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Analysis of the context-switch effect upon retrieval of the information

The influence of an increase in the prediction error
on information processing

Análisis del Efecto de Cambio de Contexto en la Recuperación de la Información

La influencia del aumento en el error de predicción
en el procesamiento de la información

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Juan Manuel Rosas Santos, Catedrático de Psicología Básica de la Universidad de Jaén, y José Enrique Callejas Aguilera, Profesor Titular de Psicología Básica de la Universidad de Jaén,

Garantizan que:

La Tesis Doctoral titulada: “Analysis of the context-switch effect upon retrieval of the information: The influence of an increase in the prediction error in the information processing”, realizada por el doctorando José Andrés Alcalá Martín, ha sido elaborada bajo nuestra dirección y reúne las condiciones de calidad, originalidad y rigor científico necesarias para que se proceda a su defensa pública de acuerdo con la legislación vigente.

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Contradiction is the root of all movement and vitality.

La contradicción es la raíz de todo movimiento y vitalidad.

Georg W. Hegel

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El objetivo último del doctorado puede ser sintetizado en forma de manuscrito, al igual que el corredor de maratón persigue traspasar la línea de meta. No obstante, en ambos casos la experiencia, aprendizaje y apoyos recibidos sobrepasan cualquier meta o conclusiones alcanzadas. En este sentido, las comparaciones entre correr una maratón y terminar un doctorado me resultan bastantes claras. No sólo hace falta correr una determinada distancia, o presentar una tesis, es necesario mucho más. Los apoyos comienzan mucho antes de plantarte en la línea de salida de ambas carreras. Una vez situado en la línea de salida, una larga distancia separa la memoria inicial de la final, pero recorrer todo el trayecto es más sencillo recibiendo sostén en cada paso recorrido.

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Abstract

There is a large body of research suggesting that the experience of associative interference leads to changes in the attentional resources used by the organism. Associative interference implies alterations in the prediction error that appears when the organism receives something unexpected. Explanations offered by different associative learning models vary in how attention is assigned to different elements inside the learning situation. For instance, one set of theories suggests that attentional changes are specific to the stimulus for which the prediction error appears. In that line, Pearce and Hall (1980) theory predicts that attention to a given stimulus is greater the greater the prediction error tied to that stimulus (but see Mackintosh, 1975). Extending this idea, experiencing increases in prediction error may enhance an attentional explorative pattern in the organism, searching for a way to eliminate the uncertainty of the situation (Le Pelley, Mitchell, Beesley, George, & Wills, 2016). Alternative approaches focus the attentional change in the context in which associative interference was generated, so that retrieval of the information that turns ambiguous after the experience of associative interference becomes context-depend (Bouton, 1993, 1997). Extending Bouton ideas, Attentional Theory of Context Processing (ATCP) suggested that the experience of associative interference boosts attention to the context, and that retrieval all the information learned within an attended context becomes context-specific (Rosas, Callejas-Aguilera, Ramos-Álvarez, & Abad, 2006). Finally, some studies suggest that experiencing changes in the prediction error may affect the subsequent rate of learning (Courville, Daw, & Toureszky, 2006). This last result suggests that the influence of associative interference in attention may not be bound to the context but to involve an increase in the exploratory pattern of behaviour that facilitates learning (Le Pelley et al., 2016). Taking all these ideas in account, the three studies gathered in this dissertation tried to evaluate whether experiencing associative interference only facilitates learning about contexts, as ATCP predicts (Rosas et al., 2006), or whether it leads to a general facilitation in subsequent learning, as suggested by other studies (Courville et al., 2006).

The first study explored the effect of experiencing associative interference upon concurrent conditioning of a non-interfered conditioned stimulus (CS) and the context in rats' appetitive conditioning. According to ATCP, experiencing associative interference should increase attention to the context, expecting greater context conditioning in the animals that had the experience of associative interference. Contrarily, if the increase in attention is not specific to the context, both context and CS conditioning should be facilitated. Animals exposed to discrimination reversal showed greater context conditioning than animals that did not have the experience of associative interference, while no differences were found in CS conditioning. This result suggests that the alleged increase in attention that the experience of associative interference produces was specific to the context, as ATCP predicts (Rosas et al., 2006).

The second study explored further the effect of associative interference upon new learning. In that line, the study tested whether the experience with discrimination reversal may enhance both, temporal and context conditioning that takes place after, and not concurrently to the experience of associative interference. Experience of previous interference facilitated the acquisition of temporal conditioning, regardless of the duration of the interval between food administrations (i.e., 30s or 60s). However, context conditioning was not facilitated after the interference experience.

The third study explores whether experiencing associative interference facilitates subsequent new learning about space in a water-maze in rats. Animals were trained in a spatial learning task, in which interference took place or not (interference was reached by changing the position of the platform in the water-maze). Results coming from two different experiments found that the group exposed to associative interference learned faster a new position of the platform than different control groups.

Taken together, the three studies present a dual pattern of results. Context, but not CS conditioning was facilitated by the concurrent experience of associative interference in the first study. A somewhat opposite pattern of results was found in the second study, finding that interference facilitated subsequent new learning about time, but it did not facilitate context conditioning. Finally, the last study found that interference facilitates subsequent new learning in the spatial domain. Thus, the general pattern of results show that the experience of interference may facilitate both, learning about context, and also learning about time and space, at least under certain conditions. These results suggest that the current formulations of retrieval (Bouton, 1997) and ATCP theories (Rosas et al., 2006) need to be reformulated in their account of the effects of context change on retrieval of the information. Additionally, these results suggest that there are boundaries in the effects of associative interference on subsequent learning and context dependence of the information that are yet to be explored.

Preface

Animals are exposed to a large amount of information throughout their lives. Their ability to classify that information, detecting predictors of relevant outcomes as quickly as possible, is essential for their growth, reproduction, and survival. It is this ability what allows them to adapt their behaviour to the changing conditions of the environment. A rat and myself may predict the location of a water source based on the type of herbage of a given area, and I can inhibit the natural reaction to flee when I see a tiger in the safe environment of the zoo. We can build new and different associations using different sources of information, and then use those associations in our interest. In other words, we are able to learn, and the ability to learn gives us an evolutionary advantage.

Understanding the processes by which human and non-human animals learn to respond to neutral stimuli that predict changes in the environment has been a goal of behavioural research since the seminal studies conducted by Pavlov (1927). Pavlov's dogs were not biologically ready to salivate to the sound of the metronome. They might have startled, but the salivation reflex was not the "natural" response to the sound of the metronome. However, when the sound of the metronome was followed by the delivery of food, the sole presentation of the sound triggered the salivation response in anticipation. His experiments set up the basic procedures and principles of what has been known as classical or Pavlovian conditioning ever since. Pairing neutral and biologically relevant stimuli produces a change in the animal's responding to the neutral stimulus, so that its behaviour adapts to the future presentation of the biologically relevant stimulus. In the case of a stimulus that anticipates delivery of food, the animal performs anticipatory responses such as approaching the magazine in which the food is usually delivered. Contrarily, if a stimulus signals an aversive outcome, the organism performs defensive responses such as freezing or fleeing. For instance, animals tend to freeze (defensive response) when one stimulus anticipates a shock in a situation where no fleeing is possible. In this situation it is generally assumed that the animal establishes associations between the predictor and the outcome that follows it (S-O associations, Colwill & Motzkin, 1994), though it also seems to learn to perform a given response in the presence of the predictor (S-R associations; Rescorla, 1973).

Animals also learn to perform responses to manipulate the environment in order to reach their goals. A hungry rat learns to follow a given path to find the food at the end of a maze. Animals may even learn to perform behaviours that are not natural for them. It is easy to visualize the iconic image of a rat pressing a lever inside an operant box. Rats are not ready to press a neutral, and a priori irrelevant lever. However, if the contingencies are arranged so that lever presses are followed by delivery of food, hungry rats soon learn to press the lever. In this free operant or instrumental learning situation, rats are assumed to establish associations between distinctive responses and the outcome (R-O associations; e.g., Bouton, Todd, Vurbic, & Winterbauer, 2011; Colwill & Rescorla, 1985). Likewise, the instrumental conditioning situation may be established so that responding is followed by the outcome only in the presence of a distinctive stimulus, but not in its absence, in what it is known as discriminative instrumental conditioning (Skinner, 1938). Moreover, animals are able to execute complex patterns of chaining, showing specific responses in the presence of particular discriminative stimuli, which subsequently elicit different types of responses under the control of different discriminative stimuli (e.g., Thrailkill, Trott, Zerr, & Bouton, 2016). In these complex situations, animals have been found to establish associations between responses and outcomes (R-O; e.g., Colwill & Rescorla, 1985), between the discriminative stimulus and the response (S-R; e.g., Colwill, 1994), between the discriminative stimulus and the outcome (S-O; e.g., Colwin & Rescorla, 1988), as well as hierarchical associations in which the R-O association is modulated by the presence of the discriminative stimulus (S[R-O]; e.g., Colwill & Rescorla, 1990; Gámez & Rosas, 2007). In addition, the context may also play a modulatory role of these associations (Bouton & Swartzentruber, 1986), or even enter into direct associations with each of the elements involved in the instrumental situation (e.g., Gámez, León, & Rosas, 2017).

Studies of classical and instrumental associative learning show the great ability the organisms have to adapt to changes in the environment, and to use the available stimuli to guide their behaviour. Decades of research have shown that the ability to develop associative learning is a general mechanism of adaptation to the environment across different animal species, including humans (e.g., Johnston, 1982; Mackintosh, 1974). The usefulness of this mechanism of adaptation depends on how the organism sorts out the meaning of the multiple stimuli that are available in natural environments.

Animals confront complex environments conformed by hundreds of stimuli, and they have to learn which stimuli are informative and which are not. How the organism ends attending some stimuli and how it learns not to attend to others is not a simple question. We could assume that animals' attention is captured by stimuli with some particular features, such as natural predators (e.g., Johnson, Gall, & Brodie, 2013), physically salient stimuli (e.g., Yantis & Yonides, 1984), or fear relevant stimuli such as snakes (e.g., Öhman, Flykt, & Esteves, 2001). Other sources of information, in spite of being relevant, do not attract attention directly, so they may be initially unattended by the organism. The proper use of its attentional resources to detect relevant information that does not naturally attract the organism's attention is crucial for the organism’s survival (e.g., Hullinger, Kruschke, & Todd, 2014). For instance, attending to the colour of some berries may be important for the animal, because berries’ colour could predict whether they are edible or not. Successful learning may represent the difference between a tasty snack and death. Thus, attention drives learning of the organism (e.g., Mackintosh, 1975; Pearce & Hall, 1980); and vice versa, learning seems to drive attention as well (e.g., Le Pelley, Mitchell, Beesley, George, & Wills, 2016). It is not surprising that many models of associative learning involve the attentional resources of the organism in order to explain how it is learned, and what it is learned about (e.g., Kruschke, 2003; Mackintosh, 1975; Pearce & Hall, 1980; Rosas, Callejas-Aguilera, Ramos-Álvarez, & Abad, 2006; Schmajuk, Lay, & Gray, 1996).

Since Pavlov’s experiments of associative learning, researchers have been trying to emulate nature within the laboratory in order to get a better understanding of the general principles that regulate the learning process. There is an agreement in some characteristics that concern of the basic principles of associative learning, and several theories and models have been proposed trying to explain data collected across thousands of experiments with non-human and human animals within the associative learning domain. As stated in the previous paragraph, associative learning and attentional resources have become quite close in some of these models to explain some key phenomena in associative learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980). For example, a decrease in attention to the stimulus is used to explain the retardation on learning that occurs when one stimulus is followed by an outcome after been presented by itself (i.e., latent inhibition, Lubow & Moore, 1959). In another example, when two stimuli are presented together, learning about the most salient stimulus is usually higher in comparison with learning about the least salient stimulus. This difference is often attributed to the most salient stimulus receiving greater attention (e.g. overshadowing, Pavlov, 1927; see Mackintosh, 1975).

The problem of understanding how associative learning works becomes more difficult when one takes into account that learning never takes place in the vacuum. Target stimuli are always surrounded by external and internal stimuli that are conventionally defined as context. Additionally, these stimuli are continuously changing (Speekenbrink & Shanks, 2010). In natural environments, the context may include circadian and ultradian cycles such as day and night, tides, or the season of the year; and more punctate changes in the environment such as distinctive odours, shapes and colours. Internal changes in the organism have been considered as part of the context as well (Schepers & Bouton, 2017). These stimuli may affect learning and retrieval of the information about target cues and responses. Blueberries could be tasty in the summer but not in the winter and questioning the speaker may have different outcomes in the classroom and in church. Thus, one source of information could be reliable within a given context but not in a different one. The problem of understanding how learning works becomes increasingly complex when we take in account that, even within the same context, one stimulus could predict a particular outcome today, but a different one, or even none tomorrow. How animals react to this unexpected change in the relationship between the stimulus and the outcome? What happens when the target stimulus is now presented in different context? Does learning transfer across different contexts? Intuitively, one would expect that learning of individuals should be robust enough to transfer across different contexts and conditions, but at the same time it needs to be flexible enough to change according to the context, as the context may be relevant for the meaning of the cues.

The search for an answer to these and other questions has guided a large number of studies conducted with the goal of exploring the effects of changes in both, the meaning of the stimuli, and the context of learning and testing. Experimental research tries to emulate and study the role of natural contexts by manipulating distinctive environmental cues (olfactory, tactile, visual, etc.). Experimental settings mimic the changing features of the environment by using different procedures in which the contingency between stimuli is changed throughout the experimental situation. The combined study of both, the effect of changing the meaning of the stimulus and the effect of changing the context where learning and testing takes place, has been largely studied within the experimental extinction paradigm. In the extinction procedure, contingency between the conditioned stimulus or the response and the outcome is changed, so that one stimulus (or response) that used to be followed by a given outcome, is not followed by that outcome anymore. Understanding the way in which an organism reacts when the expected food is not delivered is one of the most intriguing and explored topics within the field of associative learning (Lattal & Lattal, 2012). Research has been focused on how animals deal with this ambiguous situation, in which the same source of information was first followed by an outcome and then it was not (Bouton, 1993, 1994). Extinction is just one of the experimental methods more commonly used to produce associative interference. In general terms, associative interference may be understood as the result of applying those particular procedures in which animals are exposed to information that is in conflict with their previous knowledge (e.g., latent inhibition or counterconditioning).

The focus of this dissertation is to get a better understanding about the role of associative interference in subsequent learning about contexts and cues. The ultimate goal of this line of research will be to understand the role of associative interference on new learning in both human and non-human animals. The research gathered in this dissertation was conducted only with non-human animals, fitting our general comparative approach to learning and memory research which develops step by step (Papini, 2008). This strategy of research has been shown to be quite productive in the past, unveiling impressive parallelisms between non-human and human animals within the associative learning domain (e.g., Rosas, Gámez, León, González, & Nelson, 2017). In that sense, it is fairly safe to think that the results reported here may open an interesting field of research in human beings that might end extending the parallel between human and nonhuman animals with respect to the role of basic associative processes.

The present dissertation was developed following the experimental principles of generalization and replication of the effects. Replication is an important issue within scientific research. Open Science Collaboration (2015) estimated that two thirds of the psychological research have not been replicated in subsequent attempts. Even assuming that there may be some estimation error (Gilbert, King, Pettigrew, & Wilson, 2016), replication is an essential requirement within experimental research, and the studies presented within this dissertation were conducted with that rule in mind. While replication ensures the reliability of the phenomenon, generalization ensures its relevance. As the studies presented here were conducted with rats, generalizability of their results is still under evaluation. However, the first step on this exploration was reached by testing the same phenomena within different learning domains. Subsequent research should expand the exploration of the phenomena discovered in this dissertation to other species, including humans.

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1. State of the Art

1.1. Associative Learning

Most current definitions of learning assume that learning is a process by which there is a relatively permanent change in the underlying mechanisms of behaviour as a result of the experience (e.g., Anderson, 1995; Domjan, 2010). This change in behaviour is defined as "relatively permanent", so that the organism that uses learning processes can get long-term benefits from that use. However, the key of this definition lays in the word "relatively". The fact that two elements have been presented together in the past does not imply necessarily that they will be presented together in the future. The environment changes, and successful organisms are prepared to cope with those changes. Learning is the mechanism organisms have to both, learn about the environment, and adapting to environmental changes, updating their knowledge to fit the new environmental features.

In a sense, learning may be understood as the mechanism that allows the organism to disambiguate its environment, eliminating uncertainty. Associative learning is the type of learning by which organisms establish links among mental representations of elements in the environment. For most theories of associative learning, the mechanism of learning starts working when the expectancies of the organism are disconfirmed by the environment. Learning is associated to the surprise that produces in the organism the disconfirmation of an expectation (Kamin, 1965). That is, when the organism receives something that does not expect, either because it does not expect anything or because it does expect something different from what the organism receives. From this point of view, surprise is defined as the discrepancy between what the organism expects to happen and what actually happens. This has been quantified in learning models through the prediction error, that is updated with some type of delta rule.

According to classical models of associative learning, prediction error is assumed to drive learning of the organism (Mackinstosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972; Sutton & Burton, 1981). Prediction error is usually formalized as ($\lambda - \sum V$). Lambda (λ) is the maximum level of learning allowed by a given outcome, and it is conventionally assumed to go between 0 and 1 (0 when the outcome is not present, and 1 when the outcome is present); the sum of the associative strength of all the stimuli (predictors) presented in the situation is symbolized by the $\sum$ of V. Before learning, when the organism does not have an expectation about the role of the present stimuli, the associative strength (the predictive power of all the stimuli present in the situation) equals 0. If the outcome appears in that trial, prediction error will be at its maximum level ($1 - 0 = 1$). Within these formal models, learning is defined as the correction of the prediction error using a delta rule. As training progresses, associative strength of reliable predictors increases until reaching a level close to 1. Concurrently to this increase of associative strength, prediction error progressively decreases towards 0 and learning becomes gradually smaller. Learning stops when the organism receives what the organism expects, and therefore prediction error disappears.

The Delta rule at the core of classical models of associative learning has been supported by neural correlates in the activity of dopaminergic neurons (Nasser, Calu, Schoenbaum, & Sharpe, 2017; Waelti, Dickinson, & Schultz, 2001). Most classical models of associative learning conceptualize the error term in a similar way. Differences among models come from the way in which the predictors (conditioned stimuli, CS) are conceptualized, and from the role attention plays within the model. The elemental model of Rescorla and Wagner (1972) supports the idea that each stimulus involved in the learning situation is separately able to gain or lose associative strength. Within this model, the associative strength of a compound stimulus equals the sum of the associative strength of its elements, with each element of the compound competing with the others for predicting the outcome. Prediction error in this model is computed by comparing the asymptote of learning with the sum of the associative strength accrued by the elements of a given compound. When the compound is partially changed, the associative strength of the new compound will equal the sum of the associative strengths of the elements of the new compound. Alternatively, configural models such as Pearce’s (1987) assume that the organism counts with a sensory buffer that is always full, and that everything that is within that buffer at a given moment plays the role of the CS. Responding, or the lack of responding to different CSs is then explained by generalization. Any change in the CS will make it different from the original one, so that the associative strength displayed by the new CS will be the one it borrows from the original one (Pearce, 1987, 1994, 2002).

Traditional associative learning models also differ in the role they give to attentional mechanisms. Rescorla and Wagner (1972) took a simple approach to this issue, by assuming that attention to the CS and the US only depends on the physical features of the stimuli, and that this attention is fixed throughout the learning process. However, attentional associative models of learning such as the ones developed by Mackintosh (1975) or by Pearce and Hall (1980) assume that attention depends on the predictive value of the CS, and that the attention received by a CS changes as learning progresses. Both models differ in the assumptions about how learning affects attention to the CSs. According to Mackintosh (1975) the greater the predictive value of a cue, the greater the attention that cue receives. In other words, the lower the prediction error for a given stimulus, the higher the attention it receives (for a review, see Le Pelley, 2004).

Alternatively, Pearce and Hall (1980) assume that there is a reverse relationship between the predictive value of a CS and the attention the CS receive. In other words, organisms pay attention to stimuli that are poor predictors of their outcomes, discarding those that are consistent predictors of the presence or the absence of outcomes. According to these authors, the higher the prediction error, the higher the attention a given CS receive (e.g., Kaye & Pearce, 1984; Swan & Pearce, 1988).

As contradictory as they are, both approaches “make sense” from a rational perspective: it is reasonable to assume that the organism will pay more attention to the most relevant stimuli (Mackintosh, 1975), as it is reasonable to assume that the organism will pay more attention to those stimuli which outcomes are uncertain (Pearce & Hall, 1980). In fact, experimental research has given support to both assumptions, suggesting that the different results backing up one model or the other may depend on the situation, and the time in the training process in which the test is conducted (e.g., Halsegrove, Esber, Pearce, & Jones, 2010). Hereof, recent theoretical approaches tend to develop hybrid models that allow for an integration of the two different approaches about how learning affects attention, and vice versa (e.g., see a review of different models in Mitchell & Le Pelley, 2010). Within this context the approach recently developed by Le Pelley, Mitchell, Beesley, George, and Wills (2016), separating attentional exploitation from attentional exploration, results particularly relevant for the studies that will be reported in this dissertation. According to these authors, the *attentional exploitation mechanism* would enter in effect in those situations in which the outcomes of the cues are certain. In agreement with this idea, people spend more time looking at cues that are good predictors of their outcomes than looking at cues that are poor predictors of them (Le Pelley, Beesley, & Griffiths, 2011), and reaction times to respond to predictive cues are lower than reaction times to respond to non-predictive cues (Le Pelley, Vadillo, & Luque, 2013). Alternatively, the *attentional exploration mechanism* is assumed to enter into play in situations with high level of uncertainty, leading the organism to spend more time looking at cues that are poor predictors of the outcomes, rather than looking at the ones that are good predictors. In these situations, the attentional mechanism is engaged with the goal of exploring all the possibilities within that particular learning set up (Beesley, Nguyen, Pearson, & Le Pelley, 2015). Recent results are in agreement with this general idea, suggesting that high predictiveness attracts the organism’s attention to the cues, while uncertainty may lead more to holding attention to the cues (Koenig, Kadel, Uengoer, Schubö, & Lachnit, 2017; Koenig, Uengoer, & Lachnit, 2017; Luque, Vadillo, Beesley, & Le Pelley, 2017).

1.2. Associative Interference

Associative interference appears when the meaning of a stimulus or a response changes once learning has taken place. Associative interference can be categorized into two general types: *retroactive interference and proactive interference*; and can be generated by multiple techniques and procedures (e.g., Miller & Escobar, 2002; Polack, Jozefowiez, & Miller, 2017). In the case of *retroactive interference*, the information that is learned second interferes with retrieval of what it was learned first. In *proactive interference*, what it was learned first interferes with both learning and retrieval of what it was learned second.

The most common procedures for studying *associative retroactive interference* are extinction and counterconditioning. In the *extinction* procedure a conditioned stimulus (CS) or an instrumental response (R) that is regularly followed by a given outcome (O), stops being followed by O during the second stage of learning, leading to a decrease in the conditioned response (CR) (e.g., Pavlov, 1927) or in the instrumental response (e.g., Nakajima, Tanaka, Urushihara, & Imada, 2000). This decrement in the CR is found regardless of the type of learning procedure used. It may be observed as a decrease on magazine entries over extinction trials in appetitive conditioning (e.g., Ricker & Bouton, 1996), as a reduction in the freezing time in fear conditioning (e.g., Harris, Jones, Bailey, & Westbrook, 2000), as an increase in the intake of a rejected flavour in taste aversion (e.g., Rosas & Bouton, 1997), or as a decrease in the skin conductance in human fear conditioning (e.g., Álvarez, Johnson, & Grillon, 2007) among many other responses and procedures. If extinction training is long enough, the CR decreases to a level similar to the one displayed by a stimulus that has never been conditioned before. In the case of c*ounterconditioning*, after training a CS with a given outcome (O1), the original outcome is replaced by a new outcome (O2) with a motivational value opposite to the value of O1. Note that this procedure integrates two sources of interference, the extinction of the CS-O1 association, and the new learning about the CS-O2 association. For example, if the CS is followed by delivery of food during first stage, the CS will be followed by a shock during the second stage (Peck & Bouton, 1990), of vice versa. In these procedures, researchers usually focus on how what it is learned during the second phase interferes retrieval of prior learning.

Within associative *proactive interference*, the most common procedure is *latent inhibition* (e.g., Lubow & Moore, 1959). Procedurally, latent inhibition is the mirror of extinction: the CS is presented first without O, and then followed by O during a second stage of training. The organism learns about the CS-O relationship more slowly than if the CS was never presented before. Similar results are found after *learned irrelevance,* in which learning about the CS-O relationship is retarded when the CS and the O are previously presented uncorrelated (e.g., Mackintosh, 1973). Retardation of learning, and thus proactive interference, is also reported when the CS is first paired with a weak shock and then paired with a strong one, in a procedure labelled as negative transfer (e.g., Hall & Pearce, 1979).

Although for the sake of clarity we have presented separately examples of proactive and retroactive interference, both types of interference always coexist within the same procedure. Procedures are classified in one type of interference or the other depending on where researchers focus their interest, rather than in the specifics of the procedure used. For instance, in counterconditioning, presenting the CS followed by O2 interferes retroactively with retrieval of the CS-O1 relationship, at the same time that the experience of CS-O1 pairings interferes proactively with CS-O2 learning. An example in which coexistence of both types of interference is clearly shown is in *Discrimination Reversal* procedures. In these procedures, two stimuli are presented intermixed during an initial stage of training, CS1 paired with O1, and the CS2 paired with O2 (or with the absence of outcome). During the second stage of training, relationships between stimuli and outcomes are reversed, so that now CS1 is followed by O2, while CS2 is followed by O1, or by the absence of outcome (e.g., Üngor & Lachnit, 2006).

1.2.1 Explaining Associative-Interference with traditional models of Associative Learning

The explanation of associative interference involves an important challenge in the field of associative learning. In a sense, understanding how animals deal with the interfering and interfered information may be considered at the core of learning, as it will lead to an understanding of how animals adapt to a changing environment. The first and simplest approach to this problem is to consider that the increase in the prediction error that appears when a cue changes its meaning, activates the learning process so that the new learning erases the information that was acquired before. Most learning models are built upon that assumption, allowing for a single relationship between a cue and the outcome that is adjusted as environmental conditions change (e.g., Rescorla & Wagner, 1972). Alternatively, the new environmental conditions could conduct to developing of a new association that would coexist with the association already learned before the conditions changed (e.g., Konorski, 1948).

When interference appears, classical models of associative learning assume that there will be a simple fit of the organism's predictions to the new environmental conditions (i.e., associative strengths), which will be readjusted over trials until prediction error reaches zero again (e.g., Rescorla & Wagner, 1972). With this assumption, classical models of learning are able to fit the loss of the conditioned responses observed during extinction. However, they are not able to explain the remarkable body of research showing that the change in conditions do not fully eliminate the originally learned information, as that information can be retrieved even when there is no behavioural evidence of its presence. The simple passage of time, a change in the context, or the presentation of a new stimulus usually leads to retrieval of the original information, suggesting that the interference treatment does not erase it (e.g., Bouton & Bolles, 1979; Pavlov, 1927).

For instance, in *spontaneous recovery*, the simple passage of time after interference is enough to find a partial recovery of the first learned information (Pavlov, 1927; Robbins, 1990; Rosas & Bouton, 1996). This phenomenon is well stablished across a wide range of species. Snails have been found to show a recovery of the extinguished CR (tentacle lowering) when they are tested 3 days after extinction training was completed (Álvarez, Morís, Luque, & Loy, 2014). Similar results have been reported in rats (e.g., Dunsmoor, Campese, Ceceli, LeDoux, & Phelps, 2015), pigeons (e.g., Robbins, 1990), and human beings (e.g., Vila & Rosas, 2001) among other species. In *reinstatement,* a non-contingent outcome delivered within the test context once the interference treatment has been finished renders a recovery of the previous conditioned responses (e.g., Delamater, 1997; García-Gutiérrez & Rosas, 2003; Rescorla & Heth, 1975). In *external inhibition* or *disinhibition*, the presentation of unexpected events, such as new stimulus before the presentation of the extinguished stimulus, also leads to a relapse of the CR, as in the previously described phenomena (Pavlov, 1927). Within operant learning, *resurgence* appears when extinction of the relationship between lever 1 and the outcome is conducted while a different lever (lever 2) is reinforced. If subsequent extinction of lever 2 is conducted, the organism shows resurgence of responding to lever 1 (Bouton, Winterbauer, & Todd, 2012).

Finally, the *renewal* effect is perhaps the most studied, and theoretically more relevant phenomenon among those showing that interference does not eliminate information previously learned. Renewal of the CR appears when a given association is established within one context (context A), the associative interference training is conducted within a different context (context B), and the test is conducted within the original context (context A). This design leads to renewal of the interfered information with the return to the learning context (ABA renewal, e.g., Álvarez et al. 2007; Bouton & Bolles, 1979). Theoretically more important, ABA renewal appears in situations in which the acquisition information is well transferred to a new context, suggesting that it is extinction, and not acquisition, what becomes context dependent (e.g., Bouton, 1993).

Similar results are obtained when the test is conducted in a third context, different from the contexts where acquisition and interference take place (ABC renewal, e.g., Thomas, Larsen, & Ayres, 2003) or even when acquisition and extinction are conducted in the same context, and then test is conducted in a different one (AAB renewal, e.g., Bouton & Ricker, 1994). The common link among the three renewal designs is that in all of them there is a change between the context where extinction takes place, and the context where the organism receives the test, suggesting that the key factor in the renewal effect is that retrieval of either or both, inhibitory (extinction) or second-learned information is more context-specific that retrieval of acquisition-learning (Bouton, 1993).

Interestingly, renewal also appears when context changes are induced by changing internal states such as hunger (Schepers & Bouton, 2017), interoceptive cues as alcohol (Lattal, 2007), or external relationships such as social contexts (Nieto, Mason, & Bernal-Gamboa, 2017). Renewal is a ubiquitous phenomenon. It has been documented in rats' conditioned suppression (e.g., Bouton & Bolles, 1979), operant conditioning (e.g., Bouton, Todd, Vurbic, & Winterbauer, 2011), taste aversion (e.g., Rosas & Bouton, 1997, 1998), appetitive conditioning (Bouton & Peck, 1989), and chain behavior (Thrailkill, Trott, Zer, & Bouton, 2016). It has also been reported when the interference treatment involves counterconditioning (e.g., Holmes, Leung, & Westbrook, 2016; Peck & Bouton, 1990), discrimination reversal (e.g., Bouton & Brooks, 1993) or overexpectation (Rescorla, 2006). Renewal has been reported in mice's spatial learning (e.g., Lattal, Mullen, & Abel, 2003), pigeon's autoshaping (Rescorla, 2008; Starosta et al. 2016), or zebrafish (Kuroda, Mizutani, Cançado, & Podlesnik, 2007). Likewise, renewal has been reported with a variety of tasks and procedures in human beings –i.e., predictive learning (e.g., Paredes-Olay & Rosas, 1999; Üngör & Lachnit, 2006, 2008), instrumental learning (e.g., Nelson, Navarro, & Sanjuan, 2014; Nelson, Sanjuan, Vadillo-Ruiz, & Pérez, 2011; Neumann, 2006), fear conditioning (e.g., Effiting & Kindt, 2007), causal learning (e.g., Rosas, García-Gutiérrez, & Callejas-Aguilera, 2006), eye-blink conditioning (e.g., Grillon, Alvarez, Johnson, & Chavis, 2008), skin conductance conditioning (e.g., Vervliet, Vansteenwegen, Baeyens, Hermans, & Eelen, 2005), or associative learning evaluated by reaction time (e.g., Cobos, González-Martín, Varona-Moya, & López, 2013). Considering this large body of evidence, there seems to be little doubt that contexts in which learning and testing take place play an essential role on information retrieval.

All of these treatments have in common that information apparently erased is retrieved again after different manipulations that do not involve new learning about the original information. Indeed, some authors have claimed that all of these recovery phenomena may be different forms of renewal in which the context change is reached through different manipulations. In spontaneous recovery, renewal will be caused by the simple passage of time changing the temporal context of the organism (Bouton, 1993; Rosas & Bouton, 1998; Rosas, Vila, Lugo, & López, 2001), while in reinstatement, the presentation of the outcome within the learning context will lead to a change on the associative context between the interference treatment and the test (García-Gutiérrez & Rosas, 2003).

Beyond contextual manipulations, conditions in which learning develops also seem to influence subsequent retrieval of information. For instance, if the CS is followed by a novel non-threatening outcome during extinction, rather than by the usual absence of the outcome, spontaneous recovery seems to be reduced in both, humans and rats (e.g., Dunsmoor, et al., 2015). Relapse may be also modulated by the use of retrieval cues during learning and testing. Renewal is enhanced when the retrieval cue presented during testing matches the retrieval cue presented during acquisition (e.g., Bustamante, Uengoer, & Lachnit, 2016; Vansteenwegen, et al., 2006), but it is attenuated when the retrieval cue matches the retrieval cue used during extinction (Brooks & Bouton, 1994); similar results were found in reinstatement (e.g., Brooks & Farla, 2017) and spontaneous recovery (e.g., Brooks & Bouton, 1993; Brooks & Bowker, 2001). Renewal may be also reduced by increasing the number of extinction trials (e.g., Denniston, Chang, & Miller, 2003; Rosas, García-Gutiérrez, & Callejas-Aguilera, 2007; but see Tamai & Nakajima, 2000), by elongating the inter-stimulus interval during extinction (e.g., Le pelley, Wheeler, & Miller, 2009), or by conducting extinction in multiple contexts (e.g., Thomas, Vurbic, & Novak, 2009; but see Bouton, García-Gutierrez, Zilski, & Moody, 2006).

In summary, associative interference does not seem to generally erase the original learning. There is a large body of evidence showing that the interfered learning may be retrieved with a variety of manipulations that do not involve re-learning of the original information. This is not to say that interference cannot lead to erasing of the original information. There are some results in the literature that point out that under some specific circumstances, recovery of first learning may be not noticeable, supporting the idea that interference learning may erase previous conditioning (Myers, Ressler, & Davis, 2006; Quirk et al., 2010). However, this result is the exception to a large body of evidence, showing that interference learning is a new kind of learning (Bouton, 1993, 1994). Classical associative models fail to explain these recovery phenomena as they do not allow for multiple conflicting associations being developed with the same stimulus, neither they consider a role for the context different from that of an additional competing stimulus. Most of these models could explain renewal by assuming that the context gains associative strength, so that the return to the original context involves retrieving the associative strength that was never extinguished. Along this rationale, these models are not able to explain AAB or ABC renewal (e.g. Thomas et al., 2003). In addition, for this explanation to work, changes in the context after acquisition should lead to a decrease in performance that is not usually found. Acquisition learning usually transfers quite well across different contexts (see a review in Bouton, 1993, 1994; but see Starosta et al., 2016; Üngor & Lachnit, 2006). Thus, to fully understand these phenomena it will be necessary to appeal to retrieval theories of associative interference, such as the ones that will be discussed in the next section.

1.2.2 Retrieval Theories of Associative Interference

After showing the shortcomings of traditional models of associative learning to account for associative interference phenomena, in the present section we will review some of the retrieval theories of associative interference more relevant for the research reported in the experimental section of this dissertation. Specifically, we will briefly describe Bouton's Theory of Information Retrieval (Bouton, 1993), and the Attentional Theory of Context Processing developed by Rosas and colleagues (Rosas et al., 2006) as a conceptual development of Bouton's (1993) theory.

1.2.2.1 Bouton's Information Theory Retrieval

The *Theory Information Retrieval* developed by Bouton (1993) is probably one of the most influential models in the recent history of associative learning. This theory claims that memory is formed by nodes that represent events of the world and that relate to each other in an excitatory or inhibitory way. The representation of the events may be stored along different representations. For example, the same CS could be encoded linked to two different USs at different stages of learning (e.g. extinction). It is when the organism needs to solve this conflictive information when the context surrounding the target information becomes relevant. In that line, Bouton (1993), suggested that the key factor on retrieval of the information after interference is whether the testing context matches the context where the interference has taken place. Essentially, it is assumed that the information learned during acquisition transfers well across different contexts. However, the new information learned during the interference treatment becomes context specific, so that its retrieval will depend on whether the test is conducted within the interference context, or within a different one. Bouton (1993) suggested that both, retrieval of inhibitory and second-learned information become context specific. Subsequent research by Nelson (2002, 2009) found that the key factor for context-dependence of the information is not whether the information is excitatory or inhibitory, but whether the information is the first or the second information that the organism learns about the cue. It is second-learned information what becomes context-specific, regardless of whether that information is inhibitory or excitatory (Nelson, 2002; 2009).

On explaining why retrieval second-learned information becomes more context-dependent than retrieval of first-learned information, Bouton (1997) suggests that, during the interference treatment, the change in the meaning of the cues leads the organism to a search for an explanation for that change. This search leads the organism to pay attention to the context where the information is learned, so that retrieval of the ambiguous information presented in that context becomes context-specific. The context disambiguates the current meaning of the CS, playing a role similar to the role played by the linguistic context that allows to disambiguate the meaning of polysemic words (e.g., Bouton, 1994). This approach has been successful to explain interference-phenomena involving context-change such as renewal (Bouton, 2004). Moreover, it could be applied successfully to other kind of interference-phenomenon as spontaneous recovery or reinstatement (Bouton, 1993, 1997; García-Gutiérrez & Rosas, 2003; Rosas & Bouton, 1998; Rosas et al., 2001).

The ideas raised by Bouton (1993) set up the principles that have guided hundreds of studies trying to explain the effect of context changes on retrieval of the information within interference situations, moving the focus of interest from the particular stimuli to the interaction between stimuli and the context. The number of studies supporting the theory of information retrieval is quite large (e.g., Bouton, 2010; Pearce & Bouton, 2001). However, this research has also uncovered some weaknesses of the theory that question its main principles. As pointed out above, assuming that the context is attended only when interference takes place the theory is forced to assume that the three renewal designs (ABA, AAB, and ABC) are conceptually identical, and should lead to equivalent renewal effects. Nonetheless, there is an increasing number of studies showing that AAB and ABC renewal are weaker than ABA renewal (e.g., Nakajima, et al., 2000; Polack, Laborda, & Miller, 2013; Thomas, et al., 2003), suggesting that the acquisition context also plays a role on retrieval of the information. In the same lines, there is a number of studies suggesting that first-learned information may be affected by context-changes under some circumstances (e.g., Starosta et al., 2016; Üngor & Lachnit, 2006), particularly when acquisition is short, (e.g., Hall & Honey, 1989; 1990; León, Abad, & Rosas, 2010a, 2011), and when it takes place during or after an interference treatment involving other cues (Bernal Gamboa, Nieto, & Rosas, 2015; Rosas & Callejas-Aguilera, 2006, 2007).

1.2.2.2 Attentional Theory of Context Processing

In an attempt to cope with these shortcomings, Rosas, Callejas-Aguilera, Ramos-Álvarez and Abad (2006) extended Bouton's views in their *Attentional Theory of Context Processing* (ATCP). On explaining context-switch effects on retrieval of the information, previous theories have focused on which information (first-, second-learned, excitatory or inhibitory) becomes context specific after the interference treatment. ATCP moves the focus from the type of information to the context, assuming that retrieval of any information learned when the organism is paying attention to the context will become context specific, regardless of whether that information is ambiguous or not, first- or second-learned (e.g., Rosas & Callejas-Aguilera, 2006, 2007; Rosas et al., 2006). Once this assumption is accepted, the key issue on the study of context-dependence of the information will be to determine which factors modulate the attention contexts receive.

Rosas et al. (2006) suggested that there were five factors modulating the attention the organism pays to the context: attention to contexts was expected to be boosted when the situation is ambiguous such as in interference designs, when organisms have not yet learned about the role of the different stimuli in the situation at the beginning of training, when the salience of the contexts is increased with respect to the salience of the cues, when contexts are relevant to solve the task, and when instructions focus participants' attention on the context. These factors have been reduced to just two in recent reviews of the support received by the theory during the last decade. Alcalá, Callejas-Aguilera, and Rosas (2017) suggest that attention to the context is mainly modulated by two general factors: *subjective relevance of the context*, and *ambiguity of the information* (see also Ogállar, Ramos-Álvarez, Alcalá, Moreno-Fernández, & Rosas, 2017).

Subjective relevance of context. Different manipulations may be arranged to modulate the subjective relevance of the context for the organism. In a seminal work conducted by Preston, Dickinson, and Mackintosh (1986), they found that training rats in a context-based conditional discrimination enhanced context-dependence of simple conditioning. They trained rats in a situation in which CS1 was paired with the US, while CS2 was presented alone in context A; in context B this contingency was reversed for the Experimental group. The control group received the same training (CS1-US, CS2-noUS) in contexts A and B; thus, context was not necessary to solve the discrimination between stimuli. Additionally, both groups received training with the CS3-US relationship in context A. CS3 performance was impaired when tested in context B, but only in animals that were trained in the situation in which contexts were needed to solve the discrimination. The same pattern of results has been reported in humans trained in instrumental (León, Abad & Rosas, 2010b) and predictive learning (León, Abad & Rosas, 2008; León, Gámez, & Rosas, 2012). In agreement with an attentional explanation for context dependence in these situations, Lucke, Lachnit, Koenig, and Uengoer (2013) found that people spend more time looking at the context when contexts are necessary to solve the task. In this set of experiments, the informative value of the contexts is based on objective conditions, given that attending to the contexts is necessary to solve the discrimination. Subjective value of the context may also be manipulated by the use of instructions is human participants. Callejas-Aguilera, Cubillas, and Rosas (2018) found that context-dependence of the information increases when instructions lead participants pay attention to redundant contexts and decreases when instructions take participants attention away from redundant contexts by focusing it in the target cues (see the schematic selection of results in this line of work in Table 1).

Table 1: Selection of experimental research evaluating the role of subjective relevance of context on context processing.

Authors	Tittle	Subfactor	Subjects	Support
Preston, et al., (1986)	Contextual Conditioned Discrimination	Contextual Relevance	Rats	Yes
León, et al. (2008)	Retrieval of simple cue-outcome relationships is context-specific within informative contexts	Contextual Relevance	Human	Yes
León, et al. (2010b)	Giving contexts informative value makes information context-specific	Contextual Relevance	Human	Yes
León, et al. (2012)	Context switch effects and Context Experience in Rats ' Conditioned Taste Aversion	Contextual Relevance	Human	Yes
Lucke, et al., (2013)	The informational value of contexts affects context-dependent learning	Contextual Relevance	Human	Yes
Lucke, et al., (2014)	The impact of context relevance during extinction learning	Contextual Relevance	Human	Yes
Uengoer et al., (2018)	Attention toward contexts modulates context-specificity of behavior in human predictive learning: Evidence from the n-back task	Contextual Relevance	Human	Yes
Callejas-Aguilera, et al. (2018)	Attentional Instructions Modulate Differential Context-Switch Effects after Short and Long Training in Human Predictive Learning	Instructions	Human	Yes

Ambiguity. Includes all the situations that come from variations in the prediction error. Instability of prediction error may be reached by different manipulations: sudden changes, such as the ones that occur in associative interference, ambiguity in the cue-outcome relationship, as in partial reinforcement, or lack of confidence in the results of the predictor, like the one that takes place at the initial stages of training. The role of these manipulations on context-dependence of information learned under ambiguity conditions is summarized in Table 2. León and his colleagues tested context-switch effects at different levels of training in human instrumental conditioning (León, et al., 2010a) and in human predictive learning (León, et al., 2011). Information was found to be more vulnerable to context-switches at the beginning of training, when participants are not sure about the role played by the different stimuli, than later on it, when they had the opportunity to separate the target stimuli from the context, and the contexts are found redundant. In agreement with this idea, León, Callejas-Aguilera, and Rosas (2012) found that increasing the experience with the contexts reduced context dependence of conditioned taste aversion in rats (see also Hall & Honey, 1989, 1990; Sjöden & Archer, 1989; but see Bonardi, Honey, & Hall, 1990). In a related set of studies, prediction error was kept unstable by the use of partial reinforcement. Retrieval of information about cues trained under continuous reinforcement schedules within a context in which a different cue receives partial reinforcement has been shown to become context-specific (Abad, Ramos-Álvarez, & Rosas, 2009; Bouton & Sunsay, 2001). Similar results have been found when ambiguity is established through pseudodiscrimination training. Callejas-Aguilera and Rosas (2010) found that when two compounds sharing an element are followed by the outcome half of the time, retrieval of a cue that has been consistently followed by the outcome becomes context specific. Finally, contextual control has been also modulated by manipulating the ambiguity of the situation using associative interference procedures such as extinction (Bernal-Gamboa, Rosas, & Nieto, 2018; Rosas & Callejas-Aguilera, 2006, 2007), or latent inhibition (e.g., Bernal-Gamboa et al., 2015). In these experiments, retrieval of unambiguous information was more vulnerable to context-switches in animals and participants that had the experience of associative interference than in those that did not have the experience of associative interference (but see Nelson & Lamoureux, 2015; Nelson, Lombas, & León, 2011). Studies that used independent measures of attention to the contexts and cues support the interpretation that these differential effects of context-switching at different training levels are directly related to the attention contexts received. Aristizabal, Ramos-Álvarez, Callejas-Aguilera, and Rosas (2016) have reported that the time people spend looking to redundant contexts decreases as the level training increases. Along these lines, participants spent more time looking at familiar contexts when unexpected information was presented within them (Aristizabal, Ramos-Álvarez, Callejas-Aguilera, & Rosas, 2017). However, when contexts are relevant to solve the task, attention to them remains higher throughout training (Lucke et al., 2013).

A related set of studies suggests that the effect of associative interference in context processing goes beyond the task in which the interference is experienced, rendering context-specific retrieval of information subsequently learned within a different task. For instance, Rosas and Callejas-Aguilera (2006, Experiment 4) found that extinction of a cue within one predictive learning task led to context-dependence of a different cue subsequently trained within a different predictive learning task. Both tasks shared many features, and this could have facilitated the transfer of the effect of extinction across tasks. However, similar results have been reported with rodents using two distinctive tasks, suggesting that the effect may be reliable and could be found in different procedures and species. Bernal-Gamboa, Rosas, and Callejas-Aguilera (2014) found that the experience of extinction in a runway made context-specific retrieval of a conditioned taste aversion that was acquired in a different place, and vice versa (see Bernal-Gamboa, Callejas-Aguilera, Nieto, & Rosas, 2013, for similar effects involving time-dependence rather than context-dependence).

Table 2: *Selection of experimental research evaluating the role of ambiguity on context-processing.*

Authors	**Tittle**	**Subfactor**	**Subjects**	**Support**
Rosas & Callejas-Aguilera (2006)	Context switch effects on acquisition and extinction in human predictive learning	Ambiguity	Human	Yes
Rosas, et al., (2006)	Effects of context change upon retrieval of first and second-learned information in human predictive learning	Ambiguity	Human	Yes
Nelson & Callejas-Aguilera (2007)	The role of interference produced by conflicting associations in contextual control	Ambiguity	Human	Partially
Rosas & Callejas-Aguilera (2007)	Acquisition of a conditioned taste aversion becomes context dependent when it is learned after extinction	Ambiguity	Rats	Yes
Callejas-Aguilera & Rosas (2010)	Ambiguity and context processing in human predictive learning	Ambiguity	Human	Yes
Nelson, et al., (2011)	Concurrent extinction does not render appetitive conditioning context specific	Ambiguity	Rats	No
Bernal-Gamboa et al.,(2013)	Extinction Makes Conditioning Time-Dependent	Ambiguity	Rats	Yes
Nelson, et al., (2013)	Extinction arouses attention to the context in a behavioral suppression method with humans	Ambiguity	Human	Yes
Bernal-Gamboa, et al.(2014)	Experiencing extinction within a task makes nonextinguished information learned within a different task context-dependent	Ambigity	Rats	Yes
Gawronski et al.,(2014)	Formation, representation, and activation of contextualized attitudes	Ambiguity	Human	No
Bernal-Gamboa, et al.(2015)	Context specificity of taste aversion is boosted by pre-exposure and conditioning with a different taste	Ambiguity	Rats	Yes
Nelson & Lamoureux (2015)	Contextual control of conditioning is not affected by extinction in a behavioral task with humans	Ambigiuty	Human	No
Starosta et al.(2016)	Context specificity of both acquisition and extinction of a Pavlovian conditioned response	Ambiguity	Pigeon	Yes
Vadillo et al.,(2016)	Ambiguity produces attention shifts in category learning	Ambiguity	Human	Partially
Nelson et al., (2018)	The effects of extinction-aroused attention on context conditioning	Ambiguity	Human	Yes
Bernal-Gamboa, et al.(2018)	Extinction Makes Acquisition Context Specific in Conditioned Taste Aversion Regardless of the Context where Acquisition and Testing Take Place	Ambiguity	Rats	Yes
Hall & Honey (1989)	Contextual Effects in Conditioning, Latent Inhibition, and Habituation - Associative and Retrieval Functions of Contextual Cues	Learning experiencing	Rats	Yes
Hall & Honey (1990)	Context-Specific Conditioning in the Conditioned-Emotional- Response Procedure	Learning experiencing	Rats	Yes
Bonardi et al., (1990)	Context specificity of conditioning in flavor-aversion learning: Extinction and blocking tests	Learning experiencing	Rats	No
León, et al., (2010a)	The effect of context change on simple acquisition disappears with increased training	Learning experiencing	Human	Yes
León, et al.,(2011)	Context-outcome associations mediate context-switch effects in a human predictive learning task	Learning experiencing	Human	Yes
León, et al.,(2012)	Context switch effects and Context Experience in Rats ’ Conditioned Taste Aversion	Learning experiencing	Rats	Yes
Aristizabal et al.,(2016)	Attention to irrelevant contexts decreases as training increases: Evidence from eye-fixations in a human predictive learning task	Learning experiencing	Human	Yes
Aristizabal et al.,(2017)	Testing a cue outside the training context increases attention to the contexts and impairs performance in human predictive learning	Learning experiencing	Human	Yes
Murphy, et al., (2001)	Relative validity of contextual and discrete cues	Relative salience	Rats	Yes
Bouton & Sunsay (2001)	Contextual control of appetitive conditioning: Influence of a contextual stimulus generated by a partial reinforcement procedure	Relative salience	Rats	Yes
Abad, et al. (2009)	Partial reinforcement and context switch effects in human predictive learning	Relative salience	Human	Yes
Moreno-Fernández et al. (2011)	Context-Outcome Associations Underlie Context-Switch Effects after Partial Reinforcement in Human Predictive Learning	Relative Salience	Human	Yes

Taken together, these results strongly suggest that associative interference facilitates attention to the context (e.g., Darby & Pearce, 1995), at least as much as other forms of ambiguity (Aristizabal et al., 2017). In line with this idea, Vadillo, Orgaz, Luque, and Nelson (2016), inferring attention from participants' reaction time, found that attention moved from predictive cues to contextual cues when interference is generated. Moreover, extinction has been found to facilitate subsequent discrimination based on contextual cues (Nelson, Lamoureux, & León, 2013), and to enhance the memory of contextual cues in social situations (Garowski, Ye, Rydell, & De Houwer, 2014). However, it should be pointed out that associative interference seems to also increase attention to contexts different from the one in which interference takes place, affecting context processing in quite different tasks (see Bernal-Gamboa et al., 2014). This later result opens the possibility of associative interference affecting attention in a more general way than in the one traditionally assumed. The question that we introduce in the next section is whether the increase of attention that associative interference produce is limited to the context, or it might be a more general effect, such that associative interference increases attention to anything that happens afterwards. Answering this question will be the main goal of this dissertation.

1.3. The Potential Role of Associative Interference in Acquisition of New learning

We finished the previous section by showing that there are some results in the literature suggesting that once the interference takes place, its effects on context-dependence of retrieval of the information can be found in different tasks (Bernal-Gamboa et al., 2014). This result is somewhat surprising and opens the possibility of interference having a more general effect on information processing than the one that we have discussed so far. Thinking in evolutionary terms, it seems unlikely that increases in prediction errors would lead to increases in attention that are specific to the contexts, when the same effect could be reached if interference treatments lead to a general, unspecific increase in attention, from which attention to the contexts will be a side effect. If that were the case, the increase in prediction error would prompt the attentional exploration resources, searching for the key to solve the currently uncertain situation (Beesley et al., 2015).

In line with this idea, Courville, Daw, and Touretzky (2006), in their statistical account of conditioning, suggest that surprise signals, and therefore uncertainty, provoke animals to learn faster. Morevoer, Larrauri and Schmajuk (2008) suggest that animals respond to novelty by increasing attention to all the elements present in the situation –cue, context, and outcome (see also Schmajuk & Larrauri, 2006). Finally, Anselme (2010) postulates that some degree of uncertainty in the environment is necessary to motivate animals' behaviour, in order to explore the possibilities offered by the environment. This motivational point of view is quite similar to the attentional exploration idea (e.g., Le Pelley et al., 2016). In all these cases it is assumed that when animals do not control the relationships inside a given environment, they try to reduce uncertainty by engaging the attentional resources necessary to search for the regularities that eliminate the source of conflict.

Thus, the idea that the effect of the increase in prediction error that the interference produces may lead to a general increase in attention in the organism seems to be an idea worth to explore. A simple developing of this idea is that, once the organism has experienced interference, the general boost in attention should favour new learning in different situations. In an already classical work, Hall and Pearce (1982) found that pairing a CS with a weak shock retarded learning about the same CS when it was later paired with a stronger shock (negative transfer procedure). Remarkably, this retardation effect was attenuated by presenting a few CS extinction trials before starting pairings with the stronger shock. Hall and Pearce (1982) argued that attention to the CS was restored as a consequence of the extinction trials, favouring associability, and thus attenuating the retardation effect (see also Griffiths, Johnson, & Mitchell, 2011 for a replication in humans). Their second experiment tried to evaluate the generality of this effect by exploring the effects of conditioning and extinguishing a different CS. Extinguishing a different CS did not affect the rate of conditioning of the CS initially paired with the weak shock, suggesting that the facilitation effect was specific to the stimulus that received extinction. However, experiments conducted with the rabbits' nictitating membrane conditioning paradigm found that acquisition and extinction of one CS facilitate subsequent learning about a different CS paired with the same US (Kehoe & Holt, 1984; Kehoe, Macrae, & Horne, 1995; Kehoe, Morrow, & Holt, 1984; Macrae & Kehoe, 1999). Similarly, Ricker and Bouton (1986), in rats' appetitive conditioning, found that the rate of learning about a CS after extinction of a different CS was similar to the rate of reacquisition of the first extinguished CS, and faster than a naïve group. Thus, animals that have experienced acquisition-extinction training, seem to show better performance in subsequent learning, at least under some circumstances. Results of these experiments may be explained by either generalization across different stimuli, or by a learning-to-learn effect that is facilitated by the similarity in the stimuli used during interference and in the learning test, though regardless of the explanation, all of them suggest that the experience of extinction may affect subsequent learning.

Experimental arrangements different from extinction that also alter the prediction error seem to have an impact upon subsequent learning as well. For instance, the blocking effect was reduced when the unconditioned stimulus was changed across phases (Blaisdell, Denniston, & Miller, 1997). The orienting response to a light and its subsequent associability seem to be restored when the light becomes an inaccurate predictor or the outcome (Wilson, Boumphrey, & Pearce, 1992). De la Casa, Mena, Ruiz-Salas, Quintero, and Papini (2017) have shown that shifting the value of the reinforcer in a successive negative consummatory contrast arrangement, attenuates subsequently established latent inhibition in a fear conditioning procedure. De la Casa et al., (2017) suggest that devaluation of the reinforcer in the consummatory contrast procedure produces an increase in attention that attenuates the typical effect of neglecting the stimulus as a product of the presentation of this stimulus without an outcome. These results support the idea that unexpected events enhance the attentional exploration pattern of behaviour in animals (e.g., Le Pelley et al., 2016). Similar results are drawn when rats are exposed to high levels of uncertainty. Robinson, Anselme, Fischer, and Berridge (2014) manipulated the level of uncertainty within an autoshaping preparation. In each trial one lever was presented during eight seconds, then retracted, and reinforcement was delivered. Levers served as CSs, but there is no contingency between interaction with levers and successive reinforcement. One group of animals experienced a high level of uncertainty, with the lever being presented in any of three different positions and being partially reinforced with a random number of pellets. In the group with low level of uncertainty only position of the lever was changed. Rats in the uncertain group interacted more with the levers, enhancing explorative behaviour to non-preferred cues more than rats in the control group. Moreover, this initial effect of being exposed to high uncertainty was quite persistent, remaining through several sessions, even when conditions of uncertainty were reduced.

The enhancement of the explorative pattern by the experience of uncertainty has been also reported in humans. Easdale, Le Pelley, and Beesley (2018) trained two groups of participants with different pairs of cues (AX, AY, BX, and BY). During the first stage of training cue A was paired with O1, and cue B was paired with O2. For participants in group certain, A was always followed by O1 and B was always followed by O2, while for participants in group uncertain A and B were followed by O1 and O2, respectively, only 80% of the times. During the second phase, the previously irrelevant cues (X and Y) were always followed by O1 and O2, respectively. Group certain learned faster than group uncertain during this second phase. The authors argue that the sudden experience with uncertainty when conditions changed in group certain, led to an increase in the attention to the new target cues, something that did not occur in the group uncertain, that was exposed to a continuum of uncertainty from the beginning of the study. Backing up this interpretation, participants in group uncertain paid more attention to the new target cues, as measured by the time they spent looking at them. As we discussed above, this pattern of results may imply the activation of attentional exploration, searching for new information trying to reduce the uncertainty, an effect that does not appear with prolonged exposure to uncertainty (Easdale et al., 2018).

Altogether the studies discussed in this section seem to suggest that changes in the prediction error may have an impact upon subsequent learning by an increase in the attentional exploration mechanism (e.g., Le Pelley et al., 2016). The empirical goal of the present dissertation is to evaluate whether associative interference modulates the rate of subsequent learning in general. The increase in the prediction error that associative interference produces may lead to deployment of the animals' attentional exploration mechanism and consequently facilitate acquisition of new learning. Alternatively, we will test whether the increase in attention that seems to follow an interference treatment is specific to the context as ATCP predicts. The next section will display the specific goals that guided the studies conducted in this dissertation.

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2. Goal and hypothesis

2.1 General Goal and Hypothesis

Since the publication of Bouton's (1993) seminal work, different researches throughout the world have evaluated how context processing and the experience of ambiguous information interact. The most recent solution for this puzzle was provided by ATCP when suggesting that attention to the contexts depended on whether the contexts were relevant for solving the task, and whether the situation was ambiguous or not (Rosas, Callejas-Aguilera, Ramos-Álvarez, & Abad, 2006; see also Alcalá, Callejas-Aguilera, & Rosas, 2017; Ogállar, Ramos-Álvarez, Alcalá, Moreno-Fernández, & Rosas, 2017). Recent research suggests that the influence of interference may not be circumscribed to increase in attention to the contexts, but it might have a more general effect, increasing attention to everything that happens afterwards, and thus facilitating subsequent learning (Courville, Daw, & Touretzky, 2006; Le Pelley, Mitchell, Beesley, George, & Wills, 2016).

General Goal: Evaluating the effects of experiencing associative interference on subsequent learning about context and cues in nonhuman animals, trying to disentangle whether the experience of interference produces a general effect in attention, or whether that increase is specific to the attention contexts receive.

General Hypothesis: According to ATCP, the experience of interference should boost attention of the organism to the context (Rosas et al., 2006). Under this approach, experiencing interference should facilitate animals' learning about the relationship between the context and the outcome, but it will not facilitate new learning about alternative cues that were not part of the original training. Alternatively, if the experience of interference produces a general increase in the use of attentional resources, leading the organism to engage the attentional exploration mechanism, then the acquisition about different relationships should be facilitated by the experience of interference, regardless of whether the context is involved in those relationships or not.

2.2. Specific Goals and Hypothesis

Specific Goal 1: Testing the effect of experiencing associative interference upon concurrent conditioning of a non-interfered stimulus, and the context in rats' appetitive conditioning.

Specific Hypothesis 1: According to ATCP (Rosas et al., 2006), training animals with a discrimination reversal procedure should raise attention to the context, but not to the punctate stimuli in the situation, so that animals receiving reversal training are expected to show greater context conditioning than animals that do not have experienced a reversal discrimination, while no differences in learning about a punctate cue should be found. Alternatively, if reversal experience boosts general attention and facilitates new learning, animals receiving the reversal experience should show faster learning about both, contexts and new stimuli.

Specific Goal 2: Testing whether the experience of associative interference enhances both, temporal and context conditioning in appetitive magazine training in rats.

Specific Hypothesis 2: If the increase in attention produced by reversal training is specific to the context, then subsequent learning about context, but not temporal conditioning, will be facilitated in animals that have the experience of discrimination reversal. Alternatively, if reversal training leads to a general increase in attention, the experience of associative interference should facilitate both, context and temporal conditioning, in comparison with rats exposed to consistent training.

Specific Goal 3: Testing the effects of experiencing associative interference upon new learning about space in a rats' water maze.

Specific Hypothesis 3: If experiencing associative interference facilitates subsequent new learning about space in a water maze, animals receiving the interference treatment should learn faster about subsequent new spatial distribution in the maze than the animals that did not receive the interference experience.

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3. Empirical Studies

The dissertation collects three multi-experiment studies with the goal of exploring the effects of experiencing associative interference in new learning. The first study was conducted to explore the effect of experiencing associative interference on concurrent acquisition of context-US and CS-US learning in rats appetitive conditioning. Study 2 was conducted with the goal of exploring the influence of experiencing discrimination reversal on subsequent acquisition of temporal conditioning and context conditioning in rats appetitive conditioning. Finally, Study 3 was conducted with the goal of exploring the influence of experiencing contradictory information in a water maze on subsequent learning about space with a set of spatial cues partially modified.

The three studies are presented as independent studies. Study one has been recently published in journal *Psicológica*. Studies 2 and 3 are under current evaluation in the *Journal of Experimental Psychology: Animal Learning and Cognition*.

Study 1

Alcalá, J. A.**,** González, G., Aristizabal, J. A., Callejas-Aguilera, J. E., & Rosas, J. M. (2018). Discrimination Reversal Facilitates Contextual Conditioning in Rats' Appetitive conditioning. *Psicológica, 39,* 64-87. https://doi.org/10.2478/psicolj-2018-0004

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Discrimination Reversal Facilitates Contextual Conditioning in Rats' Appetitive conditioning

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Two experiments were conducted with the goal of exploring the effect of experiencing associative interference upon concurrent learning about conditioned stimuli and contexts in rats' appetitive conditioning. During the first training phase, two groups of rats received a conditioned stimulus (CS1) followed by food, whereas another conditioned stimulus (CS2) was presented alone. During a second training phase, discrimination was reversed in group R, while it remained the same in group D. A new conditioned stimulus (CS3) was concurrently trained followed by food during this second Phase (Experiment 1). Reversal discrimination did not facilitate concurrent conditioning of the new stimulus, but there was a trend towards facilitation of contextual conditioning, measured by magazine entries in the absence of stimuli, that was confirmed in Experiment 2. These results suggest that the interference treatment may facilitate context conditioning under circumstances and with boundaries that are yet to be established.

Keywords: Reversal Training, Ambiguity, Context, Learning, Appetitive Conditioning, Rats

Associations among different stimuli are not always stable in nature. The environment changes, and what it was certain at a given point may not be true later. Organisms have to deal with these changes by adjusting their behaviour to the new environmental conditions. These natural situations are mimicked within the laboratory by using experimental procedures in which cue-outcome relationships change across different phases of learning. This is the case of extinction, discrimination reversal or counterconditioning, among others. For instance, in a standard discrimination reversal design, two conditioned stimuli (CSs) are followed by different unconditioned stimuli (USs) in the initial stages of training (i.e., CS1-US, CS2-NoUS), and these relationships are reversed at a given point (i.e., CS1-NoUS, CS2-US) leading the organism to adapt its behaviour to the new environmental conditions (e.g., Bouton & Brooks, 1993; Üngör & Lachnit, 2006).

The ability of human and nonhuman animals to adapt their behaviour to changes in learning conditions is captured by every major learning theory. Traditional learning theories assume that the organism adapts to the new situation by erasing previous learning while acquiring the new one (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972). This idea is challenged by phenomena such as spontaneous recovery by the simple passage of time (Bouton & Brooks, 1993; Rescorla, 2007), disinhibition by the presentation of a new stimulus before the target one (Pavlov, 1927), renewal of performance with the context change (Bouton & King, 1979; Thomas, Larsen, & Ayres, 2003), and some forms of reinstatement (García-Gutiérrez & Rosas, 2003) as all have in common that the organism retrieves the original information in the absence of new learning. Taking in account these results, more recent theories assume that when a cue is sequentially followed by contradictory information, the first- and second-learned information are both independently stored in memory, so that which information is retrieved at any given time will depend on the context where the test takes place (e.g., Bouton, 1993). When the information is tested within the context where second-learned information was acquired, the organism will behave according to this second-learned information. However, if the test is conducted in any other context, first learned information will be retrieved and will compete with second-learned information for controlling behaviour (e.g., Bouton, 1993, 1994; Nelson, 2002, 2009; Rosas, Todd, & Bouton, 2013).

To explain susceptibility of second-learned information to context-changes, Bouton (1997) sustains that the change in the learning conditions raises the organism`s attention to the context where such change takes place, so that retrieval of second-learned, interfering information, becomes context dependent. The idea of interference leading to attentional changes is not new in the literature. Pearce and Hall (1980) suggested that when the learning conditions become ambiguous, animals tend to attend more to stimuli with uncertain outcomes. In agreement with this idea, Kaye and Pearce (1984) found that orienting responses in rats increase to both, extinguished stimuli and stimuli that underwent partial reinforcement, with respect to stimuli that were consistent predictors of their outcomes. Similar results have been reported in humans by using eye tracking devices, finding that participants spend more time looking at stimuli with uncertain outcomes than looking at stimuli with consistent outcomes (Beesley, Nguyen, Pearson, & Le Pelley; Hogarth, Dickinson, Austin, Brown, & Duka, 2008).

Bouton's (1997) idea that ambiguity may lead to an increase of attention to the contexts was taken up and extended by Rosas, Callejas-Aguilera, Ramos-Álvarez, and Abad, (2006) (see also Ogállar, Ramos-Álvarez, Alcalá, Moreno-Fernández, & Rosas, 2017; Rosas & Callejas-Aguilera, 2006). Rosas et al. (2006) suggested that the uncertainty of the situation leads the organism to pay attention to the context, so that *all the information* learned within that context becomes context-specific, and not only the ambiguous one (c.f., Bouton, 1997). Once assumed that context dependence of the information critically depends on whether contexts are attended or not, the focus of the research was placed on the factors that modulate attention to the contexts. Rosas et al. (2006) suggested that there were five factors that modulate the attention contexts receive: attention to the contexts was expected to be boosted by the ambiguity of the situation, when subjects have not yet learned about the role of the different stimuli in the situation at the beginning of training, when the salience of the contexts is increased with respect to the salience of the cues, when contexts are relevant to solve the task, and when instructions focus participants' attention to the context. However, recent reviews of the theory suggest that the five original factors may be reduced to two main ones: ambiguity of the situation and subjective relevance of the context (see Alcalá, Callejas-Aguilera, & Rosas, 2017; Ogállar et al., 2017). The apparently slight twist of considering that, once the organism pays attention to the context, retrieval of all the information learned within that context becomes context-specific led to a set of unique predictions that were instantiated in the Attentional theory of Context Processing (Rosas et al., 2006), and that have received a reasonable amount of empirical support from different laboratories (e.g., Bernal-Gamboa, Rosas, & Callejas-Aguilera, 2014; Lucke, Lachnit, Koenig, & Uengoer, 2013; Rosas & Callejas-Aguilera, 2006, 2007; but see Nelson & Lamoureux, 2015; Nelson, Lombas, & Léon, 2011). For instance, Nelson and his colleagues found that extinction boosted both context based bi-conditional discriminations (Nelson, Lamoureux, & León, 2013) and context-conditioning in human participants (Lamoureux, Dunstan, Fabiano, & Nelson, 2017).

A different set of studies explored the idea that attention to the contexts is modulated by the level of training, given that the level of uncertainty about the outcomes of cues and responses changes as training progresses. Irrelevant contexts were expected to be processed early in training, when the organism has not yet learned that contexts are redundant to solve the task. In agreement with this assumption, information was found to be more vulnerable to context-switches early on training, than later on training (León, Abad, & Rosas, 2010, 2011), and these effects were modulated by the experience that subjects had with the contexts involved in the training situation (León et al., 2011; León, Callejas-Aguilera, & Rosas, 2012). Recent reports suggest that the differential susceptibility of information to the effects of context switches at different moments of training may be due to changes on the attention contexts received as training progresses. Aristizabal, Ramos-Álvarez, Callejas-Aguilera, & Rosas, (2016) found that gaze dwell time to redundant contexts decreased as training progressed in human predictive learning, and that the time human participants spent looking at familiar contexts increased when unexpected information was presented within them (Aristizabal, Ramos-Álvarez, Callejas-Aguilera, & Rosas, 2017).

The effect of uncertainty upon context dependence of the information does not seem to be limited to the context where second-learned information is acquired. Bernal-Gamboa, et al. (2014), in an experiment conducted with rodents, found that extinction of the running behavior in a straight runway rendered context-specific retrieval of a conditioned taste aversion that was subsequently learned in a different physical context. And vice versa, extinction of a taste aversion rendered context specific retrieval of a subsequently learned runway behavior (see Bernal-Gamboa, Callejas-Aguilera, Nieto, & Rosas, 2013, for similar effects involving time-dependence rather than context-dependence; see also Rosas & Callejas-Aguilera, 2006, Exps. 3 and 4 for similar results in human predictive learning).

Thus, previous research suggests that uncertainty may increase attention to both, ambiguous CSs (e.g., Kaye & Pearce, 1984), and redundant contexts (Bernal-Gamboa et al. 2014; Rosas & Callejas-Aguilera, 2006, 2007; see also Darby & Pearce, 1995). Taking these two findings together suggests that the interference treatments might lead to a more general increase in attention than the one so far discussed. Larrauri and Schmajuk, (2008; also see Schmajuk and Larrauri, 2006) suggest that the organism's attention to the stimuli increases in the presence of novelty, facilitating learning about them. Changing the meaning of a stimulus generates a novel situation that may be assumed to boost attention, at least initially, until the organism adapts its behavior to the new environmental conditions. If this increase in attention were general, then interference treatments would be expected to facilitate new learning. In agreement with this general idea, Hall and Pearce (1982) found that the retardation of conditioning that is observed when the same CS is first paired with a weak shock and then paired with a strong shock can be attenuated by briefly extinguishing the CS-weak shock relationship by presenting a few trials with the CS alone before pairing it with the strong shock (see Griffiths, Johnson, & Mitchell, 2011, for a replication in humans). This effect was found to be specific of the extinguished CS being the one subsequently conditioned with the strong shock (Hall & Pearce, Experiment 2). However, this is not always the case. Kehoe, Morrow, and Holt (1984) found that extinction of one CS facilitated subsequent conditioning of a CS of different modality. Although this latter result may be also interpreted as a learning-to-learn effect, these results are also consistent with the idea that surprising events may facilitate subsequent learning (for a review see Courville, Daw, & Touretsky, 2006). Based on this idea, recent research in our laboratory found that interference treatments facilitate subsequent new learning about time and space in rats. Alcalá, Callejas-Aguilera, Lamoureux and Rosas (2017), in rats' appetitive conditioning, found that reversing the discrimination between two CSs across different phases of the experiment facilitated subsequent acquisition of temporal conditioning, though no differences in context conditioning based on the reversal experience were found. In a related study, Alcalá, Callejas-Aguilera, Nelson and Rosas (2017) found that placing the escape platform in different positions within a Morris water maze across different phases of the experiment facilitated subsequent learning about a new position of the platform.

Alternatively, attention has been found to correlate directly with the predictive value of the stimuli. This idea was raised by Mackintosh (1975) whose model suggests that attention to good predictors of the outcome increases while attention to poor predictors of the outcome decreases (for review see Le Pelley 2004; Le Pelley, Mitchell, Beesley, George, & Wills, 2016). In agreement with this idea, recent research has found that human participants spent more time looking at good predictors than looking at poor predictors (Le Pelley, Beesley, & Griffiths, 2011; but see Hogarth et al. 2008). Human participants have also found to show faster reaction times to predictive than to non-predictive cues (Le Pelley, Vadillo, & Luque, 2013). However, it is also true that in situations with high level of uncertainty participants spent more time looking at cues which results are uncertain (Beesley, et al., 2015). These apparently conflicting results may be understood is we consider that predictiveness is related with the capacity of attracting attention, while holding attention may be more influenced by the uncertainty of the cues (Koenig, Uengoer, & Lachnit, 2017).

The main goal of the study presented here was to explore whether an interference experience facilitates new learning in rats' appetitive conditioning. Specifically, we were interested in knowing whether an experience of discrimination reversal facilitates associative learning about both, the acquisition of new CS-US relationships, and the relationship between the context and the US. Experiment 1 focused on testing the effects of associative interference upon concurrent acquisition of learning about a new CS-US relationship, while Experiment 2 focused on exploring the effects of associative interference on context conditioning.

EXPERIMENT 1

The design of Experiment 1 is presented in the top section of Table 1. After magazine training, rats were initially trained on a discrimination between two CSs. CS1 was followed by the US and CS2 was not followed by the US. Subsequently, contingencies of CS1 and CS2 with the US were reversed for the rats assigned to group Reversal (CS1-NoUS and CS2-US), while they were kept constant for rats in group Discrimination. A new CS3 (a light) was paired with the US during this phase. Concurrent training was selected under the assumption that any effect of associative interference upon new learning should be more robust the greater the experienced uncertainty is. Uncertainty is assumed to be greater at the beginning of the reversal training, decreasing as training progresses and the animals learned the new discrimination. Thus, the key issue in this experiment was whether reversal training facilitates, first, concurrent acquisition of CS3, and second, context conditioning. Facilitation of learning about the new stimulus should appear as faster conditioning to CS3 in group Reversal (R) than in group Discrimination (D). Facilitation of learning about the context should appear as greater conditioned responding in the absence of the CS in group R than in group D. Note that both dependent measures are related, so that an increase in context-conditioning might attenuate, and even retard the observed speed of learning about CS3 in this experimental design. Thus, this test should be considered a conservative one when referred to the influence of the experience with associative interference on acquisition of a new CS-US relationship. This test should be considered conservative with respect to context conditioning as well, given that the outcome was not presented in the absence of the CSs during reversal training, and context conditioning is expected to be at least partially overshadowed by CS conditioning.

METHOD

Subjects. Sixteen experimentally naive female Wistar rats provided by Harlan Laboratories (Amsterdam) were used in this experiment. They were about 90 days old with a mean free-feeding weight of 197 g. (range 180-224 g.) at the beginning of the experiment. Rats were individually housed in standard Plexiglas cages inside a room maintained on a 12-12 hr light-dark cycle with the light part of the cycle at 8 a.m. Environmental conditions were kept constant throughout the experiment (21° C of room temperature and 60% humidity). After 7 days of acclimation period with free access to food (rodent chow) and water, food access was progressively reduced until rats' weight reached 85% of their free-feeding weight. Their weight was kept at this level until the end of experiment.

Apparatus. Eight identical operant chambers (Panlab Harvard Apparatus, Cornellá, Spain) were housed in the same room and in its own sound attenuating enclosure. Ventilation fans provided background noise of 60 dB, and the operant chambers were lit with one 2-W Led fluorescent tube mounted to the ceiling of the sound attenuating enclosure. Operant chambers measured 25 cm x 25 cm x 25 cm (l x w x h). Front and rear walls were made of aluminum whereas the side walls were made of methacrylate (clear for the door access in the left side, and black in the right side). Ceiling was made of aluminum except for a circular opening of 11.5 cm of diameter covered by clear methacrylate that allowed the houselight to illuminate the operant chamber. The floor was made of stainless steel grids (0.2 cm of diameter, spaced 1.7 cm) that were mounted parallel to the front wall. Magazine behavior was detected through a magnetic mechanism that was activated every time the animal entered its head within the food cup, displacing a small cover of clear methacrylate (3.5 cm high × 3.5 cm wide). A movement of approximately 3 cm of this small cover was automatically recorded as a magazine entry. A computer located within the same room controlled the apparatus.

Presentation of stimuli and recording of behavior was controlled through Packwin V 2.03 software (Panlab Harvard Apparatus, Cornellá, Spain).

Three 10 sec. stimuli were used as CSs: A 2850-Hz 85 dB tone presented through a module placed 22 cm above the floor level in the top right corner of the rear wall; an 80 dB white noise presented through a module placed 22 cm above the floor level in the top left of the rear wall; and a light (40 lux) presented through a module placed 22 cm above the floor lever on the right side of the magazine cup. Tone and white noise were counterbalanced as CS1 and CS2 across rats, whereas the light was used always as CS3. A pellet dispenser supplying 45-mg standard rat food pellets (Bio-Serv, Frenchtown, NJ, USA) to a recessed food cup (3.5 x 3.5 cm) was centered in the front wall 3.5 cm above the level of the floor. Delivery of two pellets was used as US throughout the experiment.

Procedure.

Magazine Training. All rats received 20 min sessions in which the US (two food pellets) was delivered under a 60 seconds variable time schedule. Rats received two sessions a day, an hour apart, for the first two days.

Phase I. All rats received eight 56-min sessions. Twenty-four trials were conducted within each session spared under a variable intertrial interval (ITI) of 120 s (+-30 s). In 12 of the trials the CS1 was followed by the US, while in the other 12 the CS2 was not followed by the US. Distribution of CS1 and CS2 trials during each session was pseudorandom, with the condition that the same trial type was not followed by itself more than twice. At the end of this phase rats were ascribed to groups R and D and matched on performance during acquisition training.

Phase II. All rats received 5 additional 56-min sessions with the following changes respect to Phase I. Firstly, for rats in group R the role of CS1 and CS2 as predictors of the US was reversed, so that CS2 was now followed by the US and CS1 was not. Secondly, a new CS (Light) was presented followed by the US in both groups. The ITI and the number of trials per session (24) were kept identical to the ones used in the acquisition phase. Consequently, only 8 trials of each type were presented in each session.

Table 1. Experimental Design

Experiment	Group	Phase 1	Phase 2
1	Reversal (R)	CS1-US, CS2-NoUS	CS1-NoUS, CS2-US, CS3-US
	Discrimination (D)	CS1-US, CS2-NoUS	CS1-US, CS2-NoUS, CS3-US
2	Reversal (R)	CS1-US, CS2-NoUS	CS1-NoUS, CS2-US
	Discrimination (D)	CS1-US, CS2-NoUS	CS1-US, CS2-NoUS

Note: In experiment 1: Tone and white noise were counterbalanced as CS1 and CS2; Light was used as CS3. In Experiment 2: Tone and Light were counterbalanced as CS1 and CS2. US =Unconditioned Stimulus, food. See text for details.

Dependent Variable and Statistical Analyses. Magazine entries during the 10 seconds CSs (CS) and during the 10 seconds immediately previous to each CS presentation (Pre-CS) were recorded. Dependent variable for CS conditioning was elevation ratio, computed as a ratio between the magazine entries in the presence and in the absence of the CS (CS/CS+Pre-CS entries) (e.g., Halsegrove, Esber, Pearce, & Jones, 2011). Dependent variable for context conditioning was the number of magazine entries in the absence of the CS (Pre-CS). Data were analyzed with a mixed-factorial analysis of variance (ANOVA). The rejection criterion was set at $p < .05$, and effect sizes were reported using partial eta-squared (η_p^2).

RESULTS

Figure 1 presents elevation ratios for CS1 and CS2 throughout the 8 sessions of Phase I, and the 5 sessions of Phase II in groups R and D. In Phase I, elevation ratios increased during CS1, and slightly decreased during CS2. In Phase 2 group D kept the same pattern of responses than in the previous phase, with high responding to CS1 and low responding to CS2, while the pattern of responding was reversed in group R. Statistical analyses confirmed these impressions. A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 8 Session ANOVA conducted with the elevation ratios from Phase I found significant main effects of CS, $F(1, 14) = 123.56$, MSe = .03, $p < .001$, $\eta_p^2 = .90$, and Session, $F(7, 98) = 41.69$, MSe = .01, $p < .001$, $\eta_p^2 = .75$. Most important, the CS x Session interaction was significant, $F(7, 98) = 7.86$, MSe = .01, $p < .001$, $\eta_p^2 = .36$. Subsequent analyses conducted to explore this interaction found that the simple effect of Session was significant in both, CS1, $F(7, 105) = 32.60$, MSe = .01, $p < .001$, $\eta_p^2 = .68$, and CS2, $F(7, 105) = 15.68$, MSe = .01, $p < .001$, $\eta_p^2 = .51$. The simple effect of CS was significant in Session 1, $F(1, 15) = 6.04$, MSe = .01, $p = .027$, $\eta_p^2 = .29$, but not in Session 2 η_p^2 (1, 15) = 3.83, MSe = .01, $p = .069$, $\eta_p^2 = .20$. The simple effect of CS was significant from Session 3 on, smallest $F(1, 15) = 27.19$, MSe = .02, $p < .001$, $\eta_p^2 = .64$ for session 7. No other main effect or interaction were significant, *largest F* (1, 14) = 1.13, MSe = .03, $p = .30$, $\eta_p^2 = .07$ for Group x CS interaction, showing that animals developed the discrimination between CS1 and CS2 after Session 3 regardless of the group.

Mean magazine entries during the Pre-CS period in Phase I were 2.07 (SD = 2.79) and 1.50 (SD = 2.12) for CS1, and 1.77 (SD = 1.49) and 1.40 (SD = 1.39) for CS2 in Groups R and D, respectively. A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 8 Session found a significant main effect of Session, $F(7, 98) = 14.78$, MSe = 3.11, $p < .001$, $\eta_p^2 = .51$, and a significant CS x Session interaction, $F(7, 98) = 7.57$, MSe = 1.15, $p < .001$, $\eta_p^2 = .35$. No other effect main effect of interaction were significant, largest $F(1, 14) = 3.68$, MSe = 1.49, $p = .076$, $\eta_p^2 = .20$ for the main effect of CS. Given that no differences on Pre-CS were expected, subsequent analyses were conducted to determine the importance of the CS x Session interaction. These analyses found that the simple effect of CS was significant only in Sessions 1, $F(1, 14) = 6.84$, Mse = .02, $p = .02$, $\eta_p^2 = .33$, and 2, $F(1,14) = 9.96$, Mse = 6.35, $p = .007$, $\eta_p^2 = .42$, with higher Pre-CS magazine entries in CS2 than in CS1 in Session 1, and vice versa in Session 2. Pre-CS differences seem to be localized at the very early sessions of training and did not show a regular pattern. Thus, they should not condition the interpretation of differences on the CS entries that appeared later.

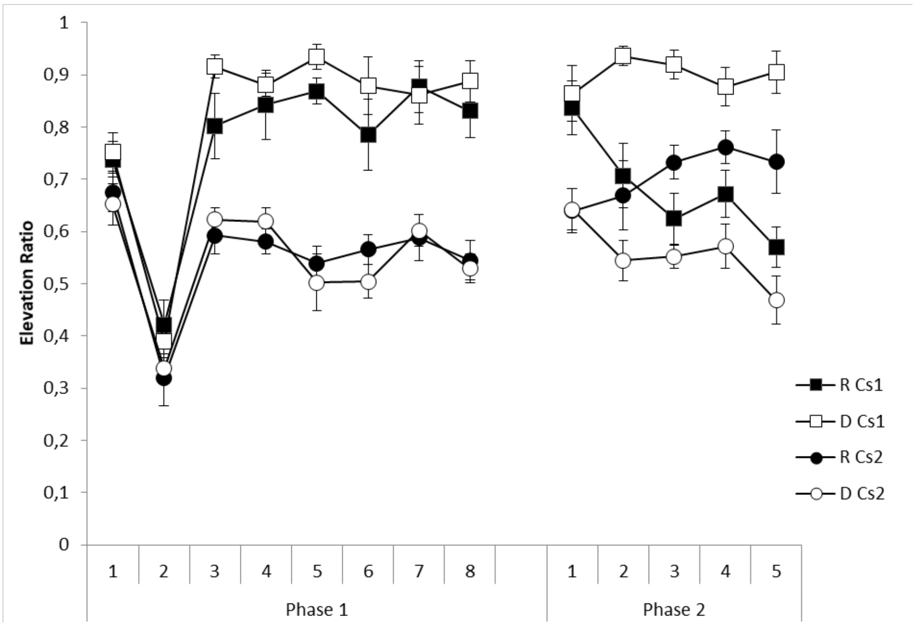

Figure 1. **Mean elevation ratios to CS1 and CS2 throughout the 8 sessions of Phase I, and the 5 sessions of Phase II in groups Reversal and Discrimination. Error bars denote standard error of the mean.**

A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 5 Session ANOVA conducted with elevation ratios from the 5 sessions of training of Phase II found a significant main effect of CS, *F*(1,14) = 31.37 , MSe = .03, $p < .001$, $\eta_p^2 = .69$, and significant Group x CS, *F*(1,14) = 42.11 , MSe =.03, $p < .001$, $\eta_p^2 = 75$, and Group x CS x Session interactions, *F*(4,56) = 11.42, MSe = .01, $p < .001$, $\eta_p^2 = .45$. Subsequent analyses conducted to explore the 3-way interaction found a significant CS x Session interaction in both, Group R, *F*(4, 28) = 8.80, MSe = .01, $p < .001$, $\eta_p^2 = .56$, and Group D F(4, 28) = 4.18, MSe = .01, $p = .009$, $\eta_p^2 = .37$. The CS x Session interaction in Group R was due to a switch in the direction of the simple effect of CS across days, with elevation ratios to CS1 being significantly greater than elevation ratios to CS2 in Session 1, *F*(1, 7) = 31.96, MSe = .01, $p < .001$ $\eta_p^2 = .82$, and vice versa in Session 5, *F*(1, 7) = 10.99, MSe = .01, $p = .013$, $\eta p^2 = .61$. However, in group D, the CS x Session interaction was due to the simple effect of Session being significant in CS2, *F*(4, 28) = 4.20, MSe = .01, $p = .009$, $\eta_p^2 = .38$, but not in CS1, *F(4,28)* = 1.74, MSe = .004, $p = .168$, $\eta_p^2 = .19$. This pattern of results shows that reversal training was effective, with group R adapting its behavior to the new circumstances while group D kept its behavior constant, though discrimination in this group seems to improve further over sessions.

Mean magazine entries during the Pre-CS period in Phase II were 2.72, (SD = 2.20) and 1.01, (SD = 1.16) for CS1, and 2.4 (SD = 2.12) and 1.36 (SD = 1.05) for CS2 in Groups R and D, respectively. A 2 Group (R vs. D) x 2 CS (CS1 vs CS2) x 5 Session conducted with Pre-Cs data only found a Group x CS significant interaction *F*(1,14) = 8.00 , MSe = .03, *p* = .013, η_p^2 = .36. No other main effect or interaction were significant, largest *F*(1, 14) = 3.68, MSe = 23.33, *p* = .076, η_p^2 = .21, for the main effect of Group. Subsequent analyses of the Group x CS interaction found that the simple effect of Group was significant in CS1 *F*(1, 14) = 4.74, MSe = 12.39, *p* = .047, η_p^2 = .25, but it was not significant in CS2 *F*(1, 14) = 2.63, MSe = 11.32, *p* = .127, η_p^2 = .16. The meaning of these differences should be taken with caution. The pseudorandom arrangement of trials made impossible for the animal to anticipate which stimuli will be presented next. In that sense, these differences between Pre-CSs seem to reflect a higher responding to the context in group R than in group D, though this difference was more remarkable in Pre-CS1 than in Pre-CS2.

Figure 2 presents the elevation ratios obtained with CS3 during the five sessions of Phase II training in groups R and D. Acquisition of new learning seems to be slightly slower in group R than in group D. In agreement with these appreciations, a 2 Group (R vs. D) x 5 Session ANOVA found significant main effects of Group, *F*(1, 14) = 9.94, MSe = .06, *p* = .007, η_p^2 = .41, Session, *F*(4, 56) = 24.63, MSe = .01, *p* < .001, η_p^2 = .64, and a significant Group x Session interaction, *F*(4, 56) = 2.73, MSe = .01, *p* = .037, η_p^2 = .16. Subsequent analyses conducted to explore the Group x Session interaction found that the simple effect of Group was significant in Session 2, *F*(1, 14) = 16.53, MSe = .02, *p* = .001, η_p^2 = .54, Session 3, *F*(1, 14) = 12.80, MSe = .02, *p* = .003, η_p^2 = .48 , and Session 5 *F*(1, 14) = 5.24, MSe = .01, *p* = .038, η_p^2 = .28. That is, contrarily to our expectations, elevation ratios to CS3 stimulus developed more slowly after the interference treatment with the CS1 and CS2.

Mean Pre-CS scores to CS3 were 2.57 (SD = 2.42) and 1.13 (SD = 1.27) for groups R and D, respectively. As it was found with the Pre-CS of CS1 and CS2, responding during the Pre-CS was higher in Group R than in Group D. However, a 2 (Group) x 5 (Session) ANOVA conducted with Pre-Cs entries did not find significant effects, largest *F* for the main effect of Group, *F*(1,14) = 3.11, MSe = 13.51, *p* = .10, η_p^2 = .18.

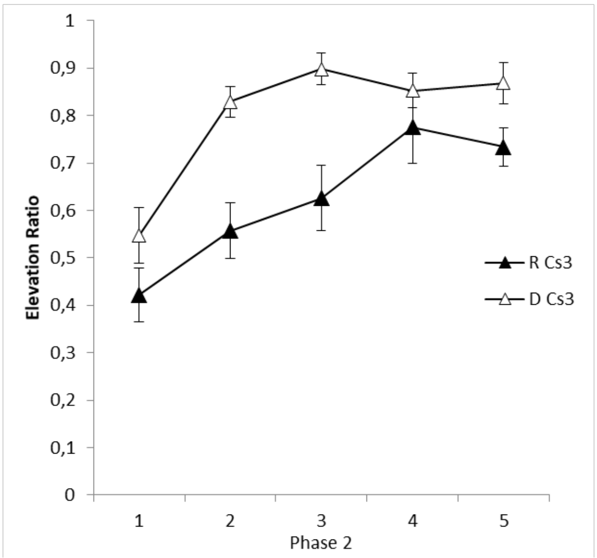

Figure 2. Mean elevation ratios to CS3 throughout the 5 sessions of Phase II training in groups Reversal and Discrimination. Error bars denote standard error of the mean.

The experience of associative interference in group R seemed to slow acquisition of the relationship between the new CS3 and the outcome, with respect to the group that did not have the experience of associative interference (group D). In general, Pre-CS magazine entries during Phase II seem to be slightly higher in group R than in group D. Though this effect did not reach significance, it could be counteracting any beneficial effect of reversal training on learning about the new CS3, as we stated above. These results are conceptually the opposite of the results recently found in our laboratory that show that the same experience with reversal training facilitates temporal conditioning without affecting context conditioning in magazine training (Alcalá, Callejas-Aguilera, Lamoureux et al., 2017). They are also in disagreement with the results reported by Alcalá, Callejas-Aguilera, Nelson et al. (2017) that found that interference facilitates subsequent new learning in the spatial domain.

The most obvious difference among the studies reporting a beneficial effect of associative interference on new learning is that those studies explored the effects of interference on time and spatial discriminations while this study explores this effect in simple conditioning. However, there is a more plausible, simpler explanation that may account for these differences on performance. In the present experiment, the effects of interference upon new learning were evaluated concurrently to the interference treatment under the assumption that any change on attention produced by the interference treatment will be greater the closer it is to the interference experience. This design was chosen with the goal of facilitating detection of the influence of reversal on context conditioning, given that it had not been reported before. Additionally, this combination would have made the effect on learning about the new CS especially strong, given that an increase in context conditioning should make more difficult to detect changes in CS conditioning, as seems to be the case. Although data are not reported, it should be noted that no differences in CS performance between groups were found when pre-CS differences were discarded, suggesting that the experience with associative interference did not facilitate simple conditioning and, if anything, it made it slower. This result suggests that there may be some boundaries on the effects of associative interference upon new learning. We will get back to this issue in the general discussion.

In summary, the results of Experiment 1 suggest that the experience of associative interference does not improve concurrent conditioning of a new CS, though there was a trend that suggests that it might facilitate context conditioning. Facilitation of context conditioning is not clear though, as numerical differences in magazine entries between groups R and D did not reach clear statistical significance, probably due to the potential weakness of the expected effect, given that contextual conditioning was expected to be partially blocked by CSs conditioning. Experiment 2 was conducted with the goal of exploring further the potential effect of associative interference upon context-conditioning by simplifying the testing situation and increasing the statistical power of the test by an increase of the sample.

EXPERIMENT 2

Experiment 2 was conducted with the goal of exploring further the possibility of associative interference facilitating concurrent context conditioning. As stated above, Experiment 1 found a trend towards higher responding to the context alone during reversal training than in the absence of reversal training. The goal of Experiment 2 was to increase the potential for detecting concurrent improvement of context conditioning by the experience of associative interference by simplifying the design, and increasing the sample. The design of Experiment 2 is presented in the bottom section of Table 1. The design was identical to the one used in Experiment 1 with the exception that no additional CS was conditioned during Phase 2. During Phase I, rats were trained in a discrimination between CS1 and CS2. During Phase II this discrimination was reversed in group R while it was kept the same in group D. The goal of this experiment was to test whether reversing the discrimination was concurrently accompanied by an increase in responding to the context in the absence of the CSs, an index of context conditioning. Context conditioning was measured concurrently to the reversal of the discrimination given that the study conducted by Alcalá, Callejas-Aguilera, Lamoureux et al. (2017) found no effect of discrimination reversal on context conditioning tested after discrimination ended in a situation similar to this one. The sample was increased up to 64 rats (32 per group) to maximize the possibility of detecting the effect.

METHOD

Subjects. Sixty-four experimentally naive female Wistar rats provided by Harlan Laboratories (Amsterdam) were used in this experiment. They were about 90 days old at the beginning of the experiment. The experiment was conducted in two replications, with 32 rats in each replication.

Apparatus. The same apparatus described in first experiment were used. Tone and Light were counterbalanced as CS1 and CS2.

Procedure. Procedure was identical to the procedure used in Experiment 1 with two exceptions: 10 56-min sessions were conducted during Phase I, rather than the 8 Sessions conducted in Experiment 1; and, this time, only CS1 and CS2 were presented during Phase II.

Dependent Variable and Statistical Analyses. As context conditioning was evaluated through Pre-CS behavior, this experiment only used raw magazine entries as a dependent variable. At any rate, the use of elevation ratios did not affect statistical conclusions about developing of the discrimination between CSs throughout training.

RESULTS AND DISCUSSION

Figure 3 presents magazine entries for CS1 and CS2 and Pre-CS periods throughout the 10 sessions of Phase I, and the 5 sessions of Phase II in groups R and D. For the sake of simplicity data are presented collapsed across replications, and Pre-CS entries are presented collapsed across CSs. In Phase I, elevation ratios increased during CS1, while slightly decreasing during CS2. In Phase 2 group D kept the same pattern of responses than in the previous phase, with high responding to CS1 and low responding to CS2, while the pattern of responding was reversed in group R. Most important for the goals of the Experiment, Pre-CS magazine entries seem to be greater in Group R than in Group D, but only during Phase II, when Group R received the reversal training. Statistical analyses confirmed these impressions.

A 2 Group (R vs. D) x 2 CS (CS1 vs CS2) x 10 Session x 2 Replication conducted with the magazine entries to CS1 and CS2 during Phase I found significant main effects of CS, $F(1, 60) = 172.98$, MSe = 19.30, $p < .001$, $\eta_p^2 = .74$, and Session $F(9, 540) = 244.16$, MSe = 6.95, $p < .001$, $\eta_p^2 = .37$. The CS x Session interaction was also significant, $F(9, 540) = 58.94$, MSe = 6.6, $p < .001$, $\eta_p^2 = .49$. Further analyses conducted to explore this interaction found that the simple effect of Session was significant in both, CS1, $F(9, 567) = 65.62$, MSe = 9.46, $p < .001$, $\eta_p^2 = .51$, and CS2, $F(9, 567) = 3.14$, MSe = 3.92, $p = .001$, $\eta_p^2 = .05$. The simple effect of CS, that was not significant in Session 1, *F(*1, 63) = 1.04, MSe = 11.34, *p* = .311, η_p^2 = .02, it was significant from Session 2 on, smallest *F(*1, 63) = 30.94, MSe = 12.12, *p* < .001, η_p^2 = .33 for Session 2, suggesting that discrimination between CS1 and CS2 developed uneventfully.

No other effects or interactions were significant, largest *F(*9, 540) = 1.47, MSe = 6.60, *p* = .155, η_p^2 = .02 for the Group x CS x Session interaction. Same analyses conducted in the Pre-CS data found a significant effect of Session *F(*9, 540) = 5.58, MSe = 3.09, *p* < .001, η_p^2 = .08, and a Group x Session interaction, *F(*9, 540) =3.01 , MSe = 3.09, *p* =.002, η_p^2 = .05. No other main effect or interaction were significant, largest *F(*1, 60) = 2.34, MSe = 30.57, *p* =.131, η_p^2 = .04, for the Group x Experiment interaction. Subsequent analyses conducted to explore the Group x Session interaction found that the simple effect of group was significant in the first-three sessions of Phase I, *F(*1, 62) = 5.33 , MSe = 4.80, *p* =.024 , η_p^2 = .08; *F(*1, 62) =15.07, MSe = 3.28, *p* < .001 , η_p^2 = .20; and *F(*1, 62) = 6.14, MSe = 6.18, *p* =.016 , η_p^2 = .09 for Sessions 1, 2 and 3, respectively, but it was not significant after Session 4, largest *F(*1, 62) = 3.40 , MSe = 7.96, *p* =.07 , η_p^2 = .05. As both groups received the same treatment throughout Phase I, these differences may be explained as random variations on behavior in the initial stages of the discrimination training, when the situation is still ambiguous for the subjects.

A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 5 Session x 2 Replication ANOVA conducted with the magazine entries to CS1 and CS2 during Phase II found significant main effects of CS, *F(*1, 60) = 28.82 , MSe = 95.84, *p* < .001, η_p^2 = .32, and Session, *F(*4, 240) = 5. 45, MSe = 5.64, *p* < .001, η_p^2 = .08. The interactions Group x CS, *F(*1, 60) = 94.51 , MSe = 95.84, *p* < .001, η_p^2 = .61, and Group x Session, *F(*4, 240) = 3.40 , MSe = 7.74, *p* < = .001, η_p^2 = .05, were also significant. Most importantly, the Group x CS x Session interaction was also significant, *F(*4, 240) = 42.50, MSe = 7.74, *p* < .001, η_p^2 = .41. Further analyses to explore the 3-way interaction found that the CS x Session interaction was significant in Group R, *F(*4, 120) = 52.05, MSe = 11.94, *p* < .001, η_p^2 = .63, but it was not significant in group D, *F < 1*. Similar to what it was obtained in Experiment 1, this pattern of results shows that reversal training was effective, with group R adapting its behavior to the new circumstances while group D kept its behavior constant. More relevant for the goals of this experiment, a similar analysis conducted with Pre-CS scores during Phase II found a significant main effect of group, *F(*1, 60) = 15.92 , MSe = 24.92, *p* < .001, η_p^2 = .21. No other main effect or interaction was significant, largest *F*(4, 240) = 1.41, MSe= 3.54, *p* = .22, η_p^2 = 02.

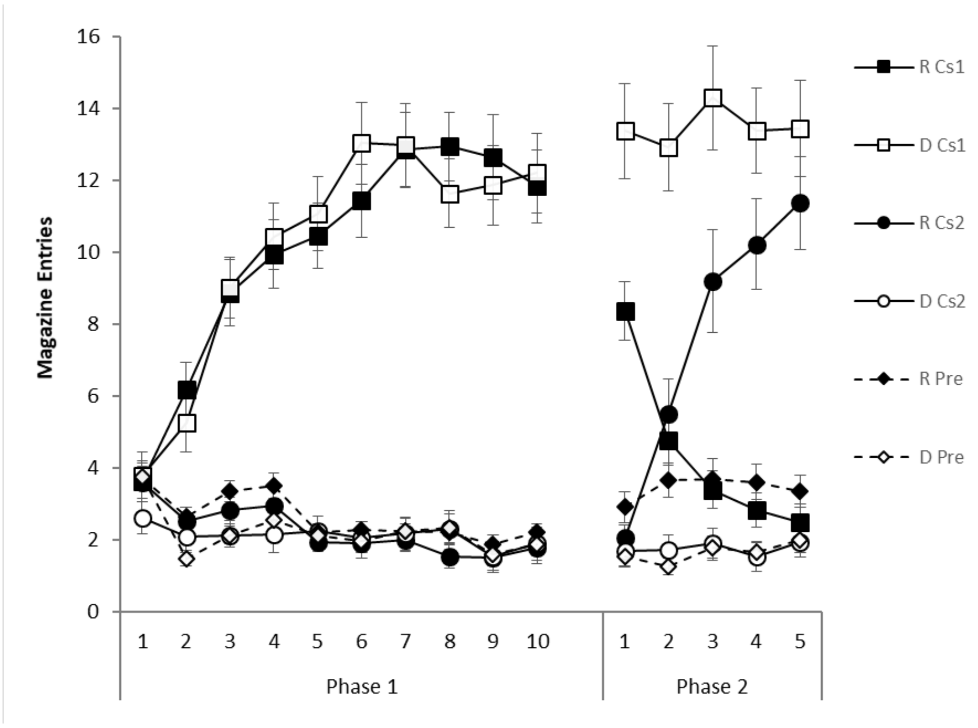

Figure 3. Mean magazine entries to CS1 and CS2 in groups Reversal and Discrimination across the 10 sessions of Phase I and the 5 sessions of Phase 2 in Experiment 2. Pre-CS entries are presented collapsed across CSs. Error bars denote standard error of the mean.

Finally, a 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 2 Phase x 5 Session complementary ANOVA was conducted with Pre-CS data from the last 5 sessions of Phase I and the 5 sessions of Phase II, with the goal of having a direct comparison of Groups R and D performance before and during reversal training. Only the interaction Group x Phase was significant, *F(*1, 60) = 7.08, MSe = 25.69, *p* = .010, η_p^2 = .11. Subsequent analyses conducted to explore this interaction found that it was due to the combination of the lack of differences between groups at the end of acquisition, *F<1*, with the greater responding during the Pre-CS in group R than in group D during Phase II, *F(*1, 60) = 15.92 , MSe = 24.92, *p* < .001, η_p^2 = .21. This pattern or results can be interpreted as a higher context conditioning during Phase II in group R than in group D.

In summary, the simplification of the design and the increase of the statistical power of Experiment 2 allowed for finding a clearer evidence of the differential effect of associative interference upon context conditioning. Reversing the discrimination increased responding during magazine training in the absence of the CS in Group R with respect to Group D. This difference only appeared in Phase 2, when the interference treatment was given to group R, but not to group D, and the difference did not disappear with the training parameters used here.

GENERAL DISCUSSION

Summarizing the results obtained in this study, discrimination reversal seemed to impair concurrent conditioning of a CS that was not involved in the discrimination (Experiment 1), while pointing towards a facilitation of context conditioning (Experiments 1 and 2). In general, combined results of Experiments 1 and 2 favour the idea that discrimination reversal facilitates context processing (Bouton, 1997; Rosas et al., 2006).

This result is similar to those obtained in the experiments conducted to test the effect of context change upon retrieval of the information after discrimination reversal in both, human and non-human animals (e.g., Bouton and Brooks, 1993, Mcdonald, King, & Hong, 2001, Üngör & Lachnit, 2008). According to Bouton (1997) the ambiguity produced by an interference treatment such as discrimination reversal lead the organisms to raise attention to the context in search for information that allows them to disambiguate the situation. The trend to greater responding in the absence of the CS found in Experiment 1, confirmed in Experiment 2, in the group that had the discrimination reversal experience, is in full agreement with Bouton's (1997) idea that the interference experience raises attention to contexts.

Retardation of CS conditioning after reversal training comes in to conflict with previous results in the literature showing that associative interference improves subsequent learning. For instance, Alcalá, Callejas-Aguilera, Lamoureux et al. (2017) found that temporal discrimination under a fixed time reinforcement schedule developed faster in rats that had previously experienced discrimination reversal than in rats that did not have the discrimination reversal experience. However, rats trained under a variable time reinforcing schedule did not show any evidence for better context conditioning after discrimination reversal (see also Bouton & Peck, 1993). It should be noted that these authors tested the influence of discrimination reversal upon new learning after the reversal phase had ended (see also Alcalá, Callejas-Aguilera, Nelson et al., 2017). In this experiment, the effect of reversing the training conditions was tested during the reversal training phase under the assumption that any effect of associative interference on new learning should be greater the closer the new learning experience is to the associative interference experience. This manipulation was aimed to favour detection an improvement in context conditioning in this experiment. According to Beesley et al. (2015), interference or uncertainty could enhance an exploration pattern of behaviour. They found that participants' attention to stimuli with uncertain outcomes was kept high, while it decreased when the stimuli outcome was certain. The idea underlying this exploration pattern is that participants would engage in a search for other sources of information in the absence of reliable predictors. In a reversal training situation such as the one used in these experiments, the outcomes of the CSs became uncertain at the start of Phase II, and that should have facilitated the engagement of the rats on exploratory behaviours that would increase context and new CSs attention in group reversal, favouring learning about context and cues when the evaluation is conducted concurrently to the associative interference treatment (see also Bouton, 1997; Ogállar et al., 2017; Rosas et al., 2006).

However, this change in the evaluation conditions with respect to previous experiments did not come without cost. As noted above, context conditioning and CS conditioning are not independent in magazine training, given that both are inferred from changes in the same dependent variable (magazine entries). As a consequence, context conditioning and CS conditioning will compete with each other so that the greater is the first, the lower the second will be. As we have seen, the design used here seems to facilitate context-conditioning during reversal training, similarly to what it has been reported by Lamoureux et al. (2017) with human participants. This facilitation reduces the opportunity for finding differences in CS conditioning. As it was found in Experiment 1, context conditioning led to retardation of the CS conditioning when measured though elevation ratios, a dependent variable that relates responding during the CS (that is presented in the context) with responding to the context alone, factoring out this way any contribution of context conditioning to the CS conditioning.

Taking in account all the results reported so far in the literature, the most reasonable conclusion will be that there are some boundaries to the facilitation effects upon new learning that discrimination reversal has. In general, it can be concluded that changes in the conditions of learning may facilitate subsequent learning about contexts and cues. However, this facilitation effect is not a strong one, and detecting one or the other may depend on parametric variables that should be studied both, to better understand the phenomenon, and to establish the boundaries for the effects of uncertainty upon new learning. Further research will need to solve the conflicting results that have been reported in the literature. For instance, it needs to be understood why the effect of associative interference upon subsequent learning is specific to the stimulus that receives the interference treatment in some situations (Pearce & Hall, 1980; Hall & Pearce, 1982), while in some others, such as in this study, is not (Alcalá, Callejas-Aguilera, Lamoureux, et al. 2017; Alcalá, Callejas-Aguilera, Nelson et al. 2017; Lamoureux, et al. 2017).

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Study 2

Alcalá, J. A., Callejas-Aguilera, J. E., Lamoureux, J. A., & Rosas, J. M. (2018). Discrimination Reversal Facilitates Subsequent Acquisition of Temporal Discriminations in Rats' Appetitive Conditioning. *Manuscript submitted to Journal of Experimental Psychology: Animal Learning and Cognition.*

Discrimination Reversal Facilitates Subsequent Acquisition of Temporal Discriminations in Rats' Appetitive Conditioning

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Abstract

Two experiments with rats assessed the effects of introducing predictive ambiguity by reversing a Pavlovianly-trained discrimination on subsequent context conditioning and temporal learning. In Experiment 1, discrimination reversal enhanced subsequent learning of a fixed temporal interval associated with unsignaled food presentation, but not simple context conditioning when the food was presented on a variable schedule. In Experiment 2 reversal enhanced learning of the fixed temporal interval, regardless of whether it was relatively short or long (i.e., 30s or 60s). Results are discussed in terms of current associative theories of human and nonhuman conditioning and attention.

Keywords: Reversal Training, Ambiguity, Temporal Conditioning, Learning, Appetitive Conditioning, Rats

The ability to learn about regularities of the environment is essential for the survival of individuals across species. However, the environment is actually unstable; the predictive value of stimuli frequently changes over time. These changes in the environment lead to situations that are ambiguous for the organism. How the animal deals with these uncertain situations has received a great amount of attention since Pavlov's (1927) initial studies on extinction. Ambiguity may be formally defined in terms of prediction error (e.g., Bush & Mosteller, 1951; Rescorla & Wagner, 1972). When the difference between what the organism expects and what the environment provides is different from zero, the situation is uncertain and the organism needs to correct the error by adapting its expectancies to the environment. This error correction is the common mechanism of learning at the root of traditional models of associative learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). In other words, learning may be understood as a mechanism that allows the organism to disambiguate its environment, eliminating uncertainty.

Let's take for instance the extinction paradigm. When a conditioned stimulus (CS) that had been previously paired with an unconditioned stimulus (US) is later presented in the absence of the US, prediction error increases; the situation becomes ambiguous and, at least until prediction error disappears, the organism must deal with uncertainty about the actual meaning of the CS. In traditional models of associative learning the extinction procedure leads to a simple adjustment of the organism's predictions (i.e., associative strengths), which are readjusted over trials until prediction error reaches zero again (e.g., Rescorla & Wagner, 1972). Attentional models such as Mackintosh's (1975) or Pearce and Hall's (1980) additionally assume that prediction errors affect the attention the CS receives, which subsequently modulates stimuli' associative strength (e.g., Kaye & Pearce, 1984; Swan & Pearce, 1988; Halsegrove, Pearce, Esber, & Jones, 2010). All of these models may explain the loss of conditioned responding (CR) that follows the extinction procedure. However, none of those models can explain why extinction, like some other forms of interference (i.e., reversal discrimination; e.g., Bouton & Brooks, 1993), does not eliminate original learning about the CS. Survival of the original CS-US learning is demonstrated by several procedures that lead to recovery of the original, extinguished, CR: the presentation of a new stimulus (i.e., external inhibition; e.g., Pavlov, 1927), the passage of time (i.e., spontaneous recovery; e.g., Bouton & Peck 1992; Brooks & Bowker, 2001; Rosas & Bouton, 1996), the presentation of the US by itself (i.e., reinstatement; e.g., Bouton, 1984; Delamater, 1997) or conducting the test outside the extinction context (i.e., renewal; e.g., Bouton & King, 1983; Thomas, Larsen, & Ayres, 2003) all lead to recovery of the original, extinguished, CR.

One potential reason for the failure of traditional models of associative learning to explain these phenomena is that they exclusively focus on the effects of ambiguity on the processing of the stimulus that becomes ambiguous. Bouton (1993) takes a different approach, suggesting that the ambiguity produced by the sudden change in the meaning of the CS has a more general effect on the behavior of the organism. According to Bouton (1997), the ambiguity produced by switching the outcome of the CS leads the organism to pay attention to the context in which training is taking place, so that the ambiguous information is now coded with the context, and retrieval of the new information thus becomes context-dependent. This is a substantial change in the traditional approach to learning, as it is assumed that prediction errors influence not only the perception of the CS, but also perception of all the stimuli that are present in the situation in which the error arises. This approach has been successful in explaining most of the effects of context change on extinction (e.g., Bouton, 2004) and other forms of interference (e.g., Peck & Bouton, 1990; Rescorla, 2006; 2007). Moreover, by assuming that contexts may be temporal (e.g., Rosas & Bouton, 1997, 1998) or even associative (e.g., García-Gutiérrez & Rosas, 2003), Bouton’s (1993, 1994, 1997) approach explains most of the results obtained in studies of spontaneous recovery and reinstatement.

Based on the ideas of Bouton (1997), Rosas, Callejas-Aguilera, Ramos-Álvarez, and Abad (2006) went one step further and proposed the Attentional Theory of Context Processing (ATCP), suggesting that when predictive ambiguity appears, all the information present in the training situation, and not only the ambiguous information, comes under contextual control. In other words, it is assumed that prediction error leads the organism to pay attention to the context, so that everything that is learned within that context becomes context-specific, regardless of whether what is being learned about that particular stimulus is ambiguous or not (see also Bernal-Gamboa, Rosas, & Nieto, 2018; Rosas & Callejas-Aguilera, 2006, 2007). In several studies, attention to the context has been manipulated by modulating the relevance of the context to solve the task. When the context is made relevant to solve the task, all the information learned within that context seems to become context specific (León, Abad, & Rosas, 2010a; Lucke, Lachnit, Koenig, & Uengoer, 2013). Similarly, when the task leads participant to pay attention or to ignore specific features of the contexts, they end controlling or not controlling behavior within a different task unrelated to the one in which the contextual elements have been raised or diminished (Uengoer, Lucke, & Lachnit, 2018). More relevant for the present experiments, contextual control has been modulated by manipulating the ambiguity of the situation, either by specific training (e.g., Bernal-Gamboa, Nieto, & Rosas, 2015; Callejas-Aguilera, & Rosas, 2010; Garowski, Ye, Rider, & De Houwer, 2014; Nelson, Lamoureux, & León, 2013; but see Nelson &

Lamoureux, 2015; Nelson, Lombas, & León, 2011), or by exploring the effects of switching the context after different levels of training (e.g., León, Abad, & Rosas, 2010b). Testing this last manipulation, recent studies have found that information is context-specific early in training, when the situation may be naturally more ambiguous, but not later, after the organism may have learned about the regularities of the situation, resolving any predictive ambiguity (León et al., 2010b, León, Callejas-Aguilera, & Rosas, 2012). These variations in contextual control seem to correlate with direct measures of attention to redundant contexts, which seem to diminish over the course of discriminative training (Aristizabal, Callejas-Aguilera, Ramos-Álvarez, & Rosas, 2016, 2017).

An interesting set of experiments within this literature investigated the effects of ambiguity across different learning tasks. In their original studies, Rosas and Callejas-Aguilera (2006) found that extinction of a cue within one predictive learning task led to context-dependence of a different cue subsequently trained within an entirely different predictive task. The tasks used by Rosas and Callejas-Aguilera (2006) shared many features, as both were computer tasks in which human participants had to predict the outcomes (gastric illness or growing of plants) of different cues (food or garden products) within different contexts (restaurants or farms). These similarities may have facilitated the transfer of the effect of extinction across tasks. However, Bernal-Gamboa, Rosas, and Callejas-Aguilera (2014) recently found, using rodents, that the experience of extinction in a runway made subsequent taste aversion in a different place context-specific, and vice versa, suggesting that extinction prompts attention to distinctly different contexts, regardless of whether or not the contexts were involved in extinction (see Bernal-Gamboa, Callejas-Aguilera, Nieto, & Rosas, 2013, for similar effects involving time-dependence rather than context-dependence).

Once shown that the influence of ambiguity on attention may be transferred to ostensibly unambiguous tasks, an important subsequent question is whether the increase on attention is specific to the context or not. Thinking in evolutionary terms, it seems more plausible that increases in prediction error would lead to a more general increase in attention than to specific increases in attention to contextual cues alone. In fact, a general increase in attention would include increased attention to the context as well as to other potentially important cues. In line with this idea, Larrauri and Schmajuk (2008) and Schmajuk and Larrauri (2006) suggest that animals respond to novelty by increasing attention to the environment. This increase in attention is assumed to lead to learning (i.e., decrease in prediction error), and learning leads to a subsequent reduction in novelty, and in attention as well, closing the circle (see also Schmajuk, Lam, & Gray, 1996).

There are several results in the literature that seem to support the direction suggested by Schmajuk and his colleagues that predictive changes result in greater overall attention, and thus faster learning. An interesting review conducted by Courville, Daw and Touretstky (2006) highlights studies in which surprise affects the speed of learning, giving some grounds to the Schmajuk et al. (1996) approach. For instance, the effect of blocking is reduced when the US is changed across phases (Blaisdell, Denniston, & Miller, 1997), and the orienting response to a CS seems to be restored when the learning situation changes (Wilson, Boumphrey, & Pearce, 1992). The presentation of unreinforced trials may also influence subsequent learning. Hall and Pearce (1982) found that the retardation effect of pairing a CS with a weak US on subsequent conditioning of the same CS with a stronger shock was attenuated by the presentation of the stimulus alone before the final conditioning phase (see also Griffiths, Johnson, & Mitchell, 2011). Similarly, Kehoe and their colleagues, using the nictitating membrane conditioning paradigm, have found that conducting acquisition and extinction with one CS facilitates subsequent acquisition of the relationship between a second, different CS and the same US (Kehoe, Morrow, & Holt, 1984; Kehoe, Macrae, & Horne, 1995; Macrae & Kehoe, 1999). Finally, in appetitive conditioning, Ricker and Bouton (1986) found that previous acquisition and extinction of one CS could enhance the subsequent conditioning of a second CS compared to a naïve control group, producing rates of learning similar to a group of rats that received reacquisition training with the same CS after extinction. Taking these results together with those described above indicating that extinction may both increase attention to the context, and enhance context processing, it seems reasonable to suggests that the ambiguity that extinction produces may enhance the rate of subsequent learning.

In agreement with this idea, a recent study from our laboratory has found that rats learned about the location of a hidden platform in a water-maze faster after having experienced reversal training than in the absence of it, suggesting that the experience of reversal may facilitate learning of new information (Alcalá, Callejas-Aguilera, Nelson, & Rosas, 2018). However, this facilitation of learning by the interference experience is not necessarily ubiquitous. In a recent study, Alcalá, González, Aristizabal, Callejas-Aguilera, and Rosas (2018) tested whether conditioning of a new stimulus was facilitated by the experience of concurrent reversal training in rats’ appetitive conditioning. Initial training of a CS1+/CS2- discrimination was reversed during a second stage for half of the rats. Within this second phase all rats received a new CS followed by food, intermixed with the other two CSs. Contrary to expectations, rats exposed to the reversal training showed a retardation in learning about the new CS compared to rats that did not receive the reversal experience. On the other hand, reversal training led to greater context conditioning, as indexed by responding during the Pre-CS intervals, suggesting that the facilitation effects of interference in appetitive conditioning were restrained to context processing, and did not to concurrent learning about a new, discrete conditioned stimulus under the conditions used by Alcalá, González et al., 2018). In that study, the authors used a novel CS to test the effects of interference on new learning. It might be assumed that attention to a new CS is already at a high value, however, and may benefit less from an attention-boosting mechanism than would a highly familiar context, which likely controlled very little attention after such prolonged exposure. Context conditioning enhanced by attention could also interfere with cue conditioning, making it difficult to determine the extent to which interference had an effect on the conditioning of the new cue.

The goal of the experiments presented here was to further test this prediction in appetitive conditioning by evaluating the effects of reversing a discrimination between the outcomes of two different stimuli on the subsequent acquisition of context and temporal conditioning. The use of a discrimination reversal procedure should maximize predictive ambiguity produced in the second phase of training and the context and temporal conditioning tasks may provide for more sensitive tests than those used by Alcalá, González et al. (2018; see also Hall & Pearce, 1982), especially when they are conducted after, rather than concurrent with discrimination reversal training. Rats were trained in an appetitive conditioning situation in which CS1 was followed by the US while CS2 was not. Discrimination was then reversed (or not, depending on the group) so that CS1 was not followed by the US while CS2 was now followed by it. During the final phase, rats were trained either in a temporal conditioning situation in which the food was presented either at regular times or at random times. According to the hypothesis that prediction errors may produce a more general boost in attention to the entire learning situation, learning about both time and context was expected to be faster in groups that received reversal training than in those that did not.

Experiment 1

The goal of Experiment 1 was to test whether the ambiguity produced by reversing a discrimination modulates the speed of subsequent context and temporal conditioning that occur within the same context in which the initial discrimination and reversal training were conducted. The use of a magazine approach task and the same context throughout the experiment was intended with the goal of avoiding potential effects of novelty caused by the change in tasks and apparatus, which could hinder the hypothetical attention increase that reversal training is expected to produce (see Larrauri & Schmajuk, 2008).

The design of Experiment 1 is presented in the top section of Table 1. Four groups of rats received a simple discrimination between two conditioned stimuli, CS1-US and CS2-noUS, within an appetitive conditioning situation in which the CSs were a tone and a light, the US was the presentation of food pellets, and magazine entries were recorded as the CR. During the second phase, the outcomes of CS1 and CS2 were switched in R- groups (Reversal; CS1-noUS, CS2-US), while they remained the same in A- groups (Acquisition; CS1-US, CS2-noUS). During the test, rats in FT (Fixed Time) groups received food on a fixed time 60 s schedule, while rats in VT (Variable Time) groups received the same amount of food on a variable time 60 s schedule.

Table 1: Experimental design

Experiment and Group	Phase I	Phase II	Test
Experiment 1			
R-FT	CS1-US, CS2-noUS	CS1-noUS, CS2-US	FT60
R-VT	CS1-US, CS2-noUS	CS1-noUS, CS2-US	VT60
A-FT	CS1-US, CS2-noUS	CS1-US, CS2-noUS	FT60
A-VT	CS1-US, CS2-noUS	CS1-US, CS2-noUS	VT60
Experiment 2			
R-FT60	CS1-US, CS2-noUS	CS1-noUS, CS2-US	FT60
R-FT30	CS1-US, CS2-noUS	CS1-noUS, CS2-US	FT30
A-FT60	CS1-US, CS2-noUS	CS1-US, CS2-noUS	FT60
A-FT30	CS1-US, CS2-noUS	CS1-US, CS2-noUS	FT30

Note: The first letter of the group's label reflects the treatment received by the groups in Phase 2 (R = Reversal Training; A = Acquisition Training). The last two letters in the group names and test phase of the first experiment indicate the schedule in the Test phase (FT= Fixed Time; VT= Variable Time). Numbers in the final Test stage of both experiments, and in the group names of the second experiment, reflect the schedule on which food was delivered: 60 seconds and 30 seconds, respectively. Tone and light were counterbalanced as CS1 and CS2. "US" = reinforced with food; "noUS"= not reinforcement with food.

In summary, only R groups had the experience of ambiguity. If ambiguity produces a general increase in attention that facilitates subsequent learning then R groups should learn faster than A groups. In general, R groups should show faster context conditioning than A groups, though we expect the topography of responding to differ between VT and FT groups. Specifically, in FT groups, we expect to see the development of temporal conditioning, as evidenced by temporally-graded responding. We predict better learning of this temporal interval in group R-FT than in A-FT. Similarly, we expect better non-temporally-graded context conditioning in the R-VT group than the A-VT group. Alternatively, if attentional increases caused by ambiguity are specific to attention to the context alone (Bouton, 1997; Rosas et al., 2006), differences would be observed only in the overall responding to the context, rather than in the temporal distribution of performance (as expected in FT groups).

Method

Subjects

The present experiments were approved by the bioethical committee of the Universidad de Jaén, reference JA-U1 2013.

Thirty-two experimentally-naive female Wistar rats provided by Harlan Laboratories (Amsterdam) were used in this experiment. They were about 90 days old with a mean free-feeding weight of 197 g (range 180-224 g) at the beginning of the experiment. Rats were individually housed in standard Plexiglas cages inside a room maintained on a 12-12 hr light-dark cycle with the light part of the cycle at 8 a.m. Environmental conditions were constant (21° C, 60% humidity).

After a seven-day acclimation period with free access to food (rodent chow) and water, food access was progressively reduced until rats' weights reached 85% of their free-feeding weight. Their weight was kept at this level until the end of experiment.

Apparatus

The experiment was conducted at the Laboratory of Animal Behavior and Cognition of the Centre of Animal Production and Experimentation of the University of Jaén. Eight operant chambers housed in the same room served as the apparatus, each in its own sound attenuating enclosure. Ventilation fans provided background noise of 60 dB, and the operant chambers were lit with one 2-W LED fluorescent tube mounted to the ceiling of the sound attenuating enclosure.

All operant chambers had the same design (Panlab S.L., Barcelona), measuring 25 cm x 25 cm x 25 cm (l x w x h). Front and rear walls were made of aluminum whereas the side walls were made of methacrylate (clear for the door access in the left side, and black for the right side). The ceiling was made of aluminum except for a circular opening 11.5 cm in diameter covered by clear methacrylate that allowed the houselight to illuminate the operant chamber. The floor was made of stainless steel grids (0.2 cm in diameter, spaced 1.7 cm apart) that were mounted parallel to the front wall, and a cup containing Vicks VapoRub (Proctor & Gamble, Cincinnati, OH, USA) was placed outside the operant chamber. Magazine behavior was detected through a magnetic mechanism that was activated every time the animal inserted its head into the food cup, displacing a small cover of clear methacrylate (3.5 cm high × 3.5 cm wide). A movement of this small cover, approximately 3 cm, was automatically recorded as a magazine entry. A computer located within the same room controlled the apparatus, including the presentation of stimuli and the recording of behavior, using Packwin V 2.03 software (Panlab, S.L. Barcelona, Spain).

The auditory CS was a 10s presentation of a 2850-Hz, 85 dB tone presented through a speaker placed 22 cm above the floor level in the top right corner of the rear wall (Panlab, SL. Model LE100X41). The light CS was a 10s presentation of a high intensity light (240 lux) though a module placed 15 cm above the floor in the right of the magazine (Panlab, SL. Model LE100X677). Tone and light were counterbalanced as CS1 and CS2 across rats. A pellet dispenser (Panlab S.L., Model LE100X52) supplying 45-mg standard rat food pellets (Bio-Serv, Frenchtown, NJ, USA) to a recessed food cup (3.5 x 3.5 cm) was centered in the front wall 3.5 cm above the level of the floor.

Procedure

Magazine Training. All rats received 20 min sessions in which food (two pellets per presentation) was delivered on a 60s VT schedule. Rats received two sessions per day, one hour apart, for the first two days.

Acquisition. All rats received ten 56-min daily sessions. Twenty-four trials were conducted within each session with a variable intertrial interval of 120s (+/-30s). In 12 of the trials CS1 was followed by food, while in the other 12 CS2 was not followed by food. Distribution of CS1 and CS2 trials during each session was pseudorandom, with the condition that the same trial was not repeated more than twice.

Reversal Training. All rats received 5 additional 56-min sessions identical to the ones conducted during acquisition with the exception that for half of the rats the role of CS1 and CS2 as predictors of food was switched, so that CS2 was followed by food and CS1 was not (R Groups). A Groups received training identical to the acquisition phase.

Test. Two 80 min sessions were conducted. Half of the rats (groups R-FT and A-FT) were exposed to a fixed time 60s food delivery schedule. The other half (groups R-VT and A-VT) received the same number of reinforcements per session (80) but according to a variable time 60s (±45s) schedule. Food presentations within the VT groups was arranged so that the number of reinforcements received by this groups equated the reinforcements received by FT groups every 10 min. This arrangement allows for the blocking of data as small as six 10-trial blocks per session, though in the present study data were analyzed in larger, 40-trial blocks.

Dependent Variable

Magazine entries were recorded as the dependent variable across all phases of the experiment. During acquisition and reversal phases magazine entries were recorded during the 10-s CSs (CS), and during the 10-s immediately prior to the presentation of each CS (Pre). During the test, each of the 80 presentations of food per session in the FT groups was considered a trial. Trials were grouped in 40-trial blocks. Only the first three blocks of testing (i.e., all of Test Session 1 and the first half of Test Session 2) are reported, as all groups achieved asymptotic levels of responding by Block 3.

A temporal conditioning index was computed as a ratio between the 10 seconds preceding food presentation (f), and a 10-s interval starting 5 seconds after food delivery –the comparison period (c)– in the form of f/f+c. The first 5 seconds of the inter-food interval were discarded from all the analyses conducted with test data to avoid the confound of pellet consumption activity on the feeder immediately after food consumption from the previous trial (see Boakes, Paterson, Kendig, & Harris, 2015). Temporal conditioning should be shown as higher entries in the interval preceding food delivery than in the comparison interval (i.e., temporal discrimination indices greater than 0.5). Since magazine entries were not expected to be temporally-distributed in the VT groups, the total number of magazine entries during f intervals was used as a measure of context conditioning during testing of VT groups. Two rats were excluded from the experiment (one in group R-FT and another one in group R-VT) because they exhibited no magazine approach behavior during the first stage of training.

Results and Discussion

Acquisition and Reversal Training

Figure 1 presents the mean magazine entries during the Pre and CS-periods of CS1 and CS2 throughout the 10 sessions of acquisition (left side) and in the 5 sessions of reversal (right side) in R and A groups. For the sake of simplicity, data from groups FT and VT were collapsed within each R and A condition. Similarly, Pre-data were collapsed for CS1 and CS2. However, the analyses were conducted with all factors and levels. All rats seemed to learn the discrimination between CS1 and CS2 during the acquisition stage, gradually responding significantly more to CS1 than CS2. During reversal training, magazine entries increased in the presence of CS2, while decreasing in the presence of CS1 in the R condition, while remaining at levels similar to the acquisition phase in the A condition. Statistical analyses confirmed these impressions.

A 2 (Training, Acquisition vs Reversal) x 2 (Test Schedule, FT vs VT) x 2 (CS, CS1 vs CS2) x 10 (Session) ANOVA conducted on CS magazine entry data from the Acquisition stage found a significant main effect of CS *F(*1, 26) = 79.70, MSe = 100.82, *p* < .001, η^2p = .75, 95% CI [.58, .82] and Session, *F*(9, 234) = 14.21, MSe = 7.41, *p* < .001, η^2p = .35, 95% CI [.35, .50]. The Cue x Session interaction was also significant, *F*(9, 234) = 21.47, MSe = 7.98 *p* < .001, η^2p = .45, 95% CI [.25, .40]. No other main effect or interaction was significant, largest *F(*1, 26) = 1.35, *p* = .26, for the Test Schedule x CS interaction. The same analysis conducted on pre-CS magazine entries did not reveal significant main effects or interactions, largest, *F*(1, 26) = 2.26, *p* = .15 for the Training x Test Schedule interaction. Thus, rats learned the discrimination between CS1 and CS2 by the end of Acquisition, with higher responding to CS1 than to CS2.

A 2 (Training) x 2 (Test Schedule) x 2 (CS) x 5 (Session) ANOVA conducted on CS magazine entry data from the Reversal stage revealed significant main effects of CS, *F*(1, 26) = 8.92, MSe = 96.22, *p* =.006, η^2p = .26, 95% CI [.05, .44], and Session, *F*(4, 104) = 2.98, MSe = 3.73, *p* = .02, η^2p = .10, 95% CI [.01, .17]. Training x CS, *F*(1, 26) = 40.64, MSe = 96.22, *p* < .001, η^2p = .50, 95% CI [.25, .64], and CS x Session, *F*(4, 104) = 15.03, MSe = 9.85, *p* < .001, η^2p = .37, 95% CI [.23, .45], interactions were also significant. Most relevant for the goals of the experiment, the Training x CS x Session interaction was significant, *F*(4, 104) = 15.20, MSe = 9.85, *p* < .001, η^2p = .37, 95% CI [.23, .45]. No other main effects or interactions were significant, largest *F*(1, 26) = 1.66, *p* = .21, for the Training x Test Schedule interaction. Subsequent analyses conducted to explore the Training x CS x Session interaction found that the CS x Session interaction was significant for the R training condition, *F* (4, 52) = 17.61, MSe = 15.83, *p* < .001, η^2p = .58, 95% CI [.39, .66], but it was not significant in the A condition, *F* < 1. Subsequent analyses showed that the CS x Session interaction in the Reversal condition came from a switch in differential responding to CS1 and CS2 across Reversal sessions. Responding to CS1 was greater than responding to CS2 in Session 1, *F* (1, 12) = 45.85, MSe = 15.63, *p* < .001, η^2p = .79, 95% CI [.51, .86], but this pattern was reversed in Sessions 3, 4, and 5, smallest *F* (1, 12) = 7.78, MSe = 45.22, *p* = .016, η^2p = .39, 95% CI [.05, .60] in Session 3. The same analyses conducted on pre-CS magazine entries did not reveal any significant main effect or interaction, largest *F* (4, 104) = 2.22, *p* =.083 for Training x Session interaction.

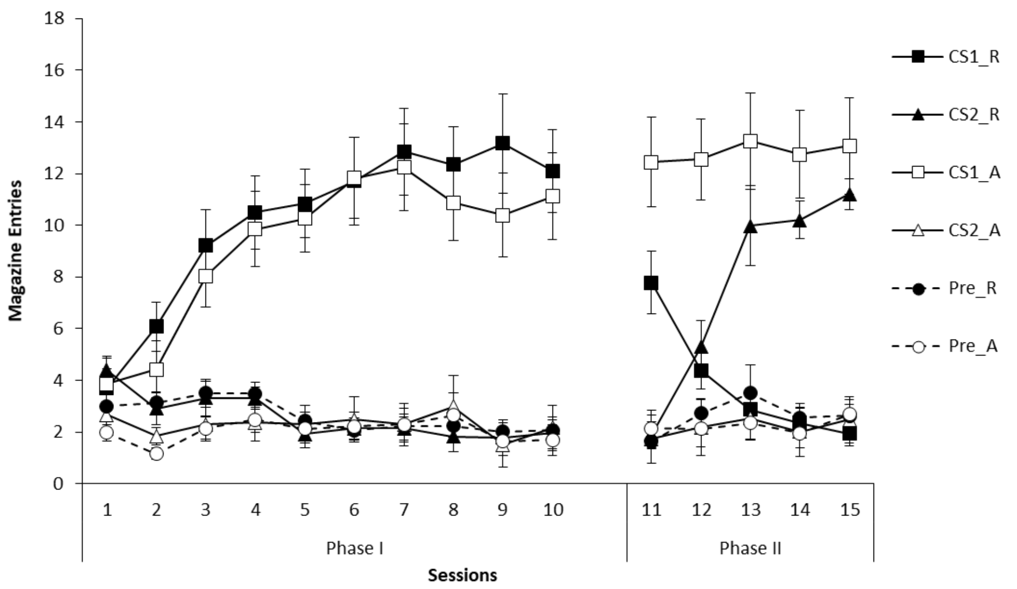

Figure 1. *Mean Magazine Entries for both CSs in each session of Acquisition and Reversal Training. Mean Pre-CS magazine entries are shown for each training condition, collapsed across CSs and test schedule. For simplicity, mean CS response data are shown collapsed across Reversal and Acquisition Training Condition, regardless of test training schedule. Error bars denote standard error of the mean.*

Test

Context Conditioning Test. Mean magazine entries and standard deviations (in brackets) in each of the three 40-trial blocks of testing in groups trained under the VT condition was 1160 (648), 1010 (504), 1014 (639) for group R-VT, and for group 976 (910), 869 (956), 814 (873) A-VT, respectively. A 2 (Training) x 3 (Block) ANOVA found no main effects or interaction, largest, F (2, 26) =1.80, p = .184 for the main effect of Block. Thus, there was no evidence of either greater overall responding or faster contextual conditioning in the Reversal condition than in the Acquisition condition in the groups that were tested with variable food presentations in which differences in context conditioning should appear uncontaminated by temporal distribution of responding.

This lack of an effect was observed regardless of the size of the trial-blocks used in the analyses (analyses not shown) suggesting that either context conditioning is not enhanced by reversal training (c.f., Alcalá, González, et al., 2018; Bouton, 1997; Rosas et al., 2006), or that this particular task and procedure are not sensitive enough to detect presumably subtle differences in contextual conditioning. Note that context-switch effects reported by Alcalá, González et al. (2018) were found when tested during the reversal training phase itself, and the effects were only reliable when 32 rats were trained in each condition (reversal and control). Given that interference treatments such as extinction have been shown to increase context processing in other published reports, so that retrieval of the information learned within learning contexts becomes context specific (Rosas & Callejas-Aguilera, 2007; Bernal-Gamboa et al., 2015; Bernal-Gamboa et al., 2018), or increases context processing within different tasks in which the animals are subsequently trained (Bernal-Gamboa et al., 2014), the failure to observe differences in context conditioning between the R and A groups with VT training may point towards a lack of sensitivity of this task to detect differences in context conditioning favored by the reversal training similar to the lack of general effects of extinction on learning reported by Hall and Pearce (1982).

Temporal Discrimination Test. Figure 2 presents the mean temporal discrimination index during the first 3 40-Trial blocks of Testing in groups R-FT, R-VT, A-FT, and A-VT. As expected, temporal discrimination indices increased in both FT groups, while they remained around 0.5 in both VT groups. The most important data with respect to the main goal of this experiment was that the temporal discrimination index increased significantly faster in group R-FT than in group A-FT. Statistical analyses confirmed these initial impressions. A 2 (Training) x 2 (Test Schedule) x 3 (Block) ANOVA conducted on the test data revealed significant main effects of Training, $F(1, 26) = 5.44$, $MSe = .04$, $p = .028$, $\eta^2p = .17$, 95% CI [.01, .36], Test Schedule, $F(1, 26) = 29.88$, $MSe = .04$, $p < .001$, $\eta^2p = .54$, 95% CI [.29, .67], and Block, $F(2, 52) = 3.57$, $MSe = .15$, $p = .035$, $\eta^2p = .12$, 95% CI [.001, .31]. Additionally, the Test Schedule x Block, $F(2, 52) = 3.42$, $p = .04$, $\eta^2p = .12$, 95% CI [.005, .24], and, most crucially, Training x Test Schedule, $F(1, 26) = 4.83$, $MSe = .04$, $p < .037$, $\eta^2p = .16$, 95% CI [.01, .35], interactions were significant. The three-way Training x Test-Schedule x Block interaction was not significant, $F(2, 52) = .356$, $MSe = .015$ $p = .70$, $\eta^2p = .01$, 95% CI [.000001, .07].

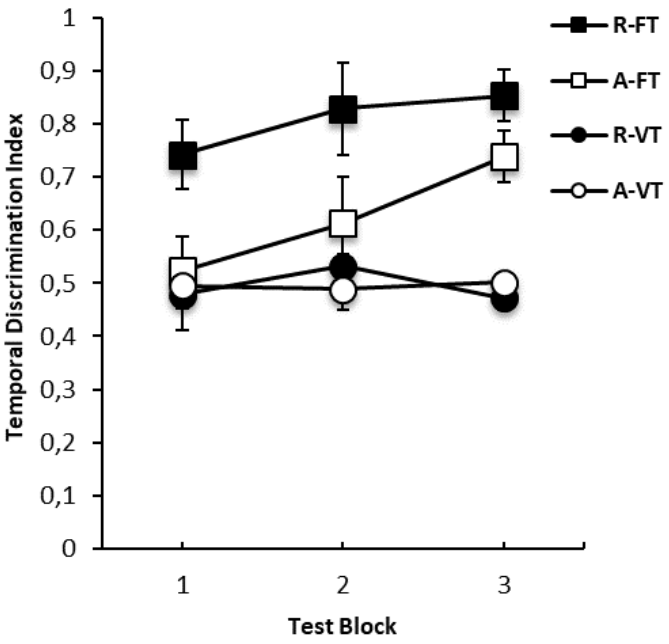

Figure 2. *Mean temporal discrimination indices of the first 3 40-trial Blocks of testing. R groups received Reversal training in Phase 2; A groups received continued Acquisition training. FT groups received food presentation at fixed times in the test phase; VT groups received variable presentation of the food. Error bars denote standard error of the mean.*

According to the main goals of the experiment, we focused on the analyses of the Training x Test-Schedule interaction. Firstly, we explored the simple effect of Test-Schedule at each level of the Training condition (R and A), to test whether temporal indices were greater in the FT condition than in the VT condition, as expected. Analyses showed that the simple effect of Test-Schedule was indeed significant in both, Reversal, *F*(1, 12) = 36.22, *MSe* = .03, *p* > .001, η^2p = .75, 95% CI [.44, .84], and in Acquisition condition *F*(1, 14) = 4.75, *MSe*= .04, *p* = .047, η^2p = .25, 95% CI [.001, .49]. Thus Temporal Discrimination was developed in both conditions of training, as we expected. Secondly and most important to our goals was to explore the effect of Reversal Training in the FT and VT conditions, independently. In the FT condition, a main effect of Block *F*(2,26) = 7.22, *MSe* = .014, *p* = .003, η^2p = .36, 95% CI [.10, .51] and most interestingly of Training *F*(1, 13) = 5.50, *MSe* = .07, *p* = .036, η^2p = .30, 95% CI [.01, .53] was observed, although the interaction between Block x Training was not significant, *F* < 1, *p* = .398. In the VT condition, no significant effects were observed, largest *F* < 1, for the Training x Block interaction. Thus, the effect of reversal training only appeared in the FT condition, whereas under the VT schedule there was a null effect of prior training.

Temporal conditioning developed faster after discrimination reversal than after simple acquisition. The only difference between R and A groups was the experience of reversal in groups R. This result supports the idea that the ambiguity produced by interference produces a more general increase in attention than the specific context-attention increase that some theories have posited (e.g., Bouton, 1997; Rosas & Callejas-Aguilera, 2006). This more general attentional increase may have facilitated subsequent learning, allowing rats in the R-FT condition to better learn the temporal interval associated with food presentation in the test phase. This result is made even more noteworthy by the explicit lack of an effect of reversal training on context conditioning in the VT groups. Specifically, reversal training produced a learning advantage in a task in which no general context conditioning advantage was apparent following reversal. Experiment 2 was designed as a replication of the main result of Experiment 1, intended to confirm the main result by showing that the better temporal conditioning is not specific to one interval, but rather is observed across different temporal durations.

Experiment 2

The results of Experiment 1 suggest that predictive ambiguity produced by interference treatments facilitates subsequent temporal discrimination while not affecting context conditioning. As far as we know, this result is a new one in the animal learning literature (but, see Nelson, Fabiano, & Lamoureux (in press) for a related example in human beings) so, before taking it at face value, it is important for the finding to be replicated. This was the goal of Experiment 2. The design of the experiment is presented in the bottom section of Table 1. Training (Reversal vs Acquisition) was again manipulated in this experiment, as well as the new variable Test Interval, comprised of two fixed temporal durations for food presentations (FT60 vs FT30), manipulated in a 2 x 2 design. Based on the results of Experiment 1, and the predictions of the idea that reversal may produce a general boost in attention, temporal conditioning should be better in both R groups than in both A groups, regardless of the between-food interval duration. Additionally, this effect should be observed at specific temporal intervals, relevant to the Test Interval employed in each groups' training.

Substantial prior work on the scalar properties of time (Gibbon, 1977) has revealed a phenomenon known as the superposition effect, which has been observed in both nonhuman animals (Drew, Couvillon, Zupan, Cooke, & Balsam, 2005; Church & Gibbon, 1982; Rosas & Alonso, 1996) and humans (Molet, Callejas-Aguilera, & Rosas, 2007). Specifically, when a conditioned response is recorded in units proportional to the interval duration (e.g., every third of the criterion time), the response of the organism to different interval durations tends to superimpose. In Experiment 2, we used two intervals (30s and 60s) that allowed us to measure performance in relative response bins (i.e., sixths of the inter-food interval). However, it should be noted that, as the first 5-s intervals after food delivery were excluded from the analyses, the comparison index was not computed with the exact same sixths of the inter-food interval in groups 30 and 60. Regrettably, this aspect of the analysis should make the detection of the scalar property of timing more difficult. But at any rate, the temporal distribution of responding in the groups should show a similar trend regardless of the length of the inter-food interval. Moreover, this trend should appear faster in groups R than in groups A, even if the superposition results are not precise.

Method

Subjects and Apparatus.

Forty-eight naïve female Wistar rats participated in the experiment. Rats were provided by Harlan Laboratories (Amsterdam) and their mean free-feeding weight at the beginning of the experiment, before deprivation began, was 195g (range 179-220g). The general experimental conditions and apparatus were the same as in Experiment 1.

Procedure

Rats received identical training to that received by rats in Experiment 1, with one exception. During the test stage all rats were trained under a FT food delivery schedule. Half of the rats in each condition (Reversal and Acquisition) were trained under a FT(60s) schedule, while the other half were trained under a FT(30s) schedule. So, by the time of testing there were four groups of rats: R-FT60, R-FT30, A-FT60, and A-FT30. With the goal of keeping the number of trials identical across different conditions, the duration of the test sessions was different in groups FT60 (80 min) and in groups FT30 (40 min).

Dependent variable and statistical analyses

Dependent variables were the same as in Experiment 1. As the periods used for computing the temporal conditioning index were sixths of the between-food interval, they were 5-s periods in groups FT30 and 10-s periods in groups FT60. As in Experiment 1, the five first seconds after delivery of food were excluded from the subsequent analyses.

Results and Discussion

The food dispenser of one of the operant boxes failed during the second phase of training. The five rats affected by this problem were thus excluded from the experiment, so that the final number of rats in the different groups was: 10 for R-FT60, 12 for A-FT60, 11 for R-FT30, and 10 for A-FT30.

Acquisition and Reversal Training.

Figure 3 presents the mean magazine entries during the Pre- and CS-periods of CS1 and CS2 throughout the 10 sessions of Acquisition (left side) and the five sessions of Reversal (right side) in the R and A conditions. Unlike in Experiment 1, the interaction among Test Interval, CS, and Session was statistically significant. This result was unexpected, and seems to be due to a higher level of responding in groups FT30 than in groups FT60 only in acquisition Session 4, and only in CS2, *F*(1, 41) = 4.62, *MSe* = 7.75 *p* < .038, η2p = .10, 95% CI [.003, .25]. As this result was not based on any differences in training procedures and was only a transient effect that was not observed at the end of the initial Acquisition phase, it appears to be a random difference at the beginning of training. Thus, the remainder of the data are presented the same, collapsed format used in Experiment 1. Results of this experiment were similar to those reported in Experiment 1, with higher responding to CS1 than to CS2 during acquisition, which reverses during the Reversal phase in groups in the Reversal condition.

A 2 (Training) x 2 (Test Interval) x 2 (CS) x 10 (Session) ANOVA conducted with the CS acquisition data found significant main effects of CS *F(*1, 39) = 58.87, *MSe* = 161.75, *p* < .001, η^2p = .60, 95% CI [.42, .70], and Session, *F*(9, 351) = 8.16, *MSe* = 9.13, *p* < .001, η^2p = .17, 95% CI [.10, .21]. The CS x Session interaction was significant, *F*(9, 351) = 27.18, *MSe* = 6.85 *p* < .001, η^2p = .41, 95% CI [.33, .45]. The Test Interval x CS x Session interaction was also significant, F (9, 351) = 1.99, *MSe* = 6.48, *p* =.039, η^2p = .05, 95% CI [.002, .07], as explained above. No other main effects or interactions were significant, largest *F(*9, 351) = 9.13, *p* = .15, for the Test Interval x Session interaction. The same analysis conducted on pre-CS magazine entries revealed a significant main effect of Session, *F*(9, 351) = 9.17, *MSe* = 4.24 *p* < .001, η^2p = .19, 95% CI [.11, .23], and a Test Interval x Session interaction, *F*(9, 351) = 2.67, *MSe* = 4.24 *p* = .005, η^2p = .06, 95% CI [.01, .08]. No other main effects or interactions were significant, largest *F*(9, 234) = 1.49, *p* = .15 for the Training x Test Interval x Session interaction. Subsequent analyses conducted to explore the Test Interval x Session interaction did not reveal significant simple effects of Test Schedule at any level of Session, nor a significant simple effect of Session at any level of Test Interval, largest *F(*1, 41) = 3.05, *p* = .09, for Session 4. The significant interaction appeared to be due to a slightly faster decrease in Pre-CS magazine entries in the FT-30 group in the first few sessions.

A 2 (Training) x 2 (Test Interval) x 2 (CS) x 5 (Session) ANOVA conducted on CS magazine entry data during Reversal training found significant main effects of CS, *F*(1, 39) = 13.23, *MSe* = 112.70, *p* =.001, η^{2}p = .25, 95% CI [.07, .41], and Session, *F*(4, 156) = 6.88, *MSe* = 3.56, *p* < .001, η^{2}p = .15, 95% CI [.06, .22]. Training x CS, *F*(1, 39) = 56.97, *MSe* = 112.70, *p* < .001, η^{2}p = .59, 95% CI [.41, .69], CS x Session, *F*(4, 156) = 35.32, *MSe* = 6.25, *p* < .001, η^{2}p = .48, 95% CI [.34, .51], and Training x Session interactions, *F*(4, 156) = 4.16, *MSe* = 3.56, *p* = .003, η^{2}p = .10, 95% CI [.03, .16] also were significant. Finally, there was a significant three-way Training x CS x Session interaction, *F*(4, 156) = 33.70, *MSe* = 6.25, *p* < .001, η^{2}p = .47, 95% CI [.36, .53]. Subsequent analyses conducted to explore the 3-way interaction revealed that the CS x Session interaction was significant in the Reversal condition, *F*(4, 80) = 48.00, *MSe* = 8.75, *p* < .001, η^{2}p =.71, 95% CI [.60, .76], but not in the Acquisition condition, *F* < 1. The CS x Session interaction in the Reversal condition was further revealed to be the result of a switch in the direction of the differences in responding between CS1 and CS2 across Reversal sessions. Responding to CS1 was greater than responding to CS2 in Session 1, *F* (1, 19) = 38.19, *MSe* = 9.12, *p* < .001, η^{2}p = .67, 95% CI [.41, .77], and this pattern was reversed in Sessions 3, 4, and 5, smallest *F*(1, 19) = 22.60, *MSe* = 19.72, *p* <.001, η^{2}p = .54, 95% CI [.25, .69] for Session 3.

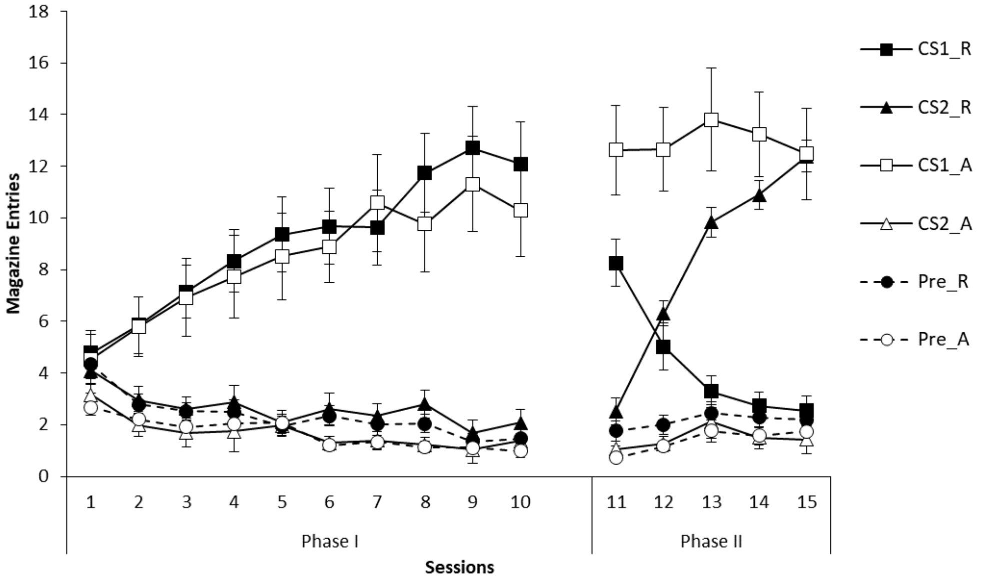

***Figure 3**. Mean Magazine Entries during Phase I and Phase II in Experiment 2. For simplicity, mean magazine entries for CS1, CS2, and the Pre-CS interval are collapsed across Reversal and Acquisition groups in both phases, regardless of final test interval. Pre-CS magazine entry rates are further collapsed across both CSs. Error bars denote standard of the mean*

These results suggest that the discrimination reversal treatment was effective, so CS1 and CS2 stimuli reversed their relative predictive values, but only in the Reversal condition. The same analyses conducted on pre-CS magazine entries found only a significant main effect of Session, *F*(4, 156) = 3.09, *MSe* = 3.15, *p* = .018, η^2p = .07, 95% CI [.005, .12]. No other main effect or interaction was significant, largest *F*(4, 156) = 1.89, *p* = .115, for the Test Interval x CS x Session interaction.

Temporal Discrimination Test.

In accord with the first experiment the first 120 trials of the temporal discrimination test were considered in the subsequent analyses (i.e., one and a half sessions). Trials were divided into three 40-trial blocks. Figure 4 presents the mean temporal discrimination indices during the first three 40-trial blocks of testing in groups R-FT60 and A-FT60 (left) and in groups R-FT30 and A-FT30 (right). In general, temporal discrimination was greater in groups R than in groups A, regardless of the duration of the fixed time interval, though discriminative performance seemed to be better in group R-FT60 than in the other groups. A 2 (Training) x 2 (Test Interval) x 3 (Block) ANOVA conducted on the test data found significant main effects of Training *F*(1, 39) = 11.81, *MSe* = .05, *p* = .001, η^2p = .23, 95% CI [.06, .39], Test Interval, *F*(1,39) = 1,39, *MSe* = .05, *p* = .005, η^2p = .18, 95% CI [.03, .34], and Block *F*(2, 78) = 24.38, *MSe* = .008, *p* < .001, η^2p = .38, 95% CI [.23, .48]. No other main effect or interaction was significant, largest *F*(2, 78) = 2.85, *p* = .064, for Test Interval x Block interaction. Planned comparisons conducted with each FT condition found that the simple main effect of Training was significant in both the FT60, *F*(1, 20) = 6.12, *MSe* = .08, *p* = .022, η^2p = .23, 95% CI [.02, .44], and FT30, *F*(1, 19) = 7.58, *MSe* = .022, *p* = .013, η^2p = .28, 95% CI [.04, .49], conditions. Thus, performance was significantly better in Reversal groups than in Acquisition groups, regardless of Test Interval. Performance was also better in FT60 groups than in FT30 groups, as shown by the main Test Interval effect. Finally, the main effect of Block was due to a general increase in performance as training progressed.

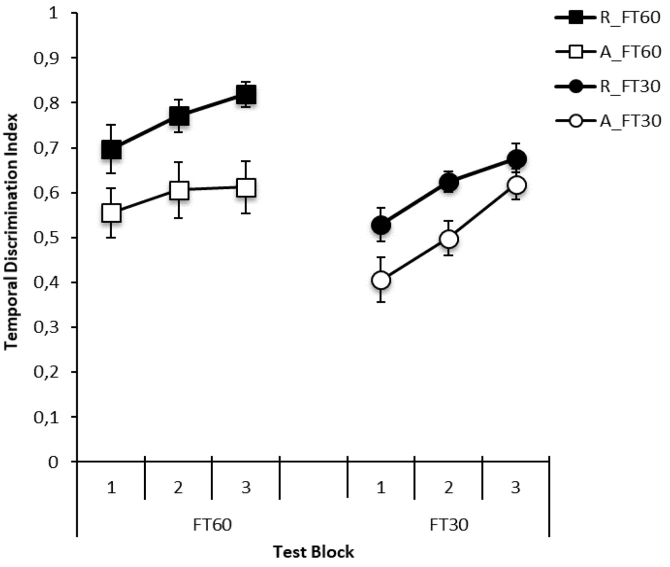

Figure 4. *Mean temporal discrimination indices in the first 3 40-Trial blocks of testing in Experiment 2. The first letter of each group indicates the treatment received (Reversal vs Acquisition) and the number represents the temporal interval in which food was delivered (fixed time 30 seconds vs fixed time 60 seconds). Error bars denote standard error of the mean.*

The overall pattern of results observed in Experiment 2 replicates the facilitation effect of discrimination reversal on subsequent acquisition of temporal conditioning observed in Experiment 1, extending the results to an additional fixed time interval. Temporal discrimination performance was better with the 60s training interval than with the 30s interval, which might suggest a poor correlation to the superposition result commonly observed in timing studies (LaBarbera & Church, 1974). However, we should remember that eliminating the 5s post-food period in both groups to avoid counting feeding behavior as anticipatory conditioned responding affects the two Test Interval conditions differentially. The sixth of the interval used for comparison in group FT30 would be the second sixth bin of the interval, which unfortunately cannot precisely match the bins used in the FT60 groups. Rather, it corresponds to half of the first and half of the second bins in the FT60 groups. Thus, this task may be a difficult one in which to obtain precise superposition effects. Additionally, it should be pointed out that the superposition effect has been found to be weaker with short intervals in time production tasks like the one we are using here (see Rosas & Alonso, 1996). Moreover, the null effect reported here is only the first of its kind, and could be a Type II error. Perhaps most importantly, since the present experiment was designed to investigate the rate of learning across many trials, rather than evaluating the temporal allocation of asymptotic responding as is typical of superpositioning experiments, it is not all that surprising that the rate of increase in our more rudimentary temporal index does not overlap across temporal intervals precisely. Indeed, the main difference between the 30s and 60s groups appears to be in overall response levels, something that is often seen, but normalized, when analyzing responding to cues of different durations in classic superpositioning experiments. Altogether, the lack of superposition effect in this experiment should be taken with caution. At any rate, the presence or absence of superposition is not a relevant issue for the main goal of these experiments, and does not compromise the primary conclusion that discrimination reversal facilitates subsequent temporal conditioning, regardless of whether temporal discrimination was particularly robust (with the FT60 groups) or more modest (in the FT30 groups).

General Discussion

The goal of this experimental series was to explore whether the ambiguity produced by discrimination reversal training in an appetitive classical conditioning situation would increase attention to the contexts in which reversal training takes place, as Bouton (1997) and Rosas et al. (2006) suggest, or whether it would lead to a more general attentional arousal or increase that would facilitate any kind of subsequent learning, regardless of whether the context is involved or not. Overall responding to the context (i.e., context conditioning) was not different at testing based on whether the discrimination was previously reversed or not. However, temporal conditioning was facilitated by prior reversal training, regardless of whether the duration of the interval was 60 s (Experiments 1 and 2) or 30 s (Experiment 2). A similar result was recently reported by Nelson, et al., (in press). However, the current experiments extend that finding from humans to rats, and more importantly, confirm that the enhancement of temporal learning is seen with more than one interval. As the prior study did not test multiple intervals in the same experiment, it is unclear whether their enhanced test performance was due to temporal discrimination or simple context conditioning.

The lack of facilitation of context conditioning observed in Experiment 1 may actually fit Bouton's (1997) explanation of context switch effects on renewal, as he posited that the increase in attention to the context should only affect the context-specificity of ambiguous information. According to this idea, an increase in attention to the context during interference would not necessarily make contexts easier to condition. However, facilitation of context conditioning is a direct prediction of the Attentional Theory of Context Processing (Rosas et al., 2006). A logical prediction derived from the idea that interference raises attention to the context is that contexts will be able to enter into associations faster after an interference treatment than in the absence of it. The results found in Experiment 1 do not support this idea. Context conditioning developed at the same rate regardless of whether the rats had received the reversal treatment or not. This result may be surprising, given that we have recently reported enhanced context conditioning by the interference experience with the same task used here (Alcalá, González et al., 2018). There are several possible reasons for this null result. Given that there are a number of results in the literature suggesting that interference specifically enhances the context-dependence of the retrieval of information (Bouton, 1993; Bouton & Todd, 2014), it could be that interference affects context-switch effects, but does not affect direct context conditioning. This is unlikely given that some context-switch effects are actually based on differential context conditioning (Abad, Ramos-Álvarez, & Rosas, 2009; Alcalá, González et al., 2018; León, et al., 2012; Preston, Dickinson, & Mackintosh, 1986). An alternative and perhaps more plausible explanation for our null result relies on the lack of sensitivity of the measure used for detecting context conditioning. The measure of context conditioning in this procedure was exclusively measured though magazine entries. Although it is true that Alcalá, González et al. (2018) found evidence of enhanced context conditioning using magazine entries in appetitive conditioning, it is also true that the evidence of context conditioning was only reliable when the experiment was conducted in two replications, adding up to 32 rats per group, suggesting that magazine entries may not be sensitive enough to detect the effect of interference on context conditioning in this situation. Moreover, as noted above, in our prior published work, this effect was measured during the discrimination reversal phase; the present experiments measure context conditioning in a separate phase after reversal has already completed. Finally, the procedures included in a CS discrimination phase may have a significant effect on the nature of contextual responding. During a discrimination phase in which CSs are frequently turning on and off, attention may be less consistent across the session, focused by the CSs to those cues' physical features, but allowed to broaden to the context during intertrial intervals. Our present nonsignaled testing phase may result in more consistent attention across the session. Since no punctate cues can focus the rats' attention, the temporal features of the fixed-time training schedule may have become more salient than the tonic physical features of the context. In future experiments it would be interesting to explore different strategies to measure context conditioning, such as recording different kind of behaviors such as rearing, grooming or the general pattern of activity in both, appetitive and aversive tasks (e.g. Carrive, 2000), as a way to increase the sensitivity of the task to detect differences in context-conditioning. Thus, the present study provides no evidence of ambiguity favoring contextual conditioning at this point, and additional research will be needed to confirm whether this lack of difference reflects an actual lack of effect, or it is caused by an insensitive measure.

Both, Bouton's (1993, 1997) theory and ATCP (Rosas et al., 2006; Rosas & Callejas-Aguilera, 2006, 2007) are focused on the role of ambiguity on context-based retrieval of information related to CSs, but they are silent with respect to whether ambiguity should affect other types of learning. As shown in this experimental series, reversing a CS-based classical conditioning discrimination facilitates subsequent temporal conditioning in the absence of a discrete CS. This kind of result is anticipated if one assumes that the ambiguity produced by the interference treatment produces a general increase in attention, so that the increase in attention to the contexts that has been observed in prior research is only one specific case of this more general effect. This idea has been raised by Schmajuk and his colleagues (Schmajuk & Larrauri, 2006), suggesting that animals respond to novelty by increasing attention to the environment. In this view, novelty is based on a prediction error that is then reduced through learning (Schmajuk et al., 1996). Accordingly, facilitation of temporal conditioning in the Reversal groups of the present experiments would be due to the increase in prediction error during the reversal training phase, producing a general increase in attention that facilitates subsequent temporal conditioning. It is important to point out that this facilitation is not always shown, and sometimes may be stimulus specific (e.g., Alcalá, González, et al., 2018; Hall & Pearce, 1982). According to Schmajuk and Larrauri (2006), the introduction of novel tasks may produce additional novelty, such that a ceiling effect is reached, hindering the potential effects of ambiguity to facilitate new learning. In summary, the effect of ambiguity on new learning is not expected to be an overly large effect, and should depend critically on the length of the interference treatment, given that once the prediction error is corrected, novelty is expected to disappear and so the beneficial effects of interference upon new learning.

For instance, a study conducted by Weideman & Kehoe (2003) using the nictitating membrane conditioning procedure found that the number of extinction trials was a critical variable in determining whether prior extinction of one CS affects the rate of acquisition of responding to a second CS. Specifically, with a lower number of extinction trials (300), acquisition with the second CS was better than in naïve control group, but only at the beginning of the second conditioning phase. When the number of trials of extinction was increased to 600 or 1200 trials, however, these differences were not significant, although there was still a trend towards better acquisition after extinction. In the current series, 5 sessions of reversal training were chosen because they clearly produce reversal, but the asymptote of training is usually not fully established, and thus some novelty is expected to be still in effect.

Before concluding that reversal training increases attention or arousal in animals, we must consider a different explanation of these results. Ricker and Bouton (1996) found that reacquisition of a previously-extinguished CS developed faster than acquisition by a naïve control group. Additionally, they found that conditioning of a new CS was facilitated by previous conditioning and extinction of a different CS, something they interpreted as a learning-to-learn effect analogous to an effect that has been observed in nictitating membrane response conditioning (Kehoe & Holt, 1984; Kehoe, et al., 1984). For instance, Kehoe and Holt (1984) found that conditioning of one CS facilitates subsequent conditioning of a different CS. This effect survived extinction of the first CS and was interpreted as a learning-to-learn effect (Kehoe et al., 1984, Ricker & Bouton, 1986). In the experiments reported here, the difference between Acquisition and Reversal groups lies in the treatment animals receive over the last five days prior to the test phase. Animals in Acquisition groups receive the same training for 15 days, while animals in Reversal groups experience a change in the learning situation and are trained that CSs may have different meanings over time. These procedural differences may have resulted in a possible facilitation effect in the subsequent temporal discrimination. As reported thus far, the learning-to-learn effect seems to be specific to the same general kind of learning (e.g., CS excitation) and is exhibited with a cue of a different modality (Kehoe, et al., 1995). What the experiments reported here found is that reversing a stimulus discrimination facilitates a different kind of learning; thus, it is a more general effect on learning and behavior that is more plausibly interpreted as a general increase in attention that prepares the organism to confront new learning than the more constrained type of logical, learning-to-learn effects described by Kehoe.

The idea that informational incongruence may enhance the ability to utilize cognitive resources has been also discussed in the human associative literature. Le Pelley, Mitchell, Beesley, Georgen, and Willians (2016) proposed two different kinds of attentional mechanisms, based on the associative principles set forth by the Pearce and Hall (1980) and Mackintosh (1975) attentional models of learning. In this view, one type of attention –attentional exploration– is assumed to be used under conditions of uncertainty, engaging cognitive resources to explore ambiguous or uncertain cues, with the goal to use this information in future events (Beesley, Nguyen, Pearson, & Le Pelley, 2015; Hogarth, Dickinson, Austin, Brown, & Duka, 2008). A second –exploitive attentional– mechanism is assumed to focus attention on cues that are good predictors of important consequences, with the goal to exploit that congruent information (Le Pelley, 2010). This idea may be applicable to the results reported here, in the sense that ambiguous information may lead the organism to engage such an exploring attentional mechanism, focusing its resources on other features of the learning environment, facilitating subsequent learning. A similar idea was raised by Kahneman (1973), suggesting that when a response conflict is detected, people's arousal increases, generating a state of generalized alertness. Indeed, these ideas may explain our lack of a context conditioning enhancement in group R-VT in Experiment 1. Presumably, attentional exploration would lead the organism to seek out alternative, but still salient, features of the environment. Perhaps the physical context itself is not a novel enough cue to focus such enhanced attention in this paradigm, while the novel importance of temporal intervals may be much more salient.

In summary, the results reported here add to the pool of results in the human and nonhuman literature suggesting that incongruence of the information, or ambiguity, may produce a general increase in the organism arousal that may facilitate subsequent learning. This idea forces to qualify recent explanations of context-switch effects on behavior as the consequence of an increase in attention to the context generated by the interference treatments. The results reported here suggest that context-switch effects, at least to a point, may be considered only a specific outcome or one example of an effect of a more general increase in attention or arousal caused by interference.

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Study 3

Alcalá, J. A., Callejas-Aguilera, J. E., Nelson, B., & Rosas, J. M. (2018). Reversal Training Facilitates Acquisition of New Learning in a Morris Water Maze. *Manuscript submitted to Journal of Experimental Psychology: Animal Learning and Behaviour.*

RUNNING HEAD: REVERSAL FACILITATES SPATIAL ACQUISITION

Reversal training facilitates acquisition of new learning in a Morris water maze

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Abstract

Two experiments determined the effect of interference training on subsequent spatial learning in a Morris water maze. After learning that a platform was located in a quadrant whose edges were marked by landmarks A and B, rats either continued that training or received a reversal where the platform was opposite to the initially trained quadrant. On test, a new cue, C, was added and the platform was located in the new AC quadrant. Rats that had received the reversal training learned the location of the new platform faster than rats trained with the same platform throughout. In Experiment 2, Phase 1 training was conducted by placing the rats on the platforms to ensure that they were located. Experimental rats received a reversal of the platform position in phase 2. A control group received training with both platforms present, and had experience with each. When a new cue C was added and the platform was now located in the AC quadrant the rats that received reversal training learned about the new location better than those without reversal training. Results are discussed in terms of interference's effect on the arousal of general attention.

Keywords: Attention, Facilitation of Learning, Interference, Spatial learning

There is general agreement that an interference treatment renders the interfering information context dependent. The paradigmatic example of this phenomenon is the renewal effect (e.g., Bouton & Bolles, 1979). Following the extinction of a conditioned response, renewal of performance exhibited prior to the interfering extinction treatment appears when the conditioned stimulus (CS) is tested outside the context in which interference has taken place. Considering each letter as the context where a phase of learning takes place (acquisition, extinction, testing), renewal can be found in ABA (e.g., Nelson, Sanjuan, Vadillo-Ruiz, Peréz, & León, 2011), AAB, and ABC designs (e.g., Thomas, Larsen, & Ayres, 2003).

Renewal is an ubiquitous phenomenon. It has been documented in rats' conditioned suppression (e.g., Bouton & Bolles, 1979), operant conditioning (e.g., Bouton, Todd, Vurbic, & Winterbauer, 2011), taste aversion (e.g., Rosas & Bouton, 1997, 1998), appetitive conditioning (Bouton & Peck, 1989), and chain behavior (Thrailkill, Trott, Zerr, & Bouton, 2016). It has also been reported when the interference treatment involves treatments such as counterconditioning (e.g., Peck & Bouton, 1990; Holmes, Leung, & Westbrook, 2016) and discrimination reversal (e.g., Bouton & Brooks, 1993). Renewal has been reported in spatial learning in mice (e.g., Lattal, Mullen, & Abel, 2003), pigeon autoshaping (Rescorla, 2008; Starosta et al. 2016), and with a variety of tasks and procedures in human beings –i.e., predictive learning (e.g., Bustamante, Uengoer, & Lachnit, 2016; Paredes-Olay & Rosas, 1999; Üngör & Lachnit, 2006; 2008), both suppression of (e.g., Baeyens, et al., 2005; Nelson, et al., 2011; Neumann, 2006) and increases in (Nelson, Navarro, & Sanjaun, 2014), responses counts, fear conditioning (e.g., Effiting & Kindt, 2007), causal learning (e.g., Rosas, García-Gutiérrez, & Callejas-Aguilera, 2006), eye-blink conditioning (e.g., Grillon, Alvarez, Johnson & Chavis, 2008), skin conductance conditioning (e.g., Vervliet, Vansteenwegen, Baeyens, Hermans & Eelen, 2005) and associative learning evaluated by reaction time (e.g., Cobos, González-Martín, Varona-Moya, & López, 2013).

In the most widely discussed explanation of renewal (i.e., Bouton, 1993), it is assumed that inhibition is acquired in extinction (e.g., Wagner, 1981), and the retrieval of that second-learned inhibition is more affected by the context change than first-learned information (Bouton, 1993; Nelson, 2002, 2009). To explain the differential context-dependence of second-learned information, Bouton (1997) suggested that when the meaning of the cues is changed during interference, organisms' attention is automatically directed to the context in a search for something that allows them to disambiguate the situation, so that second-learned information about the ambiguous cue becomes context dependent (see also Darby & Pearce, 1995).

Rosas and his colleagues have extended Bouton’s (1997) idea that contextual control of ambiguous information results from an increase in attention to the contexts by suggesting that whenever a context is attended, *any* information learned within that context becomes context specific, regardless of whether that information is ambiguous or not, or first- or second-learned (e.g., Rosas & Callejas-Aguilera, 2006; Rosas, Callejas-Aguilera, Ramos-Álvarez, & Abad, 2006). For instance, Rosas and Callejas-Aguilera (2007) reported contextual control of a conditioned taste aversion (Y) when it had been learned after conditioning and extinguishing a different flavor (X) (see also, Bernal-Gamboa, Nieto, & Rosas, 2015; Callejas-Aguilera, & Rosas, 2010). The increase in contextual control appears to go beyond just the context in which interference takes place, contextual control occurred in tasks and contexts different from the ones in which interference was experienced. For instance, Bernal-Gamboa, Rosas, & Callejas-Aguilera (2014, Experiment 1) found that prior extinction of running in a straight alley rendered a subsequently learned taste aversion context-specific. Experiment 2 yielded similar results by extinguishing a conditioned taste aversion and testing the context-dependency of runway running (see also Bernal-Gamboa, Callejas-Aguilera, Nieto, & Rosas, 2013, for similar effects with respect to time-dependence). It is important to note that the boundary conditions for this effect are not fully known (e.g., Nelson & Lamoreaux, 2015; Nelson, Lombas, & León, 2011), but when observed the effect points to interference increasing subsequent contextual control of learning.

One explanation for these effects is that the increase in prediction error that occurs when the meaning of cues or responses change increases attention to contexts. That arousal of attention is general, rather than being specific to the particular stimulus and contexts where the interference was produced (i.e., Bouton, 1997). The idea of an increase in the level of attention as a consequence of the increase in uncertainty that accompanies the interference treatment is not new. Pearce and Hall (1980) assume that greater prediction error on a trial is associated with a greater increase in attention on the subsequent trial (e.g., Kaye & Pearce, 1984). Schmajuk, Lam, and Gray (1996) incorporate this idea in a way such that the increase in attention is not circumscribed to the stimuli that were present on the interfering trial, but rather a general state of heightened arousal and attention is induced. Schmajuk, Lam, and Gray (1996; see also Larrauri & Schmajuk, 2008) suggested that novelty leads to an increase in attention to any perceptible element (i.e., cues, contexts, and outcomes). Novelty is expressed as a function of the overall prediction error in the environment; the difference between the total environmental representation expected and that which occurs. When novelty increases, organisms' attention also increases, enhancing the expression and formation of associations among the elements present in the situation. As learning progresses and the environment is better represented, attention is assumed to decrease progressively. According to that proposal, when interference is present the novelty of the situation increases. This idea would predict that the organism will be more aroused after an interference treatment, and learning would be expected to occur faster than in the absence of previous interference.

In agreement with the predictions above, a recent study from our laboratory has found that rats acquired temporal conditioning faster when it was preceded by a discrimination reversal than when it was preceded by simple discrimination (Alcalá, Callejas-Aguilera, Lamoureux, & Rosas,2018). In an appetitive conditioning procedure rats received CS1+/CS2- training in acquisition, followed either by more acquisition training or a reversal (CS1-/CS2+). Afterwards, food was delivered every 60 (Experiments 1 and 2) or 30 (Experiment 2) seconds. Rats showed temporal conditioning in the form of greater responding prior to the delivery of food relative to after its delivery, and that discrimination along time was acquired more rapidly in the reversal group. Presumably, the reversal produced novelty and interference, increasing attention to the elements of the situation. A similar result has recently been demonstrated in humans (Nelson, Fabiano, & Lamoureux, in press). In the presence of a sensor predicting an attacking spacecraft, participants learned to either respond on a keyboard (Experiment 2), or suppress responding on a mouse (Experiment 1) to prepare for the attack. Then, half the participants underwent extinction where the sensor occurred without the attacking spaceship. On a subsequent test, the spaceship arrived unsignalled on a fixed interval. In two experiments using different game methods, participants learned to expect the unsignalled spaceship more rapidly when prior extinction had occurred than when it had not.

The goal of the study we report here was to further explore the effects of interference on new learning using spatial learning in rats. Despite some controversy in the literature, there seems to be little doubt today that spatial learning involves many of the same principles as other forms of associative learning (e.g., Chamizo, 2003, Pearce, 2009; but see Jefrey, 2010). Basic associative learning phenomena have been found in spatial learning such as latent inhibition (Prados, Chamizo, & Mackintosh, 1999), spontaneous recovery (Prados, Manteiga, & Sansa, 2003), partial reinforcement (Prados, Sansa, & Artigas, 2008), blocking (Roberts & Pearce, 1999), and renewal (Lattal et al. 2003). The present study involved two experiments with rats conducted in a Morris Water maze in which different landmarks signaled the position of a hidden platform. The goal of the current research was to test whether an interference experience in the water maze facilitates subsequent learning about a new location of the hidden platform compared to a group of rats that did not have the interference experience.

Experiment 1

Experiment 1 determined whether training animals in a water maze with the platform sequentially hidden in two different positions facilitates learning the location of the platform in a new position with respect to animals for which the location of the platform was consistent during training. The design of the Experiment is presented in the top section of Figure 1. The experiment included 3 groups of rats. Rats in groups Reversal (R) and Acquisition-long (AL) were first trained with the platform placed between two distinctive landmarks (A and B) while rats in group Acquisition-short (AS) were kept in their homecages. During Reversal, rats in groups AL and AS received the Acquisition treatment while group R received the platform hidden in the quadrant opposite from its phase-1 position (see Lattal et al., 2003). Finally, all rats received a test in which a new landmark was added (C) and the platform was hidden in the new AC quadrant, equidistant from the prior platform placement for all the groups. Group R received an interference experience that groups AS and AL did not receive. If interference produces a general increase in attention, then the reversal experience should facilitate acquisition of new learning, as reported by Alcalá, Callejas-Aguilera, et al. (2018). Group R should more quickly associate the landmarks with the new platform location than the other two groups.

Method

Subjects

The present experiments were approved by the bioethical committee of Universidad de Jaén. The subjects were twenty-four female Wistar Rats, approximately six months old at the beginning of the experiment. The rats had experience in a classical conditioning experiment, unrelated to this one, in which they had limited access to food. They were kept three weeks with food and water available ad libitum before starting this experiment. Animals were individually housed in standard cages in a room with a 12:12 light-dark cycle, and were maintained ad libitum throughout the experiment. Experimental sessions were conducted in the first 6 hours of the light cycle (9:00 - 14:00). Rats were randomly assigned to groups AL, AS and R before starting the experiment. One of the rats in group AL was removed from the experiment as she showed behavioral symptoms of stress at the beginning of the experiment and somehow injured herself against the ceiling of the home cage. Group AL included 7 animals, while AS and R groups included 8.

Apparatus

The experiment was conducted in a circular water maze tank similar to the one used by Morris (1981). The tank measured 1.40 m in diameter and 0.6 m deep. It was filled to a depth of 0.48 m with water rendered opaque by the addition of black watercolor paint. The water temperature was maintained at 22 ± 1ºC. The pool was placed in the middle of a square room and mounted on a metal platform 0.27 m above the floor. The pool was surrounded by opaque curtains from the edge of the pool to the ceiling. A video camera was mounted 1.8 m above the center of the pool and was controlled by a computer in the adjacent room to record the rats' activity. Swimming patterns were analyzed by Smart Video Tracking Software 2.0 developed by Panlab, Harvard Apparatus S.A (Cornellá, Barcelona, Spain). A circular 0.47-m high platform of (12-cm square) was used as a hidden escape platform. Once placed in the tank the platform was hidden one centimeter below the surface of the water.

Four stimuli were used as landmarks. Two different geometrical shapes, a thin colored polystyrene circle with radius of 19.5 cm and depth of 3.4 cm or a thin black and white polystyrene square (29x29x1) were used as landmarks A and B, counterbalanced. The shapes were held from the ceiling, so that the landmark was close to the curtain and reached the edge of the pool. The lower edge of the shape was about 20 cm above of the surface of the water. A steady and flashing (120hz) yellow light were orthogonally counterbalanced as landmarks B and C. Light sources were placed in the border of the pool, 20-cm above the surface of the water.

Procedure

Following the procedure used by Chamizo, Rodriguez, Espinet, and Mackintosh (2012), three types of trials were used at different points across experiment: Pretraining trials, Training trials and Probe trials. Pretraining trials were conducted with the platform present in different quadrants, but without landmarks available. Training trials had both the platform and landmarks available. In Probe trials only landmarks, but not the platform, were available. The maximum duration of each trial where the platform was present was 90 sec. When the animal reached the platform, it was allowed to stay there for 30 sec. Rats were given 60 s to locate the platform on trials where it was present. Rats that did not locate the platform in 60 seconds were pushed toward the platform where they remained for 30 seconds. On probe trials rats were allowed to swim during 60 s, and then removed from the tank. The inter-trial interval was variable, averaging 12.5 min (range 10-15min). The design of the Experiment is presented in top panel of Figure 1.

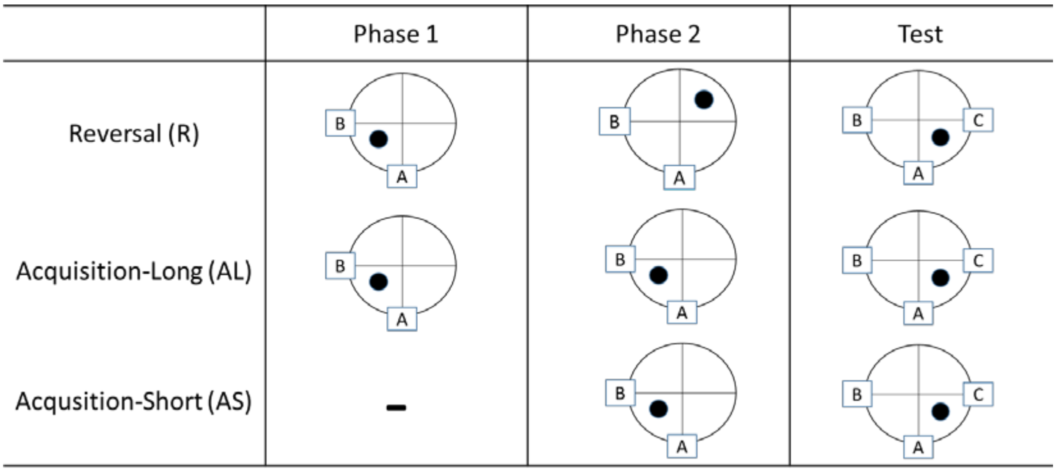
Pretraining *(Days 1-2)*. During pretraining phase all rats received 5 pretraining trials in which they were introduced into the pool with the platform hidden in a different quadrant from trial to trial, without landmarks available. Rats were introduced in the pool from a different position (N, E, S, W) each trial. Two trials were conducted on Day 1, and three on Day 2. Pretraining for group Acquisition-Short was conducted on Days 9 and 10.

Phase 1 *(Days 3-10):* Rats in groups AL and R received 48 training trials over 8 consecutive days (6 trials per day), while rats in group AS remained in their home-cages. As shown in the top panel of Figure 1, the platform was hidden in the middle of the quadrant between landmarks A and B. A probe trial was conducted at the end of each odd day of training.

Phase 2 *(Days 11-18):* The reversal phase was identical to the training phase for all groups. Group AL continued training with the landmark in the AB quadrant, and group AS began training with the landmark in the AB quadrant. In group R the position of the platform was changed, and placed in the quadrant opposite to the A and B landmarks (see Figure 1; see also Lattal et al., 2003, Exp 2).

Test Phase *(Days 19-24):* An additional landmark (C) was introduced in front of landmark B (see Figure 1). The platform was placed in the center of the quadrant defined by landmarks A and C, a place that was new and equidistant from where the platform had been hidden before in all rats. Thirty-six training trials were conducted over six consecutive days (6 per day). During the test phase, probe trials were conducted daily.

Experiment 1



Experiment 2

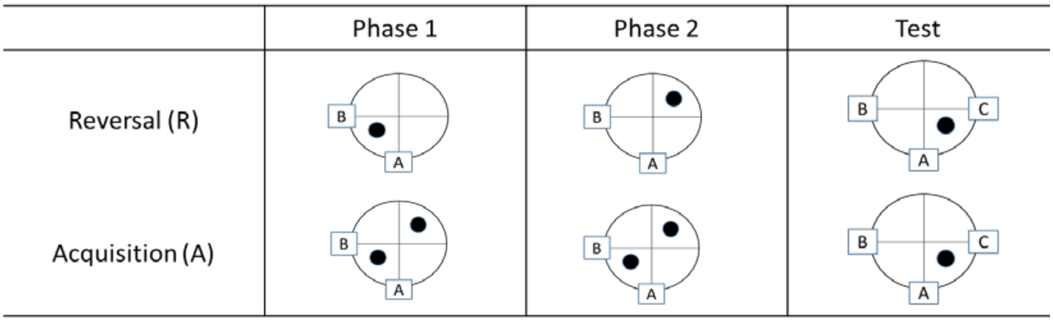


Figure 1: *Experimental designs of Experiment 1 (top panel) and Experiment 2 (bottom panel). Letters represent the landmarks. "A" was square or circle counterbalanced; B and C were fixed or flashing lights counterbalanced.*

Data analysis.

The time that rats spent swimming in each quadrant was recorded during each probe trial. Target quadrants define the quadrant where the platform was hidden at some point of the treatment, regardless of the group. During Acquisition and Reversal Phases, target quadrants were defined by their distance from the AB landmarks, being either close (AB_c) or far (AB_f). During the Test phase, the target quadrant was defined as ABC_new. For the sake of simplicity, only performance in the target quadrants during probe trials is reported. Data were analyzed with Analysis of Variance (ANOVA). Additionally, One-sample T-Tests were conducted comparing the time swimming in each quadrant with the time expected by chance. Confidence intervals on partial-eta squares (95%) were computed using software available in Nelson (2016).

Results and Discussion

Phase 1

Acquisition proceeded uneventfully. Figure 2a presents the mean time spent in each target quadrant during the probe trial conducted at the end of the Phase 1 in groups R and AL (rats in group AS spent this phase in their home cages). Rats in both groups spent more time in the AB_c quadrant, where the platform was hidden in the training trials, than in the AB_f quadrant. A 2 (Group) x 2 (Quadrant, AB_c vs AB_f) ANOVA found a significant main effect of quadrant, $F(1, 13) = 39.56$, MSe = 18.57, $p < .001$, $\eta^2_{\text{p}} = .75$, 95% CI [.39, .85]; no other main effect or interaction was significant, *F*s < 1. The time spent in the AB_c quadrant was higher than that expected by chance (15 sec), in all groups; $t(7) = 3.26$, $p = .014$, $d = 1.15$, 95% CI [.23, 2.18], and $t(6) = 3.06$, $p = .022$, $d = 1.16$, 95% CI [.16, 2.27] for groups R and AL, respectively.

Phase 2

Figure 2b presents the mean time spent in each target quadrant during the probe trial conducted at the end of the second phase in groups R, AL and AS. Performance was consistent with the treatment received by each group, with rats in group R spending more time in quadrant AB_f than in quadrant AB_c, and rats in groups AL and AS spending more time in quadrant AB_c than in quadrant AB_f. A 3 (Group) x 2 (Quadrant, AB_c vs. AB_f) ANOVA found a significant main effect of quadrant $F(1, 20) = 14.30$, $MSe = 37.33$, $p = .001$, $\eta^2_p = .42$, 95% CI [.01, .62]. Of most importance, the Group x Quadrant interaction was significant, $F(2, 20) = 19.06$, $MSe = 37.33$, $p < .001$, $\eta^2_p = .66$, 95% CI [.32, .77]. The main effect of Group was not significant, $F < 1$.

Subsequent analyses conducted to explore the Group x Quadrant interaction found that the simple effect of Group was significant in both quadrant AB_c, $F(2, 20) = 9.54$, $MSe = 37.06$, $p = .001$, $\eta^2_p = .49$, 95% CI [.12, .66], and quadrant AB_f $F(2, 20) = 20.99$, $MSe = 17.33$, $p < .001$, $\eta^2_p = .68$, 95% CI [.35, .79]. Group R spent less time in quadrant AB_c than either group AS (F (1,14) = 10.96, $p = .005$, $\eta^2_p = .43$, 95% CI [.05, .65]) or AL (F (1,13) = 18.27, $p = .001$, $\eta^2_p =$. 58, 95% CI [.15, .75]). Groups AS and AL did not differ F (1,13) = 1.21, $p = 291$. In quadrant AB_f, group R spent more time than either group AS (F (1,14) = 27.37, $p <.001$, $\eta^2_p = .66$, 95% CI [.27, .79]) or AL (F (1,13) = 30.78, $p <.001$, $\eta^2_p = .70$, 95% CI [.30, .82]), while groups S and AL did not differ $F < 1$. Student t tests found that group AL performed above chance in quadrant AB_c, $t(6) = 4.45$, $p=.004$, $d = 1.68$, 95% CI [.51, 3.07], as did group AS, $t(7) = 3.52$, p =.010, $d = 1.24$, 95% CI [.30, 2.31]. Group Reversal performed over chance only in quadrant AB_f, $t(7) = 4.24$, $p = .004$, $d = 1.50$, C95% CI [.47, 2.69].

An additional 2 (Quadrant: Platform vs. Opposite) x 3 (Group) ANOVA was conducted to ensure that all the groups showed equivalent performance at the end of the reversal training phase. Only the main effect of quadrant was significant, *F*(1, 20) = 48.35, *MSe* = 37.33, p < .001, η^2_p = .70, 95% CI [.41, .81]. No other main effect or interaction were significant, largest *F*(2,20) = 1.81, *p* = .18. Though the different groups preferred different quadrants, their preferred quadrant was the quadrant where the platform was located. Animals in group reversal reached the same level of performance in the new location as the animals in the two groups that continued acquisition training.

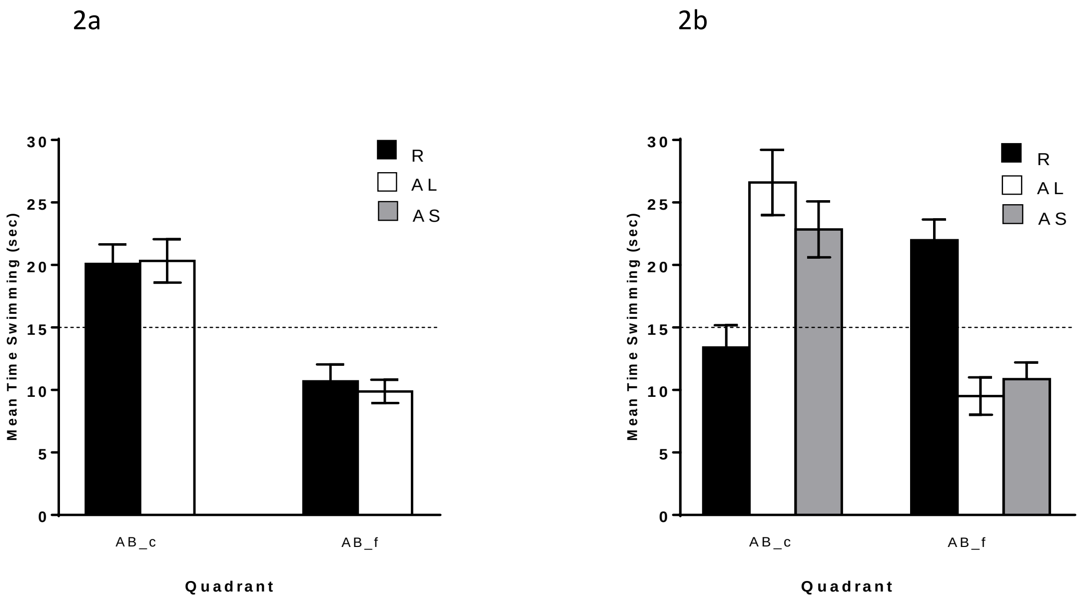


Figure 2a & 2B. *Mean time spent in each target quadrant during the probe trial conducted at the end of the acquisition phase for groups R and AL (Figure 2a), and at the end of the reversal phase for groups R, AL and AS (Figure 2b) in Experiment 1. Brackets represent standard errors of the mean.*

Test

Figure 3 presents the mean time spent in the target ABC_New quadrant during the 2 blocks of 3 probe trials conducted during the test phase for the three groups. There was an effect of Group in the first block, *F*(2, 20) = 5.00, *MSe* = 11.06, *p* = .017, η^2_p = .33, 95% CI [.01, .54]. Group

R learned within the first three trials and spent more time in the correct quadrant than chance, *t*(7) = 2.85, *p*= .025, *d* =1.01, 95% CI [.13, 1.98], and more time than either Group AL *F*(1,13) = 5.18, *p* = .04, η^2_p = .28, 95% CI [.00006, .55], or Group AS, *F*(1,14) = 8.64, *p* = .011, η^2_p = .38, 95% CI [.02, .62]. Performance did not differ from chance for either of Group AS or AL, *p*s ≥ .245. By the second block Groups AS and AL had also learned the position of the platform. All three groups responded more than chance, *p*s ≤ .018, *d*s ≥ 1.22, 95% CI [.21, 2.38], and did not differ from each other, F < 1.

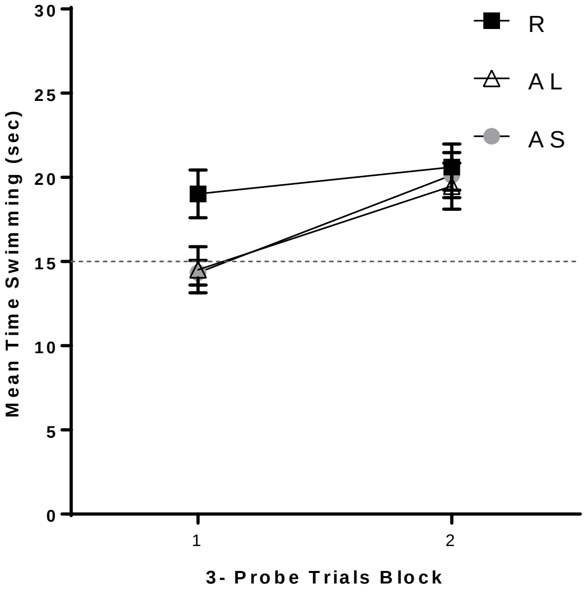


Figure 3. *Mean time spent in the target quadrant ABC_new during the 2 blocks of 3 probe trials conducted during the test phase in groups R, AL and AS in Experiment 1. Brackets represent standard errors of the mean.*

A group that received interference in the form of reversal training before testing shows better learning at test than the groups that were trained with a consistent platform location. Group R shows more evidence of learning in the first block of testing than groups AL and AS. As training progressed all groups reached the same level of performance. Thus, all groups eventually learned the new position of the platform, but acquisition in testing developed faster in group R than in the other two groups. This result is in agreement with the effect reported by Alcalá, Callejas-Aguilera, et al. (2018) with temporal conditioning, suggesting that reversal training boosted attention making acquisition of new learning easier for the group with the previous interference treatment.

It is worth acknowledging that the extended training in Group AL could have supported a strong habit to swim to the phase 2 quadrant, which would retard the acquisition of learning to swim to a new position. Thus, a deficit with respect to group R could reflect a deficit in group AL rather than an advantage in group R. Nevertheless, the amount of training to swim to the phase 2 quadrant in group AS was equal to that of group R, and there were no differences between groups AS and AL on test. Any habit supported by the extended training does not appear to produce any more or less interference than the shorter training received by Group R or AS, with only the former showing an advantage on test.

Overall, these results should be taken with caution. The design of this experiment allowed for group R to learn that the platform could be in different places with respect to the cues at different points of the experiment. Those rats had more experience searching for platforms. That experience could have facilitated learning about the new position of the platform without having to assume that it was the change in reinforcing conditions what facilitated learning. Although the actual position of the platform and the landmarks were both changed from trial to trial for all rats, the relationship between the landmarks and the position of the platform was kept constant before the test in groups AL and AS, and only changed in group R. In the light of this alternative explanation, it is not possible to rule out that facilitation of new learning was due to differential experience with different positions of platform and cues across groups, rather than to a general increase in attention based on interference produced by the reversal.

Experiment 2 was designed to determine the effect of interference on new spatial learning in a situation in which every animal had the opportunity to learn that the platform could be hidden in different places with respect to the cues, but only group R received an interference treatment. Therefore, only in group R should attention be raised and show a facilitation of new learning.

Experiment 2

The goal of Experiment 2 was to show that prior interference facilitates new learning while controlling for the differential experience with the position of the platform across groups. The design of the Experiment is presented in the bottom panel of Figure 1. Group Acquisition (A) was trained with two different platforms simultaneously placed in two different positions of the pool (close and far to the landmarks, the positions in which the platform was placed in group Reversal across phases). To ensure that rats had experienced the two positions of the platform, training during the acquisition phase involved compulsory trials where the rats were directly placed in the platform with the landmarks present. The same procedure was applied to group Reversal (R) with the exception that only one platform was used. This type of latent learning has shown to be effective in learning the location of a platform (Horne, Gilroy, Cuell, & Pearce, 2012; Sutherland & Linggard, 1982), although we are unaware as to whether it has been conducted with two platforms. During the Reversal Phase both groups were allowed free swimming. In group R the platform was placed in the opposite quadrant to the one where it was placed before, whereas rats in group acquisition had both platforms available. Therefore, both groups had the opportunity to learn that the platform could be close or far from the landmarks and by the end of training, both groups had experienced the ambiguity of the platform being placed in two different positions of the pool, but only Group R received the interference training, which should be the critical factor (see Nelson & Callejas-Aguilera, 2007). The test phase was identical to one conducted in the previous experiment with the platform placed in a new position between cue A and the added cue C.

Method

Subjects

Sixteen female Wistar Rats, approximately six months old at the beginning of the experiment, were used. As in Experiment 1, rats had prior experience in a classical conditioning experiment, unrelated to this one, in which they had limited access to food. They were maintained in the same conditions as in Experiment 1.

Apparatus

The apparatus was identical to Experiment 1, with the exception of using two platforms rather than one in the Acquisition group. The two platforms were identical in their dimensions and materials.

Procedure

The procedure was identical to procedure of Experiment 1, except where noted. Pretraining (Days 1-2) was identical to the pretraining phase from Experiment 1.

Phase 1 *(Days 3-10).* All rats received 48 compulsory trials over 8 consecutive days (6 trials per day). During these trials, rats were placed directly in the platform, without requiring them to swim to find it, and they remained on the platform for 30 seconds before being removed from the pool. As shown in the bottom panel of Figure 1, for group A two platforms were hidden in two different locations, equidistant to landmarks A and B, in the quadrant closest to the landmark and the opposite quadrant. Rats were placed in each platform the same number of times counterbalanced. A pseudorandom sequence was created for each day with the only restriction that a position (close or far from the landmarks) could not be repeated more than two times in a row (e.g. CFFCFC, FFCCFC, for first and second training`s days). For group R a single platform was hidden in the quadrant closer to the landmarks. A probe trial of free swimming was conducted at the end of each odd day of training. Probe trials were identical to the ones conducted in Experiment 1.

Phase 2 (Days 11-18). The second phase for groups R and A was identical to the one received by the corresponding groups in Experiment 1, with the only exception that group A had two platforms available on each trial.

Test (Days 19-24). The test phase was identical to the test phase conducted in Experiment 1.

Results and Discussion

Phase 1

Figure 4a presents the mean time spent in each target quadrant during the probe trial conducted at the end of the phase 1 in groups R and A. Rats in both groups spent more time in the AB_c quadrant. This quadrant is the one closer to the landmarks which may account for the preference in Group A, for which two platforms had been trained. A 2 (Group) x 2 (Quadrant, AB_c vs AB_f) ANOVA found a significant main effect of quadrant $F(1, 14) = 33.36$, $MSe = 48.90$, $p < .001$, $\eta^2_p = .70$, 95% CI [.32, .82]. Neither the main effect of Group, nor the Group x Quadrant interaction were significant, *F*s < 1. Student t tests found that both groups spent more time in the AB_c quadrant than expected by chance, t (7) = 2.74, $p = .03$, $d = 0.97$, 95% CI [.10, 1.92] and t(7) = 3.64, $p = .008$, d = 1.29, 95% CI [.33, 2.37] for groups R and A, respectively.

Phase 2

Figure 4b presents the mean time in each target quadrant during the probe trial conducted at the end of the phase 2 in Groups R and A. Group R reversed its performance, spending more time swimming in the quadrant AB_f than in quadrant AB_c. Group A showed a somewhat unexpected similar trend, though in this case the time spent in each quadrant was more similar than in group R. A 2 (Group) x 2 (Quadrant) ANOVA found a significant main effect of Quadrant *F*(1, 14) = 22.02, *MSe* = 41.36, *p* = <.001, η^2_p = .61, 95% CI [.20, .77]. The Group by Quadrant interaction fell just short of significance, *F*(1, 14) = 4.04, *p* = .064. There was no effect of Group, *F* < 1. Subsequent analyses found that the simple effect of Quadrant was significant in group R *F*(1, 7) = 25.48, *MSe* = 36.46, *p* = .001, η^2_p = .78, 95% CI [.24, .88], but not in group A *F*(1, 7) = 3.21, *MSe* = 46.25, *p* = .116, η^2_p = .31, 95% CI [.00001, .63]. Relative to chance, t tests found that group R spent more time in the AB_f quadrant, *t*(7) = 3.81 *p* =.007, d = 1.35, 95% CI [.37, 2.46] and less time in quadrant AB_c *t*(7) = -6.378, *p* < .001, *d* =2.25, 95% CI [.95, 3.83]. Group A's performance did not differ significantly from chance in either quadrant, *t*(7) = 2.17, *p* = .067, *d* =.77, 95% CI [.05, 1.65] and *t*(7) = -1.03, *p* = .337, *d* = .08 95% CI [.08, 2.09]

4a

4b

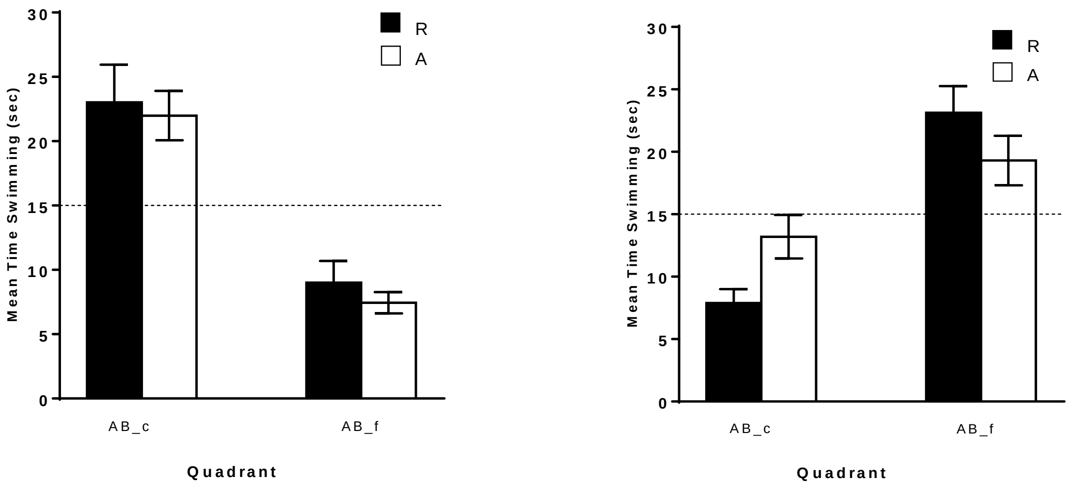


Figure 4. *Mean time spent in each target quadrant during the probe trial conducted at the end of the acquisition phase (Figure 4a), and at the end of the reversal (Figure 4b) for groups R and A in Experiment 2. Brackets represent standard errors of the mean.*

Thus, by the end of the reversal phase both groups showed performance in accordance with their treatment. Group R spent more time searching for the platform in quadrant AB_f, and group A spent more or less equal time in both areas where a platform was located, and more than in the non-platform areas.

Test

Figure 5 presents the mean time spent in the target ABC_New quadrant during the 2 blocks of 3 probe trials conducted during the test phase for both groups. Simple effect of group was significant in the first block, *F*(1, 14) = 5.25, *MSe* = 20.05, *p* = .038, η^2_p = .27, 95% CI [.00006, .54]. While group R learned within the first three trials and spent more time in the correct quadrant than chance, *t*(7) = 2.78, *p* = .027, *d* = .98, 95% CI [.11, 1.94], group A's performance not differ from chance, t(7) = .09, *p* = .92, *d* = .03, 95% CI [-.70, .77]. By the second block Group A had also learned the position of the platform. The groups did not differ on the second block, *F < 1* and both groups responded more than chance, *t*(7) = 5.17, *p*= .001, *d* = 1.83, 95% CI [.68, 3.17] , and *t*(7) = 5.59, *p* < .001, *d* = 1.98, 95% CI [.78, 3.40] for groups R and A, respectively.

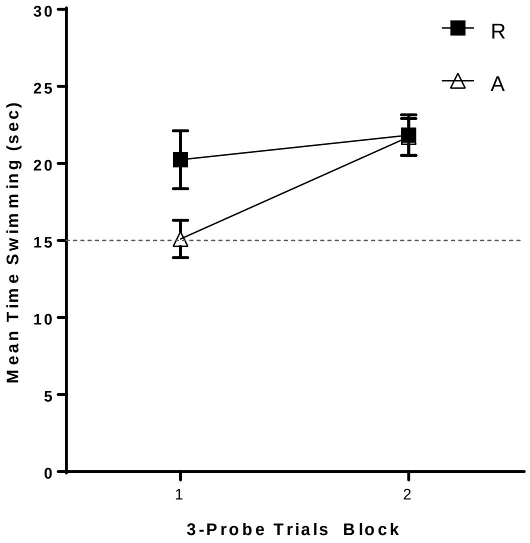


Figure 5. *Mean time spent in the target quadrant ABC_new during the 2 blocks of 3 probe trials conducted during the test phase in groups R and A in Experiment 2. Brackets represent standard errors of the mean.*

The design of this experiment was arranged so that all rats had the experience of the platform being hidden in two different positions during the initial training, though only group R received the interference treatment. As in Experiment 1, this difference turned out to be essential, as learning about the new position of the platform during the final test proceeded faster after the interference treatment.

Exposure to the two platforms in group Acquisition may have produced some ambiguity, something that has been claimed to affect context specificity of the information by itself (Rosas et al., 2006; see also Callejas-Aguilera & Rosas, 2010; but see Nelson & Callejas-Aguilera, 2007).

However, as it was the case in Nelson and Callejas-Aguilera (2007) the effect of interference upon learning surpassed any potential effect that ambiguity alone might have had. There were no controls in this experiment to test the potential effects of simple ambiguity upon new learning, though a cross-experiment comparison with test performance of control groups in Experiment 1 suggests that ambiguity alone had little effect, if any, upon acquisition of new learning. Alternatively, interference seems to produce a clear improvement in performance when rats are exposed to a new situation in which they have to search for the platform in a new position with respect to a new cue.

General Discussion

Two experiments conducted in the Morris water maze found that previous exposure to an interference treatment could facilitate subsequent acquisition of new spatial learning. In Experiment 1, reversal training facilitated learning a new platform position with respect to simple acquisition, regardless of the length of acquisition. In Experiment 2, reversal training facilitated learning about the new position of the platform compared to a group that had similar experience with the platform being placed in different positions of the pool, but that did not have the experience of interference. These results suggest that the reversal treatment facilitates subsequent new spatial learning within the water maze because of the interference it produces.

These results are in agreement with the idea that subjects' attention is boosted when the situation becomes ambiguous, in other words, when the prediction error increases because the learning situation has changed. This increase in attention has been claimed to affect stimulus (Kaye & Pearce, 1984), and context processing (Bouton, 1993; Rosas & Callejas-Aguilera, 2007). More recently, Alcalá, Callejas-Aguilera, et al. (2018) have claimed that this boost in attention may affect anything that is learned subsequently after interference has taken place, not just learning about the context. The present results are in agreement with this latter idea that interference boosts attention generally, so that learning about anything that takes place after interference may be enhanced as well. This idea is not in conflict with earlier reports in the literature, as it reasonable that attention to both discrete stimuli and contexts should be similarly boosted by interference, as well as to any other source of information present within the learning situation.

These results are quite relevant for interpretations of the renewal effect (e.g., Bouton, 1993, 1997). For instance, Bouton (1997) assumes that renewal is caused by extinction boosting the organism's attention to the context in which extinction takes place, so that retrieval of the extinguished stimulus becomes context dependent. The results reported here open the possibility of renewal being a side effect of a general increase in attention that also facilitates context processing. The effect of extinction making acquisition context specific reported by Rosas and Callejas-Aguilera (2006) may be explained in the same way, where attention to the context is a byproduct of a general increase attention produced by the experience of interference.

The facilitation effect found here and in Alcalá, Callejas-Aguilera, et al. (2018) is not necessarily ubiquitous. Alcalá, González, Aristizabal, Callejas-Aguilera, & Rosas (2018) tested whether conditioning of a new stimulus was facilitated by concurrent reversal training in appetitive conditioning. After training a simple CS1+/CS2- discrimination in appetitive conditioning the meaning of the CSs changed for half the rats in a second stage. Within this second phase a new CS (light) was introduced, intermixed with the other two CSs, and signaled the delivery of food. Results showed that the reversal group did not learn about new CS any faster than the no-reversal group. Contrary to expectations, the group exposed to the reversal showed a retardation in learning about the new CS compared to rats that did not receive the reversal. Nevertheless, reversal training led to greater context conditioning, suggesting that the facilitation effects of interference in appetitive conditioning were restrained to context processing, and did affect concurrent learning about a new stimulus. If attention to a new, novel, CS is already at a high value, it may benefit less from an attention-boosting mechanism than a highly familiar context. Thus, the context conditioning enhanced by attention could interfere with cue conditioning (e.g. Alcalá, González et al., 2018), making it difficult to determine the extent to which interference had an effect on the conditioning of the new cue.

In conclusion, this work extends the previous results found in temporal domain in which an interference treatment facilitates subsequent learning, to the spatial domain. The results support the idea that interference leads to a general increase in attention that facilitates learning to more than just the stimuli involved in the interference treatment.

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4. General Discussion

There is a theoretical tradition within the study of associative learning that suggests that changes in the prediction error lead to shifts in organisms' attention to the stimuli that are involved in those situations (Kruschke, 2001, 2003; Mackintosh, 1975; Pearce & Hall, 1980). A related set of theories assume that prediction error produced by the experience with associative interference influences the attention contexts receive, and thus, the role contexts play in retrieval of the information. Along these lines, Bouton (1997) assumes that the ambiguity experiences that associative interference produces, leads the organism to codify ambiguous information together with the context where ambiguity takes place, so that retrieval of ambiguous information becomes context-specific (Bouton, 1997). Rosas, Callejas-Aguilera, Ramos-Álvarez, and Abad (2006) went one step further, suggesting that the experience of associative interference (together with anything that leads the organism to pay attention to the context) makes context-specific retrieval of *all* the information, regardless of the context where the information is acquired (Rosas & Callejas-Aguilera, 2006, 2007). In general terms, these two sets of theories make differential predictions with respect to the role that the increase in the prediction error may have (regardless of whether this increase in the prediction error is produced by associative interference or not). The first set of theories suggests that increases in prediction error lead to an increase in attention to the stimuli that should affect learning about those stimuli (e.g., Mackintosh, 1975; Pearce & Hall, 1980). The second set of theories suggests that associative interference boosts attention to the context, so that facilitation on learning should be restricted to learning about contexts (e.g., Bouton, 1997; Rosas et al., 2006). Alternatively, there are some approaches in the literature suggesting that increases in prediction error may lead to general changes in attention that might facilitate subsequent Learning (e.g., Easdale, Le Pelley, & Beesley, 2018; Hall & Pearce, 1982; see also Schmajuk & Larrauri, 2006).

The experimental series collected in this dissertation were conducted with the goal of exploring the role of associative interference upon concurrent and subsequent new learning. Specifically, this dissertation explored the role of associative interference on new learning about contexts and stimuli in three experimental studies conducted with rats.

The first study included two experiments in rats' appetitive conditioning. The key manipulation was whether or not rats had experience with associative interference. Associative interference was reached by training animals in a discrimination between two stimuli in which CS1 was followed by food and CS2 was not, reversing the relationships with the outcome afterwards. In the first experiment we tested whether experiencing associative interference facilitates a new CS-US relationship that is learned *concurrently* to the interference experience.

At the same time, we tested whether interference facilitates *concurrent* contextual conditioning (Rosas et al., 2006). The first study found that the experience of associative interference enhanced concurrent context conditioning, measured by the increase in magazine approaches in the absence of stimuli. However, there was no evidence of facilitation of concurrent learning about the new CS.

In the second study, we explored the effects of experiencing associative interference on *subsequent* learning in rats' appetitive conditioning. Associative interference was reached with the same procedure used in the first study. Regardless of whether the animals experienced associative interference or not, they were subsequently tested for context and temporal conditioning. Rats being tested for context conditioning received random presentations of the US during the test, while rats tested for temporal conditioning received food at fixed times. The second study did not find facilitation of context conditioning after Reversal Training. Concurrent context conditioning was not behaviourally enhanced by interference either, in contrast to the results of our first study. More interestingly, learning about time was facilitated in the groups exposed to interference rather than consistent training. This facilitation effect was found regardless of temporal interval used (60s or 30s).

Finally, the last study explored whether experiencing associative interference facilitates subsequent spatial learning in a water maze procedure. Animals received initial training in which a platform was located in a particular quadrant of the pool signalled by surrounding beacons. Afterwards, rats either continued with the same conditions, or they received a reversal training where the platform was moved to the pool quadrant opposite to the initial one. In the test phase, all rats were trained with a new position of the platform and a new, additional landmark was added to the pool. Groups with the interference experience learned the new position of the platform quicker than the rats that did not in final test phase. This effect was found while controlling differential lengths of acquisition and equating experience with platforms and beacons in the control conditions.

In summary, experiencing interference facilitated contextual conditioning but not concurrent new learning (Study 1). Facilitation of new of learning was found when this was acquired after interference, although experiencing interference did not enhance contextual conditioning regardless of whether it was tested concurrently of after the interference took place (Study 2). Finally, Study 3 found evidence that the experience of interference facilitates subsequent acquisition of spatial learning.

The results found in the first study supporting the idea of associative interference facilitating concurrent contextual conditioning is somewhat in agreement with the idea that experiencing ambiguity facilitates context processing (Bouton, 1997; Rosas et al., 2006). This is not an infrequent result given that the experience of interference usually produces an increase in context-dependence of information retrieval, which is often interpreted as due to interference leading to an increase in context processing (Bouton, 1997; Nelson, Fabiano, & Lamoureux, 2018; Rosas & Callejas-Aguilera, 2006, 2007). In our study, we found an enhancement of context conditioning shown as an increase in magazine approaches in the absence of stimuli. This pattern of results is in agreement with the idea that the experience of ambiguity increases attention to the context, searching for information that helps the organism to disambiguate the situation (e.g., Bouton 1997; Rosas et al., 2006). However, these data were not replicated in the second study. In none of the two experiments of this study there was evidence of greater context conditioning concurrent or subsequent to reversal training. Considering that the experimental design during the first two phases of training was identical to the design employed in the second experiment of Study 1, the most likely explanation lies on the differences in the statistical power of each study. In agreement with this idea, there is a trend towards a higher responding in the absence of the CS in rats that receive the reversal experience, though this difference did not reach the statistical level of significance. This discrepancy suggests that differences in context conditioning caused by an interference experience are subtle when recorded through magazine approaches in this situation. This weakness is confirmed when differential effects of associative experience in context conditioning are measured sequentially, rather than concurrently. No evidence of an influence of associative interference based on differential context conditioning was found in the first experiment of Study 2, when comparing the two groups that received food at a variable times throughout the test. Although this last result may be considered in agreement with Bouton's (1997) idea that interference makes context-specific only retrieval of ambiguous information, it is in not agreement with results reported in ATCP related research showing that the experience of interference boosts attention to contexts that are even different from the one in which interference took place (e.g., Bernal-Gamboa, Rosas, & Callejas-Aguilera, 2014; Rosas & Callejas-Aguilera, 2006, 2007;). Taking into account that the effect of interference in context conditioning may be fairly weak, a plausible explanation of the discrepancy between the results of these studies comes from the lack of sensitivity of the dependent variable used in these studies. In these experiments, context conditioning was inferred from changes in the pattern of responses in the interval-time between CSs or between USs. Considering these conflictive results, it seems that magazine entries is not a sensible measure to test context conditioning, particularly when context conditioning could imply a complex pattern of behaviours involving different kind of responses including rearing and other exploratory behaviours that may be in conflict with magazine entries (e.g., Carrive, 2000). Future studies should include more direct measures of attention to the contexts, akin to the ones recently reported in studies conducted with humans (e.g., Aristizabal, Callejas-Aguilera, Ramos-Álvarez, & Rosas, 2016; Easdale et al., 2018; Vadillo, Orgaz, Luque, & Nelson, 2016).

The other target result from the first study suggests that learning about the new CS was not facilitated in rats exposed to concurrent reversal training. If anything, acquisition of the group exposed to interference seems to be slower than acquisition in the control group, though this result was actually an artefact of the increase in magazine approaches during the intertrial interval in the group that received the associative interference experience. Nevertheless, this null result should be taken with caution. First, the experience of associative interference enhanced context conditioning. Context conditioning may have counteracted any potential benefits associative interference may have had upon the new learning. Context conditioning has been found to block learning about a new CS (e.g., Bouton, Rosengard, Acenbach, Peck & Brooks, 1993; Randich & Ross, 1984). This interference may be especially plausible when the same dependent variable is used to record learning about the context and the CS, as it was the case here. Second, with the goal of making the new CS as different as possible from the CSs used in the discrimination training, the new CS was a light. Increases in attention to the light will lead rats to display orienting responses to the CS (Kaye & Pearce, 1984) that may interfere with the magazine approach used in this experiment as a measure of conditioning (Wilson, Boumphrey, & Pearce, 1992). Moreover, as the CS was new, attention to it may be at the asymptotic level regardless of the previous experience with other stimuli (Schmajuk & Larrauri, 2006). Taken together, the results discussed so far suggest that there may be grounds to think that context processing increases after the interference experience, as ATCP suggests, though such an increase did have a weak effect in context conditioning when evaluated under the parameters used in our studies. As for the influence of interference in new learning, the results of Study 1 were inconclusive, as there is no way to know whether the null effect reported in that study is due to a lack of effect of interference on new learning, or to the specific choice of task, parameters, and stimuli that might had counteracted any facilitation effect on learning that the experience of associative interference may have. To avoid this potential conflict, Studies 2 and 3 tested the effects of associative interference in new learning that took place after the experience of associative interference.

The pattern of results about new learning in successive studies was quite consistent. Learning about time was facilitated in Study 2, and spatial learning was facilitated in Study 3 after experiencing associative interference. There were several procedural changes in Studies 2 and 3 that may have simplified the detection of the influence of associative interference on new learning. In Study 2, this influence was explored by the use of temporal conditioning, rather than learning about a new CS. The use of a different type of learning should help to avoid transfer or generalization from previous learning, as it is usually found in learning-to learn effect designs (Kehoe , Morrow, & Holt, 1984; Ricker & Bouton, 1986). In addition, in Study 1, new learning was established concurrently to reversal training. Adding a new stimulus to the discrimination reversal situation could have increased the difficulty of the discrimination, and it might have led to unintended different testing conditions between groups. In Study 2, learning conditions at testing were identical for both groups, with the only difference being the previous experience of interference or not. These results fit with the explanation in terms of associative interference prompting an increase in the exploratory mechanism of attention, enhancing an explorative pattern of behaviour that facilitates subsequent learning (Le Pelley, Mitchell, Beesley, George, & Wills, 2016). Interestingly, a similar pattern of results was recently reported in human participants. Nelson et al. (2018) found that the experience of extinction enhances subsequent context conditioning, as well as temporal conditioning, as it was the case here. Participants were trained in a video game in which sensor predicted the attack of a spaceship such that they had to respond preparing the upcoming attack. Afterwards, two groups of participants received either the extinction of the previous sensor or no extinction in alternative second context. A final test was conducted in which the attacker was presented unsignalled in the second context. Conditioned responses during the test phase developed faster in the group that was previously exposed to extinction, suggesting greater context conditioning. Moreover, participants who experienced extinction also showed better temporal discrimination predicting the upcoming attack. As Nelson et al. (2018) study was conducted in human instrumental conditioning, it is difficult to pin down the reasons for the difference between their results (facilitation of both, context and temporal conditioning) and ours (facilitation of temporal conditioning, but not of context conditioning). In addition, Nelson and his colleagues used extinction rather than discrimination reversal as interference treatment. Moreover, acquisition and extinction were conducted in context A and context B respectively, while in our study all phases were conducted within the same context. However, taken the results of all the studies together, it seems that they point towards the idea that the experience of interference facilitates subsequent learning, at least to some extent. This facilitation may involve learning about contexts, but also about other features of the environment, such as temporal regularities in the US presentations. This pattern of results is also consistent with the reports showing that the experience of uncertainty facilitates subsequent learning in human participants, increasing the time that people spend looking at the target cues (Easdale et al., 2018), and with those showing that rats exposed to higher uncertainty explore more the elements inside the learning environment (Robinson, Anselme, Fischer, & Berridge et al., 2014).

The third study of the dissertation extended these results to the spatial learning domain, suggesting that the faciliatory effect of experiencing associative interference may be a general effect. Learning conditions in Study 3 followed the same experimental logic used in Study 2, so that the test was conducted after the interference experience, rather than concurrently to it. Experiment 1 of Study 3 used two different control groups. Animals in the control groups received different lengths of training (long vs short) with the idea of equating with the experimental and control groups in the experience with the pool (long training control), and in the experience with simple acquisition training (short training control). Results during the test phase pointed out that animals exposed to long-acquisition training (sixteen days of identical learning conditions) developed a trend to swim according to their previous experience during the first session of the test phase (see also Ramirez-Amaya, Balderas, Sandoval, Escobar, & Bermúdez-Rattoni, 2001). Acquisition of the habit to swim according to old learning conditions may have retarded subsequent new learning, so that the results of this experiment may be explained more by a retardation of learning in the control group, than by facilitation of learning in the experimental group. However, no retardation was found in the control group that received short-acquisition (eight days of training), giving support to the idea that the experience of associative interference facilitates new learning.

However, the results obtained with the long-acquisition group open an interesting possibility that might be worth to explore in the future. The length of training has been found to have important effects in what is learned, and in what is learned about. For instance, we have seen that contextual dependence of information depends on the level of training when contexts are redundant (León, Abad, & Rosas, 2010; León, Callejas-Aguilera, & Rosas, 2012). Additionally, extended training seems to be a critical factor for goal-directed responses becoming habits, being insensitive to subsequent reward devaluation (e.g., Adams, 1982). Thus, a potential development of this line of research would be to explore whether extended training under consistent conditions may produce a decrease in the use of the attentional exploratory mechanism, and in which conditions overtraining may lead to a retardation or facilitation of subsequent learning. There are some results in the literature suggesting that extending consistent learning may facilitate subsequent new learning, rather than impair it. For instance, animals who received overtraining developed subsequent extinction faster than animals that did not receive overtraining (Ishida & Papini, 1997; North & Stimmel, 1960). In this effect, known as the Overtraining Extinction Effect (OEE), animals showed a similar asymptotic level of performance at the end of the acquisition phase, regardless of whether they had been overtrained or not (overtraining was defined by the number of training sessions conducted after the asymptote of performance has been reached). However, the rate of extinction had a direct relationship with the number of training sessions. A similar idea is drawn from the Overtraining Reversal Effect (ORE), in which animals who received overtraining in a discrimination between two stimuli, showed a facilitation of learning when the discrimination is subsequently reversed, relative to a control group of animals that were not overtrained with the initial discrimination (Ishida & Papini, 1997; Reid, 1953; Richman, Knoblock, & Coussens, 1972). Taking together, these contradictory results suggest that there is a need for a future theoretically guided exploration of the differential effects of overtraining in attention, and in subsequent learning.

Together with the influence of the length of consistent training on facilitation and retardation of subsequent learning, the duration of the experience with the associative interference treatment should be an important issue to take in account. We have been assuming throughout this dissertation that changes in the prediction error lead to changes in attention (Bouton, 1997; Pearce & Hall, 1980; Rosas et al., 2006). However, as associative interference training advances, prediction error is also progressively corrected. Thus, there will be a point in the associative interference training in which animals have already learned to expect the current outcomes. At that point, prediction error will disappear, there will be no conflict, and thus the attentional exploration mechanism should not be longer in effect. Looking at the data from the three studies reported here, we can see that groups reversal had successfully reversed the initial discrimination by the end of the interference phase. However, subsequent facilitation of learning seems to suggest that the level of interference did not reach the point in which it had no longer effect on attention. This is probably due to the differences between learning and performance. Take in mind that even when animals show similar levels of performance, subsequent rates of learning were susceptible to be altered (e.g., OOE or ORE), indicating that an asymptote of performance does not necessarily involves asymptotic learning.

In general terms, it seems safe to assume that the attentional mechanism of exploration should depend on uncertainty and, thus, on the level of training under stable conditions, even though at this point it is not clear which is the level of training at which the effects of uncertainty disappear. Meanwhile, the attentional mechanism of exploitation will depend on the meaning of the CSs and the context, and should not be affected by the level of training once learning has stablished (e.g. León et al., 2010; Lucke, Lachnit, Koening, & Uengoer, 2013; Preston, Dickinson, & Mackintosh, 1986). In that sense, AAB Renewal has been found to be attenuated by an increase on the number of extinction trials more easily than ABA renewal, a situation in which the contexts are informative with respect to whether the CS is followed by the US or not (e.g., Rosas, García-Gutiérrez, & Callejas-Aguilera, 2007; Tamai & Nakajima, 2000; see also García-Gutiérrez, Rosas, & Nelson, 2005, for a related result concerning the reinstatement effect). Although this discussion may be seen as speculative at this point, it opens a potentially interesting development for this kind of research.

Another interesting thought comes from the manipulations used at testing in Study 3. In the test phase, a novel beacon was introduced as the key to solve the new spatial learning problem. The introduction of the new stimulus increased the novelty of the situation and then should increase the attention received by this stimulus as well (Schmajuk & Larrauri, 2006). One of the potential explanations for the null influence of associative interference on CS-US new learning in Study 1 was that the level of attention to a new stimulus should be high regardless of the previous experience. According to this rationale, the increase of attention might have been similar for all the groups in the spatial learning situation, but only the group exposed to the interference experience showed facilitation of subsequent learning. Most likely, the difference in the results of Studies 1 and 3 comes from the fact that in Study 1 the animal only had to learn about the new stimulus, while in Study 3 attending to the new stimulus was not enough to solve the spatial problem. Solving the spatial problem needed of both, paying attention to the new stimulus, but also to learn about a new relationship between the position of the platform, and the combination of the new stimulus and an old one. At any rate, this difference may show a limitation of Schmajuk and Larrauri (2006) explanation of these results.

Taking in account the evidence discussed so far, it seems quite safe to conclude that experiencing of associative interference can have a beneficial impact upon acquisition of new learning. This benefit is presumably due to a hypothetical increase in attention allegedly produced by associative interference. However, as plausible as this latter interpretation may be, this is not the only one that needs to be considered. For instance, Kehoe and Holt (1984) found that conditioning of one CS facilitates subsequent conditioning of a different CS. This effect survived extinction of the first CS, and has been interpreted as a learning-to-learn effect (Kehoe et al., 1984, Ricker & Bouton, 1986). The learning-to-learn effect seems to be specific to the same type of learning (i.e., CS conditioning), although learning can be found to transfer across cues of different modality (Kehoe, Morrow, & Holt, 1995). This idea could be easily applied to the results of Study 3, though it will need of additional assumptions to be applied to the results of Study 2. In the case of Study 2, the effect of reversal a discrimination between two CSs is found on learning about temporal conditioning. Thus, it would need to be assumed that learning-to-learn is found within procedures and stimuli that are quite different. Additionally, the explanation in terms of learning-to-learn would confront the difficulty of explaining why this transfer effect is nor found after simple acquisition in Studies 2 and 3. More properly, even if we would assume that there may be a learning-to-learn effect in the acquisition controls of Studies 2 and 3 that went undetected because those studies did not include a naïve control, it would be difficult to explain why the experience of interference produces a differentially higher effect.

An alternative explanation for the effects found in the spatial learning study may come from the specific experimental design employed. A large body of evidence suggest that successive increases in the difficulty of training facilitates learning of difficult discriminations. This pattern of results is known as the easy-to-hard effect, commonly found in perceptual learning (e.g. Lawrence, 1952; Liu, Mercado, Church, & Orduña, 2008; Moreno-Fernández, Ramos-Álvarez, Paredes-Olay, & Rosas, 2012). In Study 3, rats in groups Reversal learned first one specific relationship between the cues and the platform, and then they had to change their preference during the second phase. Finally, in the target test phase, conditions of learning changed again. Meanwhile, group Acquisition only had to learn a specific relationship until the final test phase. This difference in the sequence of training may have played a role on the final results, as the training received by groups Reversal may have lead them to pay more attention to environmental cues. Indeed, this approach is compatible with the idea of associative interference boosting subjects' attention. Along these lines, it could be suggested that easy-to-hard, learning-to-learn, and the facilitation effect reported in these experiments may be all based on changes in the attentional mechanism of exploration that facilitate subsequent learning. This idea may seem speculative at this point, but it sure seems to be an idea worth to explore further in the future.

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5. Conclusions

Taking together the experimental results of this dissertation, it seems reasonable to suggest that experiencing associative interference can facilitate new learning. This facilitation may be shown as learning about the context, or about new relationships in the environment.

The results reported in this dissertation are quite relevant for attentional interpretations of contextual dependence of information. Context-switch effects have been claimed to be based on attentional changes produced as a consequence of the experience of ambiguity (e.g., Bouton, 1997) or of other factors modulating the attention contexts receive (Rosas, Callejas-Aguilera, Ramos-Álvarez, & Abad, 2006). According to the results reported here, attention to the contexts in situations of ambiguity may be understood as a by-product of a general increase of attention produced by the experience of interference that may activate the attentional exploration mechanism (Le Pelley, Mitchell, Beesley, George, & Wills, 2016). This pattern of results suggests that both, retrieval (Bouton, 1997) and ATCP theories (Rosas et al., 2006) might need to be reformulated with respect to the role attention plays in their theoretical expositions. However, these theoretical changes should be taken with caution, considering that there are still boundaries in the effects of associative interference that are yet to be explored.

As a general conclusion, the experiments collected in this dissertation support the idea that experiencing associative interference facilitates subsequent learning about new relationships, suggesting that this experience may lead to an increase in the attention the organism pays to anything that happens in the situation. This general conclusion was based in the following specific results and conclusions:

1- Associative interference produced by the experience of reversal discrimination during appetitive conditioning enhances concurrent, but not sequentially learned context conditioning, at least under the specific parameters used in this set of studies.

2- Associative interference produced by discrimination reversal training facilitates subsequent new learning about time and space, but it did not facilitate concurrent learning about a new CS-US relationship.

3- The effect of associative interference upon new learning seems congruent with the idea that increases in the prediction error lead to a general increase in the attentional mechanism of exploration that facilitates subsequent learning.

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6. Resumen Extendido

Análisis del efecto de cambio de contexto sobre la recuperación de la información

El papel del aumento en el error de predicción en el procesamiento de la información.

6.1 Introducción

El aprendizaje es considerado un proceso que produce un cambio relativamente permanente a través de la experiencia en el mecanismo subyacente al comportamiento de los organismos (e.g., Anderson, 1995). Dentro de la perspectiva asociativa, el aprendizaje se desarrolla a través del establecimiento de asociaciones entre los diferentes eventos que se suceden en el ambiente, siendo posible establecer asociaciones entre un estímulo y su consecuencia futura (Pavlov, 1927). Igualmente, pueden establecerse asociaciones entre una determinada respuesta y la consecuencia que lleva aparejada (Skinner, 1937). Adquiriendo de esta forma la habilidad de anticipar la presencia de determinadas consecuencias, activando un complejo entramado de asociaciones entre todos los elementos involucrados en la situación de aprendizaje (Gámez, León, & Rosas, 2017). La mayoría de las teorías de aprendizaje asociativas sostienen que el aprendizaje se produce cuando el organismo recibe algo sorprendente (Kamin, 1965); bien sea porque no espera recibir nada o porque recibe algo diferente a lo esperado. Esta discrepancia ha sido cuantificada por los modelos de aprendizaje asociativo a través del error de predicción. De esta forma, el aprendizaje puede ser concebido como una disminución del término error entre lo que el organismo espera y el organismo recibe (e.g., Rescorla & Wagner, 1972).

Considerando qué cuando el organismo recibe algo diferente a lo esperado, se produce una alteración en el término error, una de las formas posibles de modificar las expectativas del animal es a través de la interferencia asociativa. La interferencia asociativa se produce cuando el significado de un estímulo cambia a lo largo del aprendizaje (Polack, Jozefowiez, & Miller, 2017). Entre los procedimientos de interferencia se encuentran la extinción, la inhibición latente, o la discriminación inversa, entre otros (Miller & Escobar, 2002). Alcanzar una mejor comprensión acerca de cómo el organismo afronta las distintas situaciones de interferencia asociativa, se ha convertido durante décadas en objeto de estudio para los modelos de aprendizaje asociativo.

Los estudios sobre los mecanismos que subyacen al aprendizaje en situaciones de interferencia han destacado el importante papel que puede desempeñar la *atención* como determinante de las asociaciones que se favorecerán, así como entre qué estímulos tendrán lugar (Mackintosh, 1975; Pearce & Hall, 1980). De esta forma, la interferencia asociativa modula la atención de los organismos hacía los diferentes elementos implicados en la situación de aprendizaje, favoreciendo el establecimiento de asociaciones entre ellos. Una de las propuestas con mayor repercusión es el modelo atencional asociativo de Pearce and Hall (1980). Dichos autores predicen que "*los malos*" predictores de la consecuencia recibirán mayor atención por parte de los organismos (c.f., Mackintosh, 1975); en otras palabras, aquellos estímulos para los que el error de predicción es grande, como ocurre en un procedimiento de extinción, recibirán mayor atención (Kaye & Pearce, 1984). Propuestas más recientes toman en consideración ésta perspectiva, y proponen que en situaciones de incertidumbre en los organismos se activa un mecanismo de exploración atencional con la finalidad de reducir la incertidumbre presente (Le Pelley, Mitchell, Beesley, George, & Wills, 2016).

Otros modelos sostienen que el aumento de la atención es más generalizado, y predicen que la atención también es dirigida hacía el contexto en el cual el aprendizaje tiene lugar. En esta línea, Bouton (1993, 1997), expone que la información ambigua es codificada como dependiente del contexto, explicando de esta forma una larga serie de fenómenos relacionados con la presencia de interferencia asociativa, como son la renovación o recuperación espontánea (Bouton & Bolles, 1979; Rosas & Bouton, 1997), y cuya explicación supusieron problemas serios a los modelos clásicos del aprendizaje asociativo (Bouton, 1994). En cualquier caso, la propuesta teórica de Bouton no está exenta de algunos problemas y resultados contradictorios. Rosas, Callejas-Aguilera, Ramos-Álvarez, y Abad (2006) propusieron la *Teoría Atencional del Procesamiento Contextual* (TACP) como una extensión de la teoría de Bouton, en un intento de resolver dichos problemas. La TACP parte de una asunción básica: cuando un contexto es atendido toda la información será codificada como dependiente del mismo, independientemente de su significado o valencia (Rosas & Calleja-Aguilera 2006; 2007). Los factores claves para que la atención sea dirigida hacía el contexto son la ambigüedad en la situación de aprendizaje y el valor subjetivo del contexto (Alcalá, Callejas-Aguilera, & Rosas., 2018). Bajo esta perspectiva, la ambigüedad en la situación provoca que información no ambigua sea vulnerable ante un cambio de contexto (Bernal-Gamboa, Rosas, & Nieto, 2018). Interesantemente, el aumento de la atención hacía el contexto y por ende la dependencia contextual de la información, no se circunscribe al contexto donde la ambigüedad tiene lugar, sino que se transfiere a diferentes contextos y tareas de aprendizaje diferente (Bernal-Gamboa, Callejas-Aguilera, & Rosas, 2014; Rosas & Callejas-Aguilera, 2006).

Estos últimos resultados sugieren que la atención podría no ser específica al contexto donde tiene lugar la interferencia, sino que podría tratarse de un aumento más general de los recursos atencionales, que incluso afectan a diferentes tipos de tarea y por lo tanto podría afectar a cualquier elemento involucrado dentro de una determinada situación (e.g., Schmajuk & Larrauri, 2006). En esta línea de razonamiento, algunos resultados apuntan a que la experiencia de información interferente afecta a la velocidad de aprendizajes posteriores (Courville, Daw & Toureztky, 2006), lo que podría subyacer a la activación de un patrón exploratorio atencional (Le Pelley et al., 2016).

En resumen, considerando el marco teórico brevemente expuesto en la introducción, la presencia de interferencia debería aumentar la atención hacía el contexto acorde a la propuesta de la TAPC, y de esta manera debería facilitar el aprendizaje acerca del contexto (Rosas et al., 2006). Sin embargo, teniendo en cuenta qué al experimentar interferencia, también se ve afectada la tasa de aprendizajes posteriores, podría representar un incremento de atención más inespecífica y que activará un patrón exploratorio, incluso facilitando la adquisición de nuevos aprendizajes (Le Pelley et al., 2016). Con el objetivo general de explorar la experiencia de interferencia se han realizado tres estudios experimentales con ratas con los siguientes objetivos e hipótesis.

6.2 Resumen Trabajos empíricos

6.2.1 Objetivos e hipótesis generales

Objetivos e hipótesis General

Objetivo General: Explorar el efecto de experimentar interferencia asociativa sobre el condicionamiento contextual y la adquisición de nuevos aprendizajes en ratas.

Hipótesis General: De acuerdo a los principios de la ATCP, la interferencia debería aumentar la atención hacía el contexto, favoreciendo el fortalecimiento de la asociación entre el contexto y la consecuencia (Rosas et al., 2006). Sin embargo, no debería facilitar el aprendizaje acerca de nuevas claves. Alternativamente, si la interferencia provoca un aumento más general de los recursos atencionales, favoreciendo un patrón de exploración en los animales, entonces deberían verse facilitados nuevos aprendizajes después de experimentar un tratamiento de interferencia (e.g., Le Pelley et al., 2016).

6.2.2 Objetivos e Hipótesis específicas y estudios empíricos

Estudio 1

Objetivo: Evaluar el efecto que tiene un tratamiento de interferencia asociativa sobre el condicionamiento posterior de una nueva relación clave-consecuencia y sobre el contexto, empleando una tarea de condicionamiento apetitivo en ratas.

Hipótesis: De acuerdo a la TAPC una situación de discriminación inversa debería aumentar la atención hacía el contexto favoreciendo el condicionamiento contextual, pero no el condicionamiento acerca de un nuevo estímulo. Contrariamente, si el incremento de la atención es generalizado, se espera encontrar una facilitación tanto en el aprendizaje acerca del contexto como del estímulo.

Con este objetivo realizamos dos experimentos de condicionamiento apetitivo en ratas en los que se evaluó el efecto de experimentar interferencia asociativa sobre el aprendizaje de nuevas relaciones estímulo-consecuencia y contexto-consecuencia. En la primera fase se realizó un entrenamiento de discriminación simple, donde el Cs1 estuvo seguido de comida, y el Cs2 se presentó en ausencia de ésta. En la segunda fase, para la mitad de los animales se invirtió la contingencia entre cada uno de los estímulos con la consecuencia, manteniéndose constante para la otra mitad. Además, de forma concurrente se introdujo un nuevo estímulo Cs3 seguido de comida. Los resultados mostraron que el aprendizaje sobre el nuevo estímulo no fue facilitado en el grupo expuesto a interferencia, incluso éste grupo parecía mostrar una menor tasa de aprendizaje en comparación al grupo sin interferencia. Al mismo tiempo, el grupo expuesto a interferencia mostró mayor condicionamiento contextual, medido a través de un incremento en el número de entradas en ausencia de estímulos. El incremento del condicionamiento contextual en el grupo expuesto a interferencia se confirmó en un segundo experimento ampliando la muestra de animales por grupo. La facilitación en el condicionamiento contextual apoya la predicción de que la interferencia aumenta la atención al contexto, facilitando consecuentemente el condicionamiento contextual (Rosas et al., 2006). Asimismo, la falta de facilitación sobre el nuevo estímulo podría suponer una limitación a un aumento general de la atención, aunque hay que considerar que el condicionamiento contextual puede interferir sobre la adquisición del estímulo, dificultando la extracción de conclusiones acerca del papel de la interferencia sobre nuevos aprendizajes.

Estudio 2

Objetivo: Evaluar si la exposición a una situación de interferencia asociativa facilita el aprendizaje contextual posterior, así como el condicionamiento temporal con un procedimiento de condicionamiento apetitivo en ratas.

Hipótesis: Si el aumento de la atención producido por la interferencia es específico al contexto, debería facilitar el condicionamiento contextual posterior, pero no un nuevo tipo de aprendizaje en condicionamiento temporal (Rosas et al., 2006). Alternativamente, si el aumento de la atención es más general, debería facilitar ambos tipos de aprendizaje, tanto acerca del contexto, como el condicionamiento temporal posterior a la fase de interferencia.

Dos estudios realizados con ratas en condicionamiento apetitivo exploran el papel de experimentar interferencia asociativa sobre el aprendizaje posterior, ya sea acerca del contexto o aprender una discriminación temporal. Los animales fueron expuestos a una fase de discriminación entre dos estímulos, Cs1 y Cs2, el primero iba seguido de comida mientras que el segundo no. En la fase siguiente, para los animales a interferencia la contingencia cambió entre los estímulos, manteniéndose constante para los grupos sin interferencia. En la fase test, se dividieron los grupos recibiendo un reforzamiento acorde a un intervalo de tiempo variable, valorando el aprendizaje acerca del contextual o presentando el reforzador acorde a un intervalo de tiempo fijo sesenta segundos, midiendo su discriminación temporal. Los resultados mostraron que no hubo diferencia sobre el aprendizaje contextual, independientemente de haber sido previamente expuestos a interferencia o no. Sin embargo, el grupo expuesto a interferencia mostró una facilitación en la discriminación temporal respecto al grupo control. Un segundo experimento fue realizado, replicando los resultados obtenidos en el experimento con un intervalo de tiempo 60 segundos, además de extenderlo a una discriminación temporal con un intervalo de 30 segundos. Los resultados apoyan la idea de que la interferencia podría aumentar la atención de forma general, facilitando nuevos aprendizajes que ocurren tras ser expuestos a la interferencia, en este caso facilita la discriminación temporal. Al mismo tiempo suponen algunas limitaciones acerca de la facilitación del condicionamiento contextual. La discrepancia respecto a los resultados del estudio 1 apuntan a que se trata de un efecto débil, al menos bajo los parámetros y condiciones de los estudios llevados a cabo.

Estudio 3

Objetivo: Evaluar los efectos de experimentar interferencia sobre la adquisición de un nuevo aprendizaje utilizando una tarea de aprendizaje espacial en ratas.

Hipótesis: Si la experiencia de interferencia asociativa facilita nuevos aprendizajes, los animales expuestos a una situación de interferencia deberían mostrar una facilitación en la adquisición de nuevas distribuciones espaciales en comparación a animales no expuestos a situaciones de interferencia.

Dos experimentos realizados con ratas exploraron la exposición a interferencia sobre la adquisición de nuevos aprendizajes en una tarea de aprendizaje espacial utilizando una piscina de Morris. En una primera fase de entrenamiento, todos los animales experimentaron que la plataforma se situaba en un determinado cuadrante respecto a las claves. Durante la segunda fase las contingencias de aprendizaje cambiaron para el grupo expuesto a interferencia, mientras que se mantuvieron constantes para los grupos sin interferencia. En la fase test, se añadió una nueva clave, cambiando la posición de la plataforma relativa a la nueva clave, generando de esta manera una situación similar de aprendizaje para todos los animales. Los resultados encontrados mostraron que el grupo expuesto a interferencia exhibió mayor rapidez en la adquisición de las nuevas condiciones de aprendizaje. Estas diferencias fueron evidentes independientemente del nivel de experiencia con condiciones de aprendizajes constantes en los grupos no expuestos a interferencia. En un segundo experimento se controlaron que los animales recibieran similar experiencia entre la plataforma y claves, destacando que la plataforma podría estar en diferentes posiciones relativas a las claves, pero únicamente un grupo experimentó interferencia en dicho aprendizaje. Nuevamente, el grupo expuesto a interferencia mostraba una facilitación en la adquisición de las condiciones espaciales en la fase test. El patrón de resultados apoya la idea que la experiencia de interferencia aumentaría la atención de los animales, facilitando la adquisición de una nueva distribución espacial en aprendizaje espacial.

6.3 Conclusiones

Tomando en consideración los experimentos expuestos durante la tesis sugieren que la exposición a interferencia asociativa podría facilitar la adquisición de nuevos aprendizajes. Aunque bajo ciertas condiciones experimentales, se observa una facilitación contextual que apoya las predicciones de la TACP (Rosas et al., 2006), en otras ocasiones se encuentra una facilitación de nuevos tipos de aprendizaje, tanto en el aprendizaje espacial como el temporal. Éste patrón de resultados puede ser integrados bajo la perspectiva de un incremento del patrón atencional de exploración (Le Pelley et al., 2016). Considerando que nuevos aprendizajes son facilitados, el aumento de la atención producido por la interferencia no sería tan específico al contexto como presupone la TAPC (Rosas et al., 2006), lo cual supondría una reformulación de la teoría. En cualquier caso, las limitaciones presentadas en los experimentos hacen necesario más información acerca del efecto de la interferencia asociativa sobre nuevos aprendizajes. Esta conclusión general puede ser descompuesta en tres resultados y conclusiones específicas:

1- La experiencia de interferencia asociativa producida por la discriminación inversa facilita el condicionamiento contextual cuando es presentado de forma concurrente a la presencia de interferencia. Sin embargo, no facilita el condicionamiento contextual cuando es presentado de forma posterior a la interferencia, al menos teniendo en cuenta los parámetros utilizados en estos estudios.

2- La experiencia de interferencia asociativa generada por la discriminación inversa facilita un aprendizaje posterior, ya sea aprendizaje temporal como espacial. Sin embargo, no facilita la adquisición de nuevas relaciones EC-EI cuando son presentadas de forma concurrentemente a la exposición de interferencia.

3- El efecto de la interferencia asociativa sobre nuevos aprendizajes es congruente con la idea de que el incremento en el error de predicción produce un aumento inespecífico de los recursos atencionales, activando un patrón de exploración que facilita nuevos aprendizajes.

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