of the US-representation and, hence, responding to the CS). Therefore, for example, the comparator hypothesis predicts that conducting preexposure and conditioning phases in different contexts will result in attenuated LI because the preexposure context, in this case, a strong comparator stimulus for the CS, has no association with the US, whereas the conditioning context, which has a strong association with the US, is a poor comparator for the CS. (In an LI experiment, the preexposure context is usually a stronger comparator stimulus for the target CS than the conditioning context because of the large number of CS-alone trials, relative to the number of CS-US pairings.) The above explanation does not apply to those cases in which a change of context follows the conditioning phase, prior to testing. In this case, the context switch should not affect responding to the target CS, basically because the status of the CS-context and context-US associations remains intact after such a manipulation. Moreover, according to the comparator hypothesis, the interpolation of a retention interval between CS-preexposure and conditioning, or between conditioning and test, should attenuate LI only to the extent that this retention interval is spent in the training context: in this case, exposure to the context will cause the extinction of either the CS-context association or the context-US association, or both, thereby reducing the indirect activation of

the US-representation and, hence, allowing the CS–US association to be strongly expressed in responding. In sum, the comparator hypothesis can only explain attenuation and enhancement of LI when contextual/temporal manipulations are performed that result in the weakening or strengthening, respectively, of the CS–context and/or context–US associations. When contextual/temporal manipulations leave these associations intact, responding elicited by the target CS should not be affected.

### Explaining time–context interactions

As reviewed in the Introduction, passage of time and contextual manipulations clearly modulate the size of the LI effect at test. Specifically, LI is attenuated in those situations in which a long retention interval is spent in the same context as the other experimental stages (e.g., Aguado *et al.*, 1994). This result is usually obtained in experiments using the conditioned taste aversion procedure, in which the experimental manipulations are typically conducted in the animals' home cages (i.e., the context remains constant throughout the experiment). In contrast, the super-LI effect appears when the long delay context is different from the context in which the rest of the experimental stages are conducted (e.g., De la Casa & Lubow, 2000). This situation occurs when the preexposure, conditioning and test stages take place in a location that is not the animals' home cage.

None of the theories of LI proposed to date (see section on Theoretical implications) seems capable of integrating the results stemming from the interaction between the delay and the context in which the delay takes place. This led Lubow and De la Casa (2005) to propose the *context differentiation hypothesis*. The rationale for the hypothesis begins by accepting the commonly held assumption that, during the different stages in an LI treatment, two associations are formed, an association between the preexposed stimulus and the absence of consequences (during preexposure), and an association between the preexposed stimulus and the US (during conditioning).

Although both associations are potentially recoverable, the essential factors that determine the context's ability to retrieve one association or another are the time elapsing following the establishment of the CS–nothing and CS–US associations and the context in which the organism spends this time. When the period following conditioning is short (typically 24/48 hours in conditioned taste aversion experiments), the context does not play an important role. The LI effect is observed, regardless of the context in which the delay has elapsed (see, for example, De la Casa & Lubow, 2000). However, when a longer time interval is interpolated following conditioning, the delay context takes on a pivotal role in the expression of the conditioned response. More specifically, when the delay elapses in the same context as the other experimental stages (preexposure and conditioning), the animal is exposed for a prolonged period to a context in which a series of biologically

significant events have occurred, but now in the absence of such events. As a result, we might expect the hypothetical links established between the context and the different associations established in its presence (CS–nothing and CS–US) to be extinguished, with further extinction taking place the longer the period of context exposure. Moreover, the extinction of the links between the context and the CS–nothing and CS–US associations presumably has a differential impact on the subsequent retrieval and/or expression of these two associations. In general, CS–US associations are relatively context-independent compared to the CS–nothing association (Bouton & King, 1983; Bouton & Peck, 1989; Lubow & De la Casa, 2005). Thus, with passage of time, the link between the context and the CS–nothing association would be extinguished, while the link with the CS–US association would remain relatively intact. As a consequence, presentation of the CS in the test stage would result in strong conditioned responding (i.e., attenuation of LI). In contrast, when the time interval is spent in a context different from that of the other experimental stages, all of the previously established associations would remain intact. To account for the *super*-LI effect that is obtained under these conditions, one might appeal to a time-induced enhancement of the *primacy* effect, the evidence that *first learning* is disproportionately strong as compared with subsequent training (Bouton, 1993; Konorski & Szwejkowska, 1952). A number of human memory experiments have shown that primacy effects increase with the length of the retention interval between study and test stages (e.g. Knoedler, Hellwig, & Neath, 1999; Neath, 1993). Thus, for instance, Neath (1993) found that increasing the delay between the study of a list of non-verbal items (i.e., pictures of snowflakes) and a recognition stage resulted in better performance for the first-learned item than for the last-learned item.

This interpretation of the role played by the long retention interval context matches the available empirical evidence on the subject, but it does not offer an explanatory mechanism for the *origin* of the bidirectional modulation of LI (i.e., attenuation of LI vs. *super*-LI). To address this limitation, Lubow and De la Casa (2005) have proposed the *context differentiation hypothesis*, which restates the processes outlined in the previous paragraph in terms of perceptual mechanisms. According to the context differentiation hypothesis, the perceived similarity of two contexts does not exclusively depend on their objective physical similarity. Additional factors that determine the *perceived similarity* between contexts include time between presentations of the two contexts and the degree of objective similarity/difference between the interval context and the other context of the other experimental stages.

The McLaren, Kaye, and Mackintosh (1989; see also McLaren & Mackintosh, 2000) analysis of perceptual learning offers an explanatory framework that is congruent with the context differentiation hypothesis. From their perspective, the perceptual differentiation between two contexts will depend on the proportion of common to unique elements. Discrimination between contexts would be facilitated by exposure to both of them since the salience of any common stimulus elements

would be disproportionately reduced compared to unique elements (i.e., there would be a greater LI effect for the more frequently exposed common stimuli than for the unique stimuli). Thus, when preexposure, conditioning, retention interval, and testing occur in the same experimental context (AAAA, respectively), the common contextual elements will receive extensive preexposure which would reduce their associability/salience. However, this process would potentiate the salience of the differential elements (including those that tend to change over time such as physiological state, uncontrolled environmental changes, etc.), and lead to an enhancement of the perceived difference between the preexposure, conditioning, and test contexts, the context-change condition that reliably disrupts LI (e.g. Channell & Hall, 1981; Hall & Channell, 1986; Hall & Minor, 1984; Lovibond *et al.*, 1984). This process of perceptive differentiation, probably together with the hypothetical extinction of the link between the context and the CS–nothing association previously discussed, would result in stronger conditioned responding being observed at test. In contrast, when the delay context is different from the other experimental contexts (AABA), the reduction in saliency of the common elements would be minimal. This, in turn, would promote the perceptual similarity of the experimental contexts, and consequently, at test, favor the retrieval of the CS–nothing association over the recovery of the CS–US association (i.e., due to the former association being more dependent on the context than the latter association), thereby producing enhanced LI.

### Applied implications

To date, practical, clinically related, applications of the LI effect have been primarily prophylactic, namely using inconsequential stimulus preexposures in order to *prevent* the acquisition of, for example, food aversions due to radiation/chemotherapy-induced nausea (e.g., Bovbjerg, 2006; Carey & Burish, 1988; Schwartz, Jacobsen, & Bovbjerg, 2006) and phobias (e.g., Davey, 1989; Eiche & Cook, 2001; for a review, see Lubow, 1998). The *post*-event time/context manipulations, which can either decrease or increase LI, also have implications increasing the efficacy of preventative measures as well as for treatment.

For example, the interaction between time and context discussed in the previous section, applied to the chemotherapy treatment, suggests that the effectiveness of food preexposure in reducing the development of food aversions would be enhanced if the chemotherapy sessions were followed by a long a period in a different context from that in which the target food was eaten. As for reducing the likelihood of developing a phobia, the typical procedure already favors the appearance of the super-LI effect. For example, many dentists require children to make several visits to the dental clinic, before any treatment, in order to familiarize them with the setting and the material used in dental operations. Eiche and Cook (2001) suggested that between two and five visits of this type should be made, each lasting about 20 minutes. To maximize prophylactic effectiveness, the first real intervention should be followed

by a relatively long period spent (as would usually be the case anyway) in a context different from that of preexposure and conditioning. In this way, the process of perceptive equalization (see section on Explaining time–context interactions) would favor the recovery of the association established during preexposure without consequences, thereby reducing anxiety responses that are characteristic of phobia.

### Conclusions

The present chapter has discussed evidence and theoretical explanations of attenuation and enhancement of LI due to inter-stage manipulations of context and time. These two key terms provide an appropriate metaphor for the relevance of LI in current research: in today's new theoretical context, and after a 50-year retention interval since the original report of the LI effect by Lubow and Moore (1959), the impact of LI research in the literature has not attenuated, it has been greatly enhanced.

If we can conclude anything from the empirical evidence discussed in this chapter, it is that the phenomenon of LI is determined by a series of variables that do not act in a linear manner. Instead, these variables interact intricately, giving rise to an enormously flexible and adaptive process. In this chapter, we have focused on the impact of two of these variables, namely, context and time, as well as on their interaction. The results from the studies that have examined this interaction do not fit easily into past or current theories of LI. As a consequence, we have described an alternative account, namely the context differentiation hypothesis (Lubow & De la Casa, 2005), which, although reasonable, is largely post-hoc and speculative. The practical difficulties involved in analyzing this interaction in certain experimental situations, particularly in the case of research with humans, present a formidable challenge, but the prospective theoretical and applied results indicate that it would be well worth the effort.

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