Context and Pavlovian conditioning

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Abstract

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Procedurally, learning has to occur in a context. Several lines of evidence suggest that contextual stimuli actively affect learning and expression of the conditional response. The experimental context can become associated with the unconditional stimulus (US), especially when the US is presented in a context in the absence of a discrete conditional stimulus (CS). Moreover, context can modulate CS-US associations. Finally, it appears that context can become associated with the CS when it is presented before the CS-US training. The purpose of the present paper is to review some of the relevant literature that considers the context as an important feature of Pavlovian conditioning and to discuss some of the main learning theories that incorporate the context into their theoretical framework. The paper starts by mentioning historical positions that considered context an important variable in conditioning and then describes how the approach to contextual conditioning changed with the modern study of Pavlovian conditioning. Various forms of measurement of context conditioning are presented and the associative strength attached to context in several experimental paradigms is examined. The possible functions that context may acquire during conditioning are pointed out and related to major learning theories. Moreover, the effect of certain neurological manipulations on context conditioning is presented and these results are discussed in terms of possible functions that the context might acquire during Pavlovian conditioning. It is concluded that contextual stimuli acquire different functions during normal conditioning. A procedure in which animals are exposed to an aversive US immediately after they are placed in the experimental context is suggested as a useful control for the study of context conditioning.

Introduction

During his experiments, Pavlov (1) noticed that during the beginning of the paring between the discrete conditional stimulus (CS) and the unconditional stimulus (US) all the different stimuli of the experimental context were able to elicit the conditional response (CR). However, these CRs to the contextual stimuli started to decrease as conditioning progressed. Pavlov termed these CRs to context as "conditioned reflexes to the environment" and explained their decline as being due to internal inhibition. Although he noticed that the contextual stimuli were not neutral (they were neutralized by inhibition), he assumed that the context did not exert a very strong control over the CR (2).

In contrast to this position, several other investigators believed that contextual stimuli might affect learning and behavioral performance. For example, Hull (3) suggested that contextual stimuli present during training could affect learning by influencing the way the CS and US are perceived. According to Hull, different contexts could alter the encoding of a given CS or US due to the "afferent neural interaction" generated by contextual stimuli. This principle states that the ability of a particular stimulus to discharge its appropriate receptors is not the same under all conditions but is modified by interaction with other stimuli present at the time. One of Hull's examples to illustrate this notion is the fact that a small gray paper on a blue background is generally seen as yellowish, but when the background is red the gray paper is seen as greenish. Based on this same principle, Hull also suggested that performance of the CR could be altered by changing context between training and testing. Following the principle of afferent neural interaction, a context shift between training and testing could alter the afferent impulse produced by the CS and thus alter the CR.

To some extent, Tolman (4,5) also acknowledged the importance of the context in behavior generation by developing the notion of "supporting stimulus". The CR to a particular CS can be affected to the extent that contextual stimuli can support the response. The importance of the context for Tolman can also be viewed from a different perspective. Tolman did not have a very mechanistic view and believed that behavior was motivated by specific purposes. He suggested that animals have a natural tendency to explore their environment and form what he called cognitive maps. This cognitive map could guide the animal's behavior through the different contextual stimuli in the environment to reach a goal reward.

Using a more associative view, Konorski (6) proposed that contextual stimuli could facilitate conditioning due to a context-US association. He argued that context is rapidly associated with the US and acquires the ability to activate a motivational state that facilitates the formation of an association between the CS and US. However, as discussed later, this suggestion does not seem to be valid. Experimental evidence available today suggests that a context with some associative value in fact reduces CS-US conditioning. Konorski (6), anticipating some recent models of conditioning (e.g. Ref. 7) also suggested that context could become associated with the CS.

McAllister and associates (8,9) saw in contextual stimuli an opportunity to extend the two-factor theory of avoidance learning (10). They noticed that during signaled avoidance learning, the context in which the CS and US were presented gained some associative strength. Following this finding, they proposed that effective reinforcement for the acquisition of an avoidance response is directly dependent on the reduction of fear that occurs with the response but also inversely related to the amount of fear generated by the context present after the response (9). The interference of aversive context conditioning with avoidance learning was demonstrated by manipulations that reduced context conditioning (11). Nonetheless, it remains unclear if avoidance learning follows the rules proposed by the two-factor theory (12-15).

Contextual stimuli were also recognized by Asratyan (16). In his switching experiments, he demonstrated that animals could learn different relationships between a CS and US when they occurred in different contexts. For example, Asratyan (16) demonstrated that dogs can associate a CS1 to food and a CS2 to shock in one context and learn exactly the opposite relationship (CS1-shock and CS2-food) in a second context. This has proved to be an interesting method to show that context can acquire different signaling functions about the CS-US association (e.g. Ref. 17).

Nevertheless, recognition of the context

as part of the conditioning process has lacked a more detailed analysis. It was only recently, with the emergence of the modern analysis of Pavlovian conditioning, that context started to receive more attention. The factors that led to this revolution in Pavlovian conditioning and its particular approach to context are discussed in the next section.

The modern study of Pavlovian conditioning: incorporating the context as part of the learning situation

Thinking about Pavlovian conditioning today is entirely different from the views held 20 or 25 years ago. The main change proposed by the more recent approach to Pavlovian conditioning is that contiguity is neither necessary nor sufficient to produce learning. Rather, modern theory of conditioning emphasizes the information that one stimulus gives about the other. This major conceptual change was stimulated by Rescorla's seminal work (18-22) on stimulus predictability and Kamin's blocking effect (23). Both of these studies agree that information, but not contiguity among stimuli, is the important variable involved in learning.

The insufficiency of contiguity for producing conditioning was demonstrated by Rescorla (18,19). In a typical experiment, animals in one condition were exposed to uncorrelated presentation of the CS and the US. Animals in a second condition received the US only when it was preceded by the CS. The important feature imposed in these two conditions was that the CS and US contiguity was the same between groups but the information that the CS gave to the US was different. In the first condition, the US was equally likely to occur in the presence and in the absence of the CS ($P_{US/CS} = P_{US/\overline{CS}}$). In the second condition, the US only occurred in the presence of the CS ($P_{US/CS} = 1$; $P_{US/\overline{CS}} = 0$). Only the animals that had the informa-

tion relationship between the CS and the US ($P_{US/CS} = 1$; $P_{US/\overline{CS}} = 0$) acquired the CR. Animals that had an uncorrelated relationship between the CS and the US did not show any sign of learning despite the presence of the CS-US contiguity. Interestingly, Rescorla (20,21) also found that if the CS only occurred in the absence of the US ($P_{US/CS} = 0$; $P_{US/\overline{CS}} = 1$), the CS acquired inhibitory properties. Variations in the $P_{US/CS}$ and in the $P_{US/\overline{CS}}$ lead to the conclusion that excitatory conditioning occurs when $P_{US/CS} > P_{US/\overline{CS}}$ and inhibitory conditioning occurs when $P_{US/CS} < P_{US/\overline{CS}}$. These findings, among others, have demonstrated that pairing is not necessary. This is because in these inhibitory conditioning experiments an association forms when the CS and US are not paired. Based on this approach, Rescorla (22) argued that the appropriate control procedure for nonassociative aspects in conditioning would be a situation in which $P_{US/CS} = P_{US/\overline{CS}}$. He termed this control procedure as the "truly random control". The distribution of these probabilities and their impact on conditioning is illustrated in Figure 1.

Using a compound conditioning preparation, Wagner et al. (24) also concluded that the informative value of a particular CS was the major determinant of conditioning. They found that the most informative stimulus of the compound not only gained more
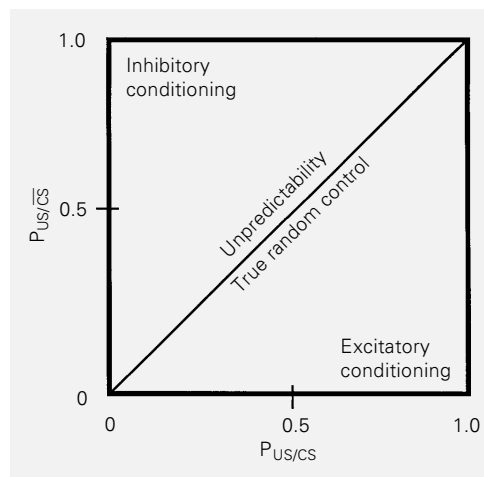

Figure 1 - Representation of excitatory and inhibitory conditioning according to the probability (P) of US occurrence in the presence of the CS or in its absence ($\overline{CS}$) (Modified from Ref. 112).

associative strength but also blocked conditioning to the stimulus that was less informative. This pattern of results emerged despite the fact that animals had the same amount of reinforcement.

The idea that temporal contiguity between the CS and US is not necessary for conditioning is also suggested by the blocking effect (23). Blocking refers to a deficit in conditioning to a specific CS2 when it is paired with a US in the presence of a second CS1 that was previously paired with the US. Thus, although CS2 is paired with the US, it does not became associated with the US. The blocking effect, together with Rescorla's and Wagner et al.'s notion of information between stimuli, was the critical finding that motivated the Rescorla and Wagner (25) model of Pavlovian conditioning. According to this model, conditioning is viewed as an active interaction among all stimuli in the conditioning situation. It is proposed that these stimuli compete for a limited amount of associative strength provided by the US. The change in associative strength of a particular stimulus depends upon the total associative strength of all stimuli present in a given trial. The model also states that contextual stimuli function as any other CS. Thus, when CS-US pairings occur in a context what is actually occurring is a compound conditioning in which the CS and the context are being paired with the US.

Suppose, for example, that a CS is paired with a US in a certain context. According to the Rescorla and Wagner model, both the CS and the context will acquire some associative strength (V). The model suggests that the increment in associative strength (ΔV) in a given trial is a function of the discrepancy between the combined associative strengths of the CS and the context, on the one hand, and a theoretical conditioning asymptote (λ) on the other. There are two learning rate parameters, one associated with the CS (α) and the other associated with the US (β). Change in associative strength to the

CS and to the context (designated A and X, respectively) is formally expressed as

$$\Delta V_A = \alpha_A \beta_1 (\lambda_1 - V_{AX}) \qquad \text{(Eq. 1)}$$

and

$$\Delta V_X = \alpha_X \beta_1 (\lambda_1 - V_{AX}) \qquad \text{(Eq. 2)}$$

where V_{AX} refers to the sum of the associative strengths of the CS and the context ($V_A + V_X$).

It should be noted that the context is still present when the US is not. Therefore, the associative strength of the context changes according to the equation

$$\Delta V_X = \alpha_X \beta_2 (\lambda_2 - V_{AX}) \qquad \text{(Eq. 3)}$$

where $\lambda_2 = 0$.

According to equation 2, context should gain some associative strength, but as training proceeds, this associative strength should decrease (equation 3). Since the context and the CS compete for a limited total possible associative strength (λ_1), the contextual stimulus will compete less effectively with the discrete CS and eventually its associative strength will approach zero.

Since the context is a continuous stimulus, and the model requires the notion of a discrete trial in order to apply the equations, Rescorla and Wagner (25) divided the experimental session into time segments of the length of the CS. Thus, the model sees the context as identical to the traditional light, tone, bell, and buzzer CSs and its associative strength can be calculated as for any other stimulus. According to this view, a CS is never presented alone but in combination with several undefined stimuli that as a group are defined as context.

Due to this new approach to conditioning, with a special treatment of contextual stimuli, strong interest in the associative value of the context started to appear. Since the context is a more complex type of stimulus and may not directly activate a specific CR, especially when a signaled US is presented, it is important to have good measure-

ments that are able to detect the associative strength to the context. These techniques are described next.

Measurement techniques for context conditioning

As Balsam (26) pointed out, there are two main strategies to measure contextual associative strength. One strategy is to examine the effect of contextual manipulations on the control of the CR triggered by a discrete CS. The other strategy is to examine a behavior that is controlled directly by contextual cues.

The most elementary context manipulation technique is the context shift. In this procedure, subjects are submitted to normal CS-US pairings but the CS is tested in a different location from the original training context. A potential difference in performance between the training and testing contexts is attributed to the influence of the context on the CR. A disadvantage of this test is that it does not assay the associative strength of the context *per se*. A different preparation that allows study of this issue is the retardation test. Increasing contextual conditioning, by presenting an unsignaled US, retards subsequent learning in response to normal CS-US training (for a review, see Ref. 27). Thus, if CS-US pairings are performed in a context with some associative strength, then the rate of acquisition of the CR to the CS should be retarded. The assumption of this test is that prior context conditioning impairs later conditioning. This assumption, which is in agreement with the Rescorla and Wagner model, has received support from several experiments and will be discussed in the US preexposure paradigm section.

Both context shift and retardation tests use the response to the CS in order to infer the influence of the context on conditioning. A different approach is to measure the associative strength of the context in the absence of any discrete CS. For example, context conditioning can be evaluated by the conditioned emotional response (CER) technique. In this procedure, which is commonly used to access conditioning to a conventional CS, an ongoing operant behavior is observed when animals are exposed to the conditioned context. It has been reported that aversive classical conditioning differentially reduces ongoing operant response rates (28,29). In a variation of this procedure, Patterson and Overmier (30) also found that the contextual stimuli influence operant response in the same way as discrete CSs do.

The preference test is another method to measure context conditioning. In this test, animals are given a choice between a pretrained and a nonpretrained context (31-33) or between two contexts that have undergone different training procedures (34). Since this test is usually employed in aversive conditioning, context conditioning is inferred from the choice that animals make. It is reasonable to assume that animals will tend to avoid the more aversive context and choose the one that is neutral or less aversive. This test has also been employed in appetitive conditioning (35) and the results parallel the aversive conditioning pattern. Animals preferred a context paired with food in contrast to a different context in which food was never presented. A slight modification of this test has been used by McAllister and associates (8,9). Briefly, animals are allowed to escape from a compartment where avoidance training occurred by jumping to a safe box. Context conditioning is measured by the latency to escape from the training context.

The most direct way to measure the associative strength of the context is to observe a CR that is differentially controlled by the contextual stimuli themselves. In appetitive conditioning, general activity is widely used as an index of contextual conditioning and it seems to be the most reliable measure. For example, pigeons tend to increase their gen-

eral activity in response to a specific context where food is presented (26,36,37). In aversive conditioning, freezing appears to be the dominant response triggered by a discrete CS or by a context paired with the aversive stimulus (38-41). Fanselow (42) has argued that freezing is the most reliable measure of aversive context conditioning. Freezing, for example, is a direct function of shock intensity (43,44), depends on the association between the experimental chamber and the shock (45,46) and is sensitive to a series of manipulations that affect context conditioning (44,47,48). What makes freezing a very attractive response is that conditioning to the CS and to the context can be measured at the same time during normal training and testing (43,49).

Using some of these several techniques, a large number of studies were conducted to investigate the associative strength of the context generated by different experimental paradigms. In the following section, some of these paradigms are presented and the possible associative strength that contextual stimuli may develop in each of these procedures is discussed.

The associative value of context in several conditioning paradigms

The US preexposure effect. Retardation in conditioning to a discrete CS is usually observed when animals are exposed to the US prior to the CS-US training (50,51). US preexposure is thought to cause context conditioning which blocks or retards subsequent CS-US learning. This interpretation is in accordance with the Rescorla and Wagner model, which predicts that all the stimuli present during the delivery of the US, including contextual cues, compete for associative strength. Since contextual stimuli already had some associative strength when the CS-US pairing occurred, conditioning to the CS will be retarded. Several experimental findings support this associative interpre-

tation (27,51). For example, the US preexposure effect can be eliminated by: 1) extinguishing the context in which the unsignaled US was presented, 2) changing context after the US preexposure or 3) signaling the US during the US preexposure phase.

An alternative explanation of the US preexposure effects is based on a performance deficit argument. The comparator hypothesis (52) and the expectancy theory (53), which will be discussed later, state that expression of a CR to a CS is inversely proportional to the associative strength of the context. So, the deficit in conditioning found in the US preexposure effect may reflect a performance problem due to the high associative strength of the context. The beneficial effects of signaling the US before the CS-US training and extinguishing or shifting the context after the US preexposure are also in accordance with this view. Excitatory conditioning to the context is reduced and so the CR to the CS can be performed better. However, it has been reported that extinction of the context after the CS-US pairings attenuates the US pre-exposure deficit (54). This result tends to support the performance failure view. Conditioning to the CS was normally acquired but was not fully expressed because of an interference with the high context associative strength. Extinction of the context after the CS-US pairing reduces its associative strength and thus enhances the probability of performance of the CR to the CS.

Independently of which theory more accurately explains the US preexposure effect, it is clear that contextual cues present during the CS-US training are important in this phenomenon. Context-US association is assumed to exist and actively interact in some way with the CS-US association or its behavioral expression.

Inter-trial interval (ITI). ITI refers to the interval between trials in a typical Pavlovian experiment. It is well established that the ITI

has a strong influence on conditioning (55). Generally, longer ITIs produce better conditioning in relation to shorter ones (56). Distinct learning models that attempt to explain this ITI effect evoke the contextual cues present during conditioning as part of their rationale. The Rescorla and Wagner model argues that conditioning performed under long ITIs produces greater extinction of contextual conditioning in relation to short ones. Since the CS competes with the context for a limited amount of association, long ITIs lead to better conditioning due to the low associative strength of the context. For different reasons, the expectancy theory also relies on the context-US association to deal with the ITI. As will be discussed later, this model asserts that a longer ITI leads to smaller context conditioning than a shorter one. Since expression of the CR is inversely related to context conditioning, performance of the CR is superior with longer ITIs.

Regardless of their individual explanations, both models are based on the assumption that it is an inverse relationship between conditioning to the context and to the CS that determines the learning (Rescorla and Wagner model) or the performance (expectancy theory) deficit produced by short ITIs. Therefore, direct contextual conditioning, induced by unsignaled USs, should not produce the learning deficit caused by short ITIs. Although this type of result has been obtained in contextual appetitive conditioning (35), exactly opposite results have been reported in aversive context conditioning (57-59). For example, Fanselow and Tighe (57) found that 2 shocks delivered 60 sec apart produced better conditioning than 16 shocks delivered 3 sec apart. It is not clear why opposite results are found in appetitive and aversive context conditioning, or even what mechanisms are involved in the ITI effect. The fact is that contextual cues presented during conditioning have been recognized as an important variable in this paradigm.

Learned helplessness. Exposure to an uncontrollable (inescapable and unavoidable) aversive stimulus induces later deficits in learning to escape from that stimulus when escape is possible (for a review, see Ref. 60). This effect has been called learned helplessness and a variety of interpretations of this phenomenon have been proposed (see Refs. 61-64 for different explanations).

It seems clear that contextual stimuli present during the induction or testing of learned helplessness play an important role in learned helplessness. Minor and LoLordo (65), for example, found that the contextual odor present in the induction or testing chambers was the variable responsible for producing learned helplessness. Rats tested in a cleaned chamber did not show the learning deficit despite exposure to uncontrollable shocks. Moreover, animals tested in a context with stress odors did not demonstrate the deficit if exposure to the uncontrollable shocks occurred in the presence of a peppermint scent. These results argue for a context conditioning interpretation of the learned helplessness phenomenon. Contextual odor becomes associated with the uncontrollable aversive event, which, in turn, produces a high level of fear. When the escape test occurs, the fear reaction induced by the contextual odor interferes with the animal's ability to learn the escape response.

The interpretation of learned helplessness in terms of aversive context conditioning is also supported by studies that show that uncontrollable shocks produce stronger context conditioning than escapable ones (66-68). Moreover it has been shown that signaled uncontrollable shocks, a procedure that should reduce context conditioning, preclude the occurrence of the learning deficit (69).

Another procedure that disrupts the occurrence of learned helplessness is the presentation of a brief signal at the end of the uncontrollable shock (feedback stimulus, 66,68,70). It has been shown that a feedback

stimulus reduces context conditioning induced by inescapable shocks (66,68). Although these results are in contrast to the Rescorla and Wagner model (the model predicts that a backward conditioning paradigm should lead to a strong context conditioning), they are in agreement with the interpretation of learned helplessness in terms of context conditioning. Finally, Minor et al. (70) have also shown that the beneficial effect of the feedback stimulus is enhanced when animals are also exposed to another stimulus that signaled the termination of the inescapable shock.

The context conditioning interpretation of the learned helplessness effect was recently challenged by Maier (71). While measuring context conditioning during the learning deficit test, he found that aversive context conditioning and learned helplessness did not covary. Manipulations that eliminate the learned helplessness effect (naltrexone and a 72-h interval between the uncontrollable shock and testing phase) did not affect context conditioning. Furthermore, manipulations that reduced aversive context conditioning (diazepam) did not affect the learning deficit. It should be noted that the absence of correlation between learned helplessness and context conditioning was found during the test phase whereas all the other manipulations mentioned above were done during the induction phase. It is not clear why there is a difference between induction and testing of learned helplessness. This suggests that other variables, besides context conditioning, are involved in this phenomenon.

Latent inhibition. Preexposure to a stimulus subsequently used as a CS generally retards subsequent learning. This phenomenon has been termed latent inhibition (72). Several experiments have shown that latent inhibition is context dependent (73-75). In all of these experiments, a change in context between the preexposure and conditioning phases alleviates latent inhibition. The simplest explanation of these results could be in terms of generalization decrement. A context change can alter the physical properties of the CS so that animals may perceive the signal differently. Lovibond et al. (75) rejected this possibility by equating several features of two distinct contexts. More direct evidence that dismisses the generalization decrement explanation is reported by Wagner (76). He found that latent inhibition could be attenuated if animals were exposed to the context alone (context-CS extinction) after CS preexposure but before CS-US training (see Ref. 74, experiment 2, for a different result). These results suggest that latent inhibition is mediated by an association between context and CS. Evidence for the existence of this type of association has been reported by Rescorla (37), who found that presentation of a discrete CS in a certain context produces a powerful context-CS association. Second-order conditioning, sensory preconditioning and extinction manipulations of the CS differentially change the associative value of the context.

Habituation. Repeated presentations of a stimulus cause a decline in the response to the stimulus. This reduction in the response rates is referred to as habituation and is considered a very simple form of learning. Procedurally, habituation and latent inhibition are equal. The difference is that during habituation the animal's response to the stimulus is observed, while latent inhibition refers to an effect on subsequent conditioning. Since latent inhibition is context dependent, one might be inclined to accept the view that habituation also depends on the context. However, this seems not to be the case. Context change does not restore the habituated response (73,77,78). A possible explanation for this result could be that the context shift was not effective, so that animals could not discriminate between the two contexts. Nonetheless, Hall and Channell (73) demonstrated in the same preparation that latent inhibition was sensitive to the

context shift manipulation, whereas habituation was not. Rats were exposed to a light and their orientation response was used to measure habituation. A flap entry response was used to measure appetitive conditioning. Animals exposed to the light showed the same orientation response regardless of the context in which the light was presented or tested. However, selective reduction in a light-food association was found when training occurred in the same context in which the light was preexposed. This dissociation between habituation and latent inhibition has strong theoretical implications (e.g. Ref. 7) and will be discussed later.

Extinction and renewal. Nonreinforced presentations of the CS after conditioning lead to a decrease in the CR. This operation has been termed extinction (1), and as Bouton (79) pointed out, this is one of the most fundamental problems in conditioning theory. It is not clear if the CS-US association is destroyed during extinction or if a new association that inhibits the CS-US association is formed. Despite the uncertainty of this phenomenon, it is now clear that contextual stimuli present during extinction are extremely important for extinction. For example, Bouton and Bolles (80) found that extinction of the CR in a different context from the training situation did not prevent the occurrence of the CR in the context where conditioning took place. Also, the CR was not affected when the CS was presented in a neutral context after being extinguished in the trained context. This survival of the CS-US association after extinction is termed the renewal effect and strongly suggests that extinction is a context-specific phenomenon.

A possible explanation for the renewal effect could be protection from extinction. It has been shown that the CR to a CS under extinction is maintained when the CS is presented with a conditioned inhibitory stimulus (81,82). Protection from extinction can be deduced from the Rescorla and Wagner model when a neutral stimulus (which will become a conditioned inhibitor) is presented in conjunction with the CS during an extinction procedure. So, it is possible that the renewal effect is a special case of protection from extinction. If this is the case, then the neutral context where the CS is extinguished should acquire inhibitory properties. Nonetheless, Bouton and King (83) showed that the neutral context where the CS was extinguished does not become a conditioned inhibitor. Additionally, renewal is also observed when the CS is extinguished in the training context (which might have excitatory but never inhibitory properties) and tested in a neutral context. How context controls the animal's performance in this situation is an interesting question. Bouton (79,84) dismissed a series of other possibilities and proposed that contextual stimuli acquire functions similar to those of occasion setters or facilitators (85,86). This position will be discussed later.

Reinstatement and inflation. Another situation in which the CR can be observed after extinction is in the reinstatement effect (87). Unsignaled presentation of the US after conditioning to the CS had been extinguished causes a restoration of the CR. It is argued that reinstatement is mediated by the animal's memory of the US (87). This explanation is also proposed to deal with a different paradigm in which the CR to a CS is inflated. Rescorla (88) found that if animals were exposed to intense unsignaled shock after CS-US conditioning, the CRs to the CS were enhanced or inflated.

Reinstatement and inflation could be viewed as a summation between context and CS conditioning. In agreement with this idea, Bouton (83,89,90) showed that reinstatement results from a summation between context conditioning induced by the unsignaled US presentation and a residual amount of conditioning from the extinguished CS. Reinstatement is only observed in the context in which animals are exposed to the US.

Moreover, reinstatement can be precluded if context conditioning is extinguished after the unsignaled US presentations. On the other hand, Bouton (89) found that occurrence of inflation was independent of context conditioning. Presentation of the stronger US in a different context or extinction of the context after the presentation of the stronger US did not affect the occurrence of inflation.

Conditioned inhibition. As already mentioned, conditioned inhibition (CS-) is produced when the CS reliably predicts the absence of the US, usually a shock. It is considered (e.g. Ref. 25) that a CS- acquires associative strength that is opposite to normal excitatory conditioning (but see Refs. 86 and 91, for a different approach). Based on this assumption, the presence of inhibitory conditioning is measured by the summation (decrease of the CR when the CS- is presented in conjunction with an excitatory CS) and the retardation (harder to transform a CS- into an excitatory CS) tests (20).

One of the most popular forms of producing conditioned inhibition was developed by Pavlov (1). In this procedure, a stimulus is always paired with the US (A+) and another stimulus is not reinforced when presented together with A (AB-). Inhibitory conditioning generated by this type of procedure reduces several CRs elicited by excitatory context conditioning, such as freezing (92) and conditional analgesia (Landeira-Fernandez J and Helmstetter FJ, unpublished results; Maier SF, unpublished results). Inhibitory conditioning can be achieved by a different procedure. Rescorla (21), for example, showed that a CS negatively correlated with the US can also acquire inhibitory properties. Indeed, this last procedure can be seen as a special case of the A+ AB- preparation. The context alone (A+) acquires excitatory properties while the CS negatively correlated with the US and presented in the same context (AB-) develops inhibitory properties. Experimental evidence supporting this interpretation

was obtained by Baker (93). He found that inhibitory conditioning produced by a negative correlation procedure was reduced when the shocks were signaled by a different CS. The rationale here is that if inhibitory conditioning induced by a negative correlation procedure is due to excitatory conditioning to the context, then signaling the shocks should reduce context conditioning and so attenuate inhibitory conditioning.

Preference for signal shocks. A well-known behavioral finding in experimental psychology is that rats tend to prefer a location in which shocks are signaled by a discrete signal over a location in which unsignaled shocks are presented (94). Fanselow (34) suggested that preference for signaled shocks can be interpreted in terms of aversive context conditioning. In his experiments, he found that although rats preferred a signaled shock context, animals avoided the context where a signal negatively correlated with shock was presented. These results might indicate that the animal's context preference is determined by the degree of aversive context conditioning. As predicted by the Rescorla and Wagner model, signaled shocks lead to reduced context conditioning, whereas a signal negatively correlated with shock increases context conditioning. Therefore, preference for signaled shock might be a reflection of a preference for a less aversive context. Fanselow (34) reviewed a series of preferences for signaled shock experiments done in the past 3 decades and all of them could be explained according to the context conditioning approach.

Taste aversion. When a rat is made sick by X-irradiation treatment or by an injection of lithium chloride (LiCl), the animal will subsequently present a strong aversion to any food ingested before the illness. This effect was coined taste-aversion learning (95). Contextual stimuli present during the food-illness pairing also seem to exert some influence on taste aversion learning (for a review, see Ref. 96).

Slotnick et al. (97) were probably the first to demonstrate the importance of contextual stimuli in taste aversion. In this experiment, saccharin (CS) was paired with apomorphine (US) in a certain context. It was found that animals avoided the CS when it was presented in the original training context, but a preference for saccharin was observed when the CS was presented in a different context. Context dependence in taste aversion is also reported by Archer and colleagues (98). Rats that had the CS extinguished in one context still presented the taste aversion when tested in the original training context. Actually, this is the renewal effect reported by Bouton and Bolles (90) in a fear-conditioning preparation.

It has been well documented that preexposure to the US also leads to a reduction in taste aversion conditioning (99,100). An explanation of this reduction in conditioning in terms of an association between context and US has been suggested. Batson and Best (99), for example, found that animals that were preexposed to LiCl before the saccharin-LiCl pairing only showed the learning deficit when training occurred in the same context in which they were preexposed to LiCl. This result supports the blocking interpretation of US preexposure in the taste aversion paradigm.

It must be noted that contextual stimuli present during taste aversion conditioning present some peculiarities that are different from the other paradigms discussed before. While during a usual CS (e.g., tone) US (e.g., shock) pairing, contextual stimuli remain equally uncorrelated with CS and US presentation, this cannot be true in the taste aversion paradigm. This is because each of the several stimuli that compose the context can have different temporal relationships with the CS and the US. For example, the bottle or the food tray that is used to present the CS has a good correlation with the CS, and the injection procedure used to administer LiCl, for example, has a good correlation

with the US. Not surprisingly, Archer and Sjodén (101,102) found that contextual stimuli that correlate better with either the CS or the US acquired better control over taste aversion than other stimuli (compartment or odor) that were present throughout the conditioning time.

Possible context functions in conditioning and their relation to learning theories

It is obvious from the previous section that the context in which conditioning takes place has some influence on the CR. However, it is not exactly clear what type of function the context develops. As already mentioned, some theories imply that the context is just like any other nominal CS, whereas in other theories, context is assumed to be a unique type of stimulus and develops a very particular function. In this section, theories that ascribe different functions to the context will be presented and experimental evidence that supports each of these theories will be mentioned.

Competition. The Rescorla and Wagner model suggests that the US can only support a limited amount of conditioning or associative strength. Indeed, Hull (3) and Bush and Mosteller (103) had already made this suggestion. Hull, for example, proposed that

$$\Delta_S E_{R_N} = i(M - {}_S E_{R_{N-1}}) \qquad (Eq.\ 4)$$

where ${}_S E_R$ = excitatory strength, M = the maximum value of excitation (determined by motivation), i = growth rate parameter, and N = number of reinforced trials. Thus, M represents the limited amount of associative strength supported by the US. In the same vein, Bush and Mosteller (103) proposed in their linear equation for response probability that

$$\Delta p = p + a\,(1-p) \qquad (Eq.\ 5)$$

where p = response probability, and a = growth rate parameter. Note that in this case

the asymptote is an analytic necessity. There is no such thing as a probability greater than 1.

Although Hull's and Bush and Mosteller's equations appear to be similar to the Rescorla and Wagner model (equations 1, 2 and 3), a major innovation was made. Rescorla and Wagner suggested that all stimuli present in the situation where the US is delivered become associated with the US. Not all stimuli, however, reach the asymptote. Only the more informative stimulus will have its associative strength increased up to λ. The increase in associative strength of one stimulus (e.g. V_A) implies a reduction of associative strength of the other (V_X). The original contribution of the model is that context was formally recognized as an important variable during conditioning and assigned an equal ability to compete for the limited amount of conditioning supported by λ (the associative strength of the CS (V_A) plus the associative strength of the context (V_X) is subtracted from λ). Following this summation rule, Rescorla and Wagner considered the context as a whole unit and functionally equivalent to any other discrete CS. Several studies support this concept (31-34,36,104,105). Odling-Smee (31), for example, found that context conditioning was directly related to the intensity of the US but inversely proportional to the probability of the CS being followed by the US.

The notion that there is a competition between stimuli to become associated with the US can also be found in theories that give emphasis to attentional factors. According to the selective attention theory (106), attention to the CS is what determines conditioning. It is assumed that the organism has a limited capacity to process information and all stimuli present during conditioning will compete for the animal's attention. The more informative a particular stimulus is the more attention it will gain. Although this approach is different from the Rescorla and Wagner model (selective attention theory assumes that conditioning is a function of variation in CS processing whereas Rescorla and Wagner state that conditioning is a function of variation in US processing), it is easy to see how the selective attention theory also assumes that context and CS compete for associative strength.

Nevertheless, the selective attention theory presented a series of problems (see Ref. 107 for a discussion). In a modified version of the model, Mackintosh (107) discarded the competition assumption. As he pointed out, "... while differential reinforcement is assumed to increase attention to relevant stimuli, there is no comparable independent mechanism for reducing attention to irrelevant stimuli." (Ref. 107, page 280).

Therefore, the modified model assumes that attention during conditioning changes but stimuli do not compete for a limited amount of attention. According to the new approach, change in conditioning is given by

$$\Delta V_A = \alpha_A (\lambda - V_A) \qquad \text{(Eq. 6)}$$

where A is any particular stimulus. Note that associative strength to A is a function of a difference between λ and its own associative strength, instead of the Rescorla and Wagner summation rule. A change in α is what determines conditioning. Mackintosh (107) suggested that α of CS_A is positive if

$$|\lambda - V_A| < |\lambda - V_X| \qquad \text{(Eq. 7)}$$

and α of CS_A is negative if

$$|\lambda - V_A| \geq |\lambda - V_X| \qquad \text{(Eq. 8)}$$

where X represents the contextual stimuli present in the conditioning situation. From equation 6 and the α change rules stated in equations 7 and 8, it can be concluded that during normal CS-US training the CS will acquire more associative strength than the context but, importantly, the associative strength of the context will not decrease as predicted by the Rescorla and Wagner model.

Obviously, the most important feature of the Mackintosh (107) model is how α changes. Although equations 7 and 8 pro-

vide such rules, these have been questioned by Pearce and Hall (108). Based on their experiment on negative transfer, Hall and Pearce (109) proposed a completely opposite mechanism to explain changes in α (but see Ref. 110, for a different interpretation). In any event, it is clear that models that assume a competition between context and CS have different predictions about context conditioning in relation to the other position in which such assumption is not made.

Expectancy. Gibbon and Balsam (53,111) developed a particular conditioning model that ascribes a different role to contextual stimuli from the one advanced by Rescorla and Wagner. Experiments dealing with appetitive conditioning are the basis for the development of the Gibbon and Balsam model, which has been known as the scalar expectancy theory (SET). Instead of a competition for associative strength between CS and context, SET argues that expectancy or excitatory strength produced by the US presentation spreads uniformly over both the CS and the context. CR to the CS occurs when the expectancy associated with the CS is greater than the expectancy associated with the context.

Specifically, SET proposes that during normal CS-US pairing the US supports a fixed amount of expectancy (H) which is equally and independently distributed over the interval when the CS is present (T) and over the interval between US presentations defined as a cycle of time (C). It is believed that T and C are inversely proportional and their asymptotic level is given by

$$h_T = H/T \qquad (Eq.\,9)$$

and

$$h_C = H/C \qquad (Eq.\,10)$$

So, the longer the stimulus duration, the lower its expectancy. Like the other models presented before, SET also states that conditioning changes according to a negative accelerated function. Change in associative strength of T (CS) and C (approximately the context) can be represented as

$$\Delta V_T = \alpha_T\,(h_T\text{-}V_T) \qquad (Eq.\,11)$$

and

$$\Delta V_C = \alpha_C\,(h_C\text{-}V_C) \qquad (Eq.\,12)$$

Finally, SET assumes that animals compare the two expectancy levels (C and T), so that when the CS is presented a ratio (r) between these two expectancies is taken by the animal.

$$r = h_T/h_C = T/C \qquad (Eq.\,13)$$

Performance of the CR occurs when the ratio exceeds some threshold level. By definition, C is always longer than T since it includes the period in which the context is present alone plus the time when the CS is on. So, conditioning to T is always greater than conditioning to C. Based on this performance rule, SET (112) explains the absence of learning when $P_{US/CS} = P_{US/\overline{CS}}$ (22) as a performance failure. Since the US occurs at high rates in the absence of the CS, expectancy or associative strength to C becomes higher, which in turn causes a failure of the CS to perform the CR. In this case, it is predicted that a CS submitted to the random control procedure should produce some CR when tested in a neutral context. Moreover, decreasing the associative value of the training context through an extinction procedure should also lead to the occurrence of the CR. So far, these experiments have not been done.

Another prediction from SET, which is also in contrast to the Rescorla and Wagner model, is that context and CS conditioning are acquired independently. A direct test for this prediction is to compare the amount of context conditioning produced when the US is signaled or unsignaled by a discrete CS. As already mentioned, there is a tremendous amount of evidence showing that signaled USs produce less context conditioning than unsignaled USs. Nevertheless, there is some

evidence that tends to support the SET prediction. For example, Balsam and Gibbon (113) found that signaled or unsignaled USs lead to the same amount of context conditioning. Interestingly, Williams et al. (59) found the same pattern of results in an aversive conditioning preparation. Context conditioning was directly measured by freezing and no difference in acquisition or extinction in context conditioning was found when signaled or unsignaled USs were delivered in a particular chamber.

Despite the incongruent results cited above, SET makes another prediction that is much more radical and not shared with any other learning model. As stated in equation 13, the motivational variable H has no impact whatsoever on conditioning. This is because H is a variable common to T and C, which is canceled by the ratio r. It is difficult to envision how variations in the quality of the US, such as intensity or duration, do not affect conditioning. It has been known that conditioning varies with the quality of the reinforcement (e.g. 114-116). Although some experiments (117,118) tend to support the SET prediction (which means the acceptance of the null hypothesis), it is possible that in these studies the CR used to measure conditioning was not sensitive enough to detect manipulations in the US. This failure of SET to predict that conditioning is probably a function of the quality of the US tends to weaken its assumption that conditioning

is a function of a ratio between the associative strength of the CS and all the stimuli present during the interval between reinforcements.

Comparison. A model similar to SET has been proposed by Ralph Miller and associates (52,119,120) and assumes that the context acquires associative strength that will be used by the animal to compare with the associative strength with the CS at the time of testing. For obvious reasons, the model was named the comparator hypothesis.

According to the model, occurrence of the CR to a given CS is a direct function of the associative strength of the CS and an inverse function of the associative strength of all the other stimuli that were present during training. It is assumed that animals have a comparator mechanism that is able to evaluate the associative values attached to the CS and to all other stimuli that were presented during the CS-US pairing. Comparison occurs at the time of testing. The greater the associative strength of the comparator stimulus the smaller the chance of the occurrence of the CR to the CS.

The comparator hypothesis assumes that during training 3 different types of association are acquired: CS-US, CS-context and context-US. Figure 2 illustrates how these associations interact. Presentation of the CS during the testing situation activates the representation of the US and the context where training occurred. Retrieval of the contextual stimuli is able to activate the US representation. Since performance of the CR is inversely proportional to context conditioning, the smaller the representation of the US by the context the stronger the CR to the CS will be.

In contrast to SET, the comparator hypothesis states that the testing context does not have to be the same context where training occurred to participate in the comparison. This is because it is the representation of the context activated by the CS that retrieves the memory of the US. Moreover, the

Figure 2 - Schematic diagram of the comparator process. Numbers 1, 2 and 3 denote the three associations assumed to underline the comparison process. 1) CS-US; 2) CS-context; 3) context-US. It is assumed that CR is a direct function of the US representation activated by the CS and inversely related to the US representation activated by the representation of the training context (Taken from Ref. 52, with permission).
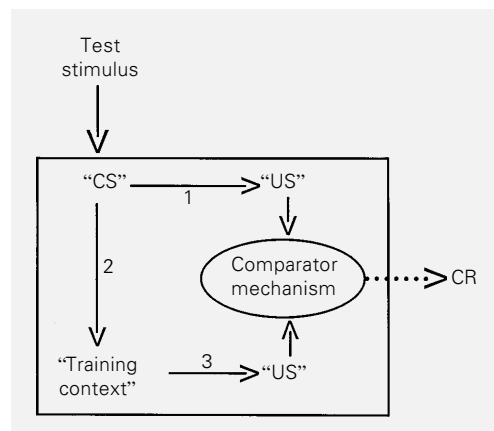
comparator hypothesis is a qualitative model and does not advance any quantitative equations as does SET in equation 13, for example. Finally, the comparator hypothesis is a model that is only concerned with response generation. It does not address how associations are acquired and in fact it can complement a model that deals with acquisition processes.

Some empirical results have supported the comparator hypothesis (54,121). As already mentioned, Matzel et al. (54) tested whether the deficit in conditioning produced by the US preexposure was a performance or an acquisition problem. The unique prediction from the comparator hypothesis is that performance of the CR to the CS is reduced due to the high amount of context conditioning produced by preexposure to the US. Therefore, decreasing the associative strength of the context should increase CR performance to the CS. In fact, Matzel et al. (54) reported that extinction of the context after training attenuated the US preexposure deficit.

Another straightforward prediction from the comparator hypothesis is that increasing the amount of conditioning of the comparator stimulus (e.g. context) should decrease performance of the CR to the CS. This prediction has not been confirmed (52,119). The post-training increase of context conditioning does not affect CRs to CS. This prediction failure could be a good reason to reject the comparator model. Nevertheless, Miller and Matzel (119) argued that the model is still useful, at least as a reference point. In their own words, "Although such approach may seem inconsistent, it just might be the wisest course to take until some new model is formulated that is able to handle the existing data and suggest interesting new experiments. Even though such strategy is contrary to the popular view of science, it is, in fact, how science proceeds. For example, the Rescorla-Wagner (25) model has been disconfirmed by at least two dozen phenom-

ena (e.g. failure of inhibitors to lose inhibitory value when they are presented alone...), but, researchers still use it when it fits their data. The reason for this is that the model continues to suggest interesting experiments and it is elegantly simple." (Ref. 119, page 85).

Priming. Alan Wagner has developed over time a model that evolved from a series of versions (rehearsal, 122; short-term memory (STM), 123; standard operating procedure or sometimes opponent process (SOP) 7; affective extension of SOP (AESOP), 124). It is beyond the scope of this paper to discuss each of these versions. Instead, a brief description of the SOP that agglomerates some features of the previous version will be presented.

Figure 3 presents a scheme of the model. It is proposed that memory is composed of three types of states: two active ones, A1 and A2, and one inactive, I. A1 and A2 can be viewed as short-term memory (STM) or working memory, while I can be interpreted as long-term memory. A1 is the focal part of the STM and has limited capacity. It receives stimuli from the external world through a sensory recorder and is connected to a response generator mechanism R1. When two events share the same A1 state they become associated through a rehearsal process. Since A1 has limited capacity, elements tend to decay to A2, which is considered a peripheral portion of the working memory. A2 also has limited capacity, although its capacity is greater than A1, and can elicit its own response R2. Eventually, elements from A2 decay to I, which has
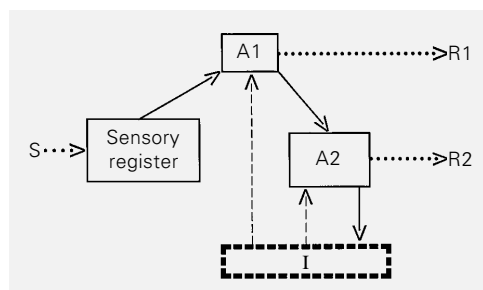

Figure 3 - Diagram of the SOP model (standard operating procedure or sometimes opponent process). External stimuli are decoded by a sensory register and sent to the focal portion of the short-term memory (STM), A1. With the passage of time, elements of the stimulus in A1 start to decay to the peripheral portion of the STM, A2 and eventually will decay to the long-term memory (LTM), I. Elements of a stimulus presented externally can be retrieved from I to A1 and stimuli associated with it can be retrieved to A2. A1 is interfaced with a response generator which provides the unconditioned response to the stimulus presented in the environment. A2 is also connected to the response generator and provides the conditioned response of the stimulus associated with the stimulus presented in the environment.

unlimited capacity. Importantly, each of these three states are connected with unidirectional links so that information always flows from A1 to A2 to I.

A very important aspect of the SOP are the priming rules. According to SOP, there are two kinds of priming: self-generated priming and retrieval-generated priming. Self-generated priming is the ability of the system to retrieve information from I to A1. Note that stimulus elements in A2 cannot be retrieved to A1. Therefore, if a stimulus is presented with short ITIs, then its processing in A1 will be reduced. Since A1 can produce its own responses, a direct prediction from SOP is that during the same experimental session, presentation of a stimulus with short ITI will cause a stronger response reduction in relation to a longer ITI. Indeed this is what is found in short-term habituation (STH; Ref. 125). Thus, SOP explains STH by a self-generated priming mechanism.

Retrieval-generated priming refers to the ability of a stimulus to prime another stimulus associated with it into A2. Thus, if one stimulus S1, previously associated with another stimulus S2, is externally presented and processed into A1, it will have the ability to retrieve the representation of S2 into A2. This mechanism deals extremely well with the fact that latent inhibition is context dependent. Assuming that an association between the context and the CS occurs during the preexposure phase, conditioning will be reduced because contextual stimuli retrieve the CS into A2, thus preventing its full processing in A1. Therefore, SOP explains the context specificity of latent inhibition in terms of retrieval-generated priming. This same mechanism also predicts that long-term habituation (LTH, habituation across sessions) should be context dependent. Context retrieves the stimulus under habituation into A2 and reduces its full response trigger through A1. Context shift prevents the retrieval-generated priming and thus should bring the habituated response to the baseline. However, LTH is insensitive to context change (73). Context shifts abolish latent inhibition but do not interfere with LTH. The inability of SOP to deal with the fact that LTH is context independent has led researchers to question its validity (e.g. Ref. 126). In any event, the present model calls attention to a possible context-CS association (already suggested by Konorski in 1967 (Ref. 6)) and successfully explains the fact that latent inhibition is context dependent.

Retrieval. One of the most well-recognized effects of context on conditioning is the detrimental consequence produced by imposing a change between training and testing locations (for a review, see Spear, Ref. 127). It is not clear why context shift produces a deficit in conditioning performance. A simple explanation could be that the novelty of the testing context elicits responses that are incompatible with the CR. However, this response competition explanation has been dismissed by Miller and Schachtman (120) who found that the reduction of conditioning produced by the context shift was not attenuated when the novel context was preexposed before testing. Generalization decrement also does not seem to be responsible for the performance deficit induced by context shift. Lovibond et al. (75) found a performance deficit in the context shift test when differences in perception of the CS were minimized between the training and the testing contexts.

Another explanation of the performance decrement of the CR to a CS induced by a context shift is that the training context acquires some associative strength that summates with the associative strength of the CS. Although increasing contextual conditioning enhances performance of the CR (89) there is evidence that the better performance of the CR in the training context is independent of the associative value of the contextual stimuli (128,129). Therefore, the associative value of the training context is

an important factor for the expression of the CR, but it cannot fully explain the detrimental effect produced by the context shift.

Given this state of affairs, it is possible that the context may acquire a special ability that interacts with performance of the CS-US association. It has been suggested that contextual stimuli have a hierarchical relationship with the CS and US presented on the context (130). This hierarchical relationship implies that the context acquires the particular function of signaling the CS-US association. Similarly, Spear (127) argues that the conditioning context acts as a retrieval cue for the CS-US association. Interestingly, the retrieval deficit found in the context shift test can be alleviated if animals are briefly exposed to the training context (131). This procedure, known as cueing, consists of exposing the subject to some components of the learning episode, such as the training context, before the retention test. Although it is not clear why cueing enhances performance, it is possible that it acts on modulatory processes developed during conditioning. Recently, modulatory processes in Pavlovian conditioning have received much attention. It has been demonstrated that stimuli can alter the CS-US association without having any measurable associative strength. These types of stimuli have been termed facilitators (86) or occasion setters (85) and it is possible that contextual stimuli might acquire such ability.

Occasion setting. In a feature-positive discrimination a compound stimulus, AX, is followed by the US while one of the CSs, X, is not. CR occurs when AX is presented but no CR to X is observed. In fact, it has been shown that X does not gain any associative strength but facilitates the CR to A by signaling or setting the occasion for its reinforcement (86).

It has been suggested that during normal CS-US training, contextual stimuli may acquire this facilitatory ability. Indeed, traditional Pavlovian conditioning can be viewed as a feature-positive discrimination if contextual stimuli are assumed to be X and the discrete CS to be A. Bouton and Swartzentruber (84) reported data that support this interpretation. In a series of experiments, they showed that the context specificity of extinction (renewal effect) was not mediated by a context-US association. Animals were submitted to CS-US pairings in context A and CS alone in context B (AX+; BX). Summation, blocking and retardation tests failed to show associative strength of contexts A and B. Moreover, exposure to context A alone after training did not affect the ability of context to control CR performance to the CS. Therefore, it seems plausible that contextual stimuli interfere with the CS-US association by mechanisms similar to facilitators or occasion setters.

Neurological manipulations

There is not much doubt that the nervous system is the structure responsible for association formation. Associative conditioning causes specific neuronal changes in several brain areas (132-136), including permanent electrophysiological changes at the very first synapses in the central nervous system (137). Therefore, neuronal manipulations, such as lesions, can be helpful to examine which functions contextual stimuli develop during Pavlovian conditioning.

It has been reported that hippocampal lesions did not affect aversive conditioning to a discrete CS but disrupted aversive context conditioning (138-140). This dissociation between CS and context conditioning suggests that the hippocampus is selectively involved in context conditioning. Contextual stimuli are present throughout the training period and are composed of several sensory modalities. Since the hippocampus is a critical structure for spatial and contextual processing (141,142), it is possible that the disruptive effect of hippocampal lesions on aversive context conditioning is due to a

deficit in contextual processing. In agreement with this interpretation is the fact that hippocampal lesions disrupt latent inhibition (143). As mentioned, latent inhibition is a context-specific phenomenon and depends on a context-CS association. Therefore hippocampal lesions might interfere with perception and/or representation of contextual stimuli. Neuroanatomical results also support the premise that the hippocampus is a sensory relay for the polymodal nature of the contextual stimuli. The hippocampus receives projections from several cortical associative areas and different sensory thalamic regions (144).

The fact that hippocampal lesions do not affect conditioning to a discrete CS is also consistent with the above rationale. Discrete CSs are unimodal stimuli and have their own sensory pathways. Auditory stimuli, for example, are carried through the inferior colliculus and the medial geniculate body. Lesions in either of these structures disrupt auditory aversive conditioning (145,146). Moreover, visual stimuli are encoded by the superior colliculus, the lateral geniculate body and the visual cortex. Lesions in any one of these sensory areas disrupt visual aversive conditioning (147). Therefore, the selective effect of hippocampal lesions on context conditioning is probably due to a sensory deficit produced by the hippocampal lesion and might indicate that contextual stimuli are perceived as a whole unit before conditioning occurs. Interestingly, it has been suggested that the hippocampus is the critical neural structure where learning occurs. (e.g. Refs. 148,149). If the presented logic proves to be true, then the participation of the hippocampus in learning might be related to sensory processing rather than being the actual site of learning.

Other evidence indicating that the hippocampus is not the place where aversive conditioning occurs is the fact that microinjection of APV (an N-methyl-D-aspartate receptor antagonist) in the basolateral nucleus of the amygdala, but not in the central nucleus, blocks acquisition of aversive context conditioning (150). This finding corroborates the notion that aversive context conditioning is mediated by a long-term potentiation mechanism (151-153) and indicates that the CS-US association may occur in the basolateral portion of the amygdala. Since electrolytic or ibotenic acid lesions in several nuclei of the amygdala (central, lateral and basolateral) interfere with performance of conditioning to the CS (152,154, 155) and to the context (156-158) it is possible that all the amygdala nuclei, except the basolateral one, are related to expression of aversive conditioning.

Recently, Sparks and LeDoux (159) reported that lesions of the septal area enhance aversive context conditioning but have no effect on aversive conditioning to a discrete CS. Again, this is further evidence showing that contextual and discrete stimuli are processed by different neural structures. It is not clear why damage to the septal area induces a selective increase in context conditioning. Because the septal area and the hippocampus are intimately related, it is possible that the destruction of the septal area enhances the ability of the hippocampus to perceive the contextual stimuli.

In the midbrain, lesions in the ventral portion of the periaqueductal gray (PAG) disrupt context and CS conditioning (160-162). Furthermore, the ventral PAG is also involved in the expression of the analgesic response triggered by aversive context conditioning (163). Therefore, this area might be a final common pathway for expression of aversive conditioning (164). On the other hand, lesions of the dorsolateral portion of the PAG enhance aversive context conditioning (161,162,165). Because there are monosynaptic projections between the dorsolateral PAG and the amygdala (166), it is possible that activation of the dorsolateral PAG has a negative impact on the acquisition of aversive context conditioning that

occurs in the amygdala (for further discussion of this possibility, see Ref. 165).

Despite the associative strength attached to context, and its particular mechanism, contextual stimuli seem also to be involved in the retrieval of the CS-US association. There is evidence that the hippocampus is the neuronal structure responsible for such ability (167-169). Interestingly, it appears that hippocampal lesions abolish acquisition of occasion setters (170, but see 171,172). Thus, neurological manipulations suggest that retrieval and occasion setting might be the same process. In fact, occasion setting might be the mechanism that underlies contextual retrieval.

Conclusion

The birth of modern theories of learning was based on the fact that contiguity is not necessary or sufficient to produce associative learning. This is best illustrated by Rescorla's contingency experiments and Kamin's blocking effect. A group of theories (7,25,107,108) argue that the CR is a direct reflection of the CS-US association. Although these models dispute whether it is a variation in CS processing or US processing that determines change in learning, all of them recognize that the most important factor in conditioning is the informational relationship between the CS and US. On the other hand, a different group of theories (52,53) stress the necessity of a distinction between learning and performance. The absence of the CR during a test might reflect a performance problem and not a learning deficit. Surprisingly, but in accordance with this particular approach, blocking and overshadowing can be reversed by manipulations that enhance performance (173-176).

It is far beyond the aim of this paper to evaluate which theory deals best with all the data available today. Instead, the paper limits itself to discuss the evidence that indicates the importance of contextual stimuli in Pavlovian conditioning. In this respect, the Rescorla and Wagner model is a landmark since it first formally recognized contextual cues as part of the conditioning situation. Since then, contextual conditioning has attracted a lot of interest and still remains an open field of study. It is clear from this review that context can acquire its own associative strength, which in turn can sum with the CS-US association. It is also plausible that context can become associated with the CS and this form of learning can alter the course of future conditioning. Moreover, contextual stimuli appear to enhance retrieval of specific CS-US associations. This retrieval ability is not mediated by any form of associative learning and is probably related to a modulatory process such as occasion setting. Therefore, context can develop more than one function during Pavlovian conditioning.

It is important to note that the modulatory function of the context might only occur when contextual stimuli are the background for a discrete CS. Having the context as the target, CS would probably preclude this function. Therefore, a simpler situation in which the US is presented alone in the context would be a more appropriate preparation for the exclusive study of associative learning. For example, the ITI paradigm, in which unsignaled shocks are presented in a context, have already proved to be a fruitful paradigm for testing several learning models (e.g. Ref. 57). An interesting control procedure for context conditioning is the immediate shock deficit (45,46). In this procedure, animals do not show any form of learning when they are exposed to a shock as soon as they are placed in the experimental chamber. It has been shown that the handling cues that immediately precede the presentation of the US or the novelty of the contextual stimuli where the immediate shock is presented are not variables responsible for the learning deficit (177). Moreover, the immediate shock deficit is not

caused by retrieval or performance deficits (Landeira-Fernandez J, Fanselow MS, DeCola JP and Kim JJ, unpublished results). Finally, an interpretation based on simultaneous conditioning has been already discarded (45). Therefore, it appears that the immediate shock procedure can be employed as a useful sensitization and pseudoconditioning control for the study of context conditioning.

The fact that the context is composed of a series of rather diffuse stimuli poses an interesting question. Does the US become associated with a particular stimulus present in the experimental chamber or with all con-

textual stimuli as a whole? Although neurological manipulations favor the latter alternative, Minor and LoLordo (65) suggested that it is the olfactory stimulus that becomes conditioned with the US. Unfortunately no study has directly addressed this issue. Indeed, this is just one of several problems that remain open for future research.

Acknowledgments

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