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Of Rats and People: A Select Comparative Analysis of Cue Competition, the Contents of Learning, and Retrieval

Juan M Rosas
Universidad de Jaén, España
A Matías Gámez
Universidad de Cádiz, España
Samuel P León
Universidad Internacional de la Rioja, España
Gabriel González Tirado
Universidad de Jaén, España
J Byron Nelson
Universidad del País Vasco, España

Abstract

Select literature regarding cue competition, the contents of learning, and retrieval processes is summarized to demonstrate parallels and differences between human and nonhuman associative learning. Competition phenomena such as blocking, overshadowing, and relative predictive validity are largely analogous in animal and human learning. In general, strong parallels are found in the associative structures established during learning, as well as in the basic phenomena associated with information retrieval. Some differences arise too, such as retrospective evaluation, which seems easier to observe in human than in nonhuman animals. However, the parallels are sufficient to indicate that the study of learning in animals continues to be relevant to human learning and memory.
Key words: associative learning, cue competition, contents of learning, retrieval processes, comparative psychology, humans, animals.

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Novelty and Significance

What is already known about the topic?

- Despite some common roots, human and nonhuman learning and memory research has largely evolved separately during the last decades.
- The separate evolution of animal and human learning and memory research may give the impression that they are independent, and findings and ideas from one field are of little interest to the other.

What this paper adds?

- The paper reviews select literature regarding cue competition, the contents of learning, and retrieval processes in human and nonhuman associative learning.
- The paper highlights strong parallels between human and nonhuman animals in cue competition phenomena, in the associative structures established during learning, and in the basic mechanisms of retrieval.
- Although differences arise, such as retrospective evaluation which is easier to find in human than in nonhuman animals, parallels show that the study of animal learning continues to be relevant to human learning and memory.

The origins of experimental research in associative learning are linked to early studies with a variety of animal species such as dogs (e.g., Pavlov, 1927), cats (e.g., Thorndike, 1898), pigeons (e.g., Skinner, 1938) and rats (e.g., Tolman, 1948). Interest

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[*] Correspondence concerning this article: Juan M. Rosas, Departamento de Psicología, Universidad de Jaén, 23071, Jaén, España. Email: jmrosas@ujaen.es. Acknowledgments: This work was funded by grants PSI2014-52263-C2-1-P and PSI2014-52263-C2-2-P from the Ministerio de Economía y Competitividad.

in such work with animals itself traces back to Darwin, who brought the idea that there is continuity among species to the forefront of scientific thought (Boakes, 1984). The idea, that "…the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind" (Darwin, 1871, pp 105) led to the emergence of comparative psychology, concerning itself with the comparison of the "intellectual" capabilities of various species. Though called "comparative" psychology, the field began by seeking to support that there is continuity among species. That is, the field was arguably looking for generality, as opposed to differences. That emerging field developed the initial methods, logic, and frame of thought needed to investigate abstract constructs, such as learning and intelligence, in nonverbal organisms. Though comparative psychology is still alive today, its approach and methods towards understanding intellectual capability gave birth to the Behaviorist schools of thought and the field of Learning Theory. Both are branches from the same tree with comparative psychology at its base (Boakes, 1984).

During the first half of the twentieth century much of the general psychological theory was based on animal research (e.g., Hull, 1943; Skinner, 1938; Tolman, 1967). With the "cognitive revolution" against the strict tenets of what was becoming "radical" behaviorism, studies of human learning and memory began to develop more independently of animal learning during the second half of the century. Animal learning lost most of its early dominance of psychology in this time. However, parallels between the results found in animal learning and those found in human instrumental, predictive, and causal learning during the last quarter of the past century show that animal research is still relevant. Both animal and human research still contribute to an understanding of general principles (see for instance, Shanks & Dickinson, 1987). The goal of this review is to provide a brief overview of some of these more recent parallels, focusing on the cases of competition between stimuli, the contents of learning, and the conditions affecting memory retrieval.

COMPETITION BETWEEN STIMULI

Blocking (e.g., Kamin, 1969), Overshadowing (e.g., Mackintosh, 1976), and Relative Validity (e.g., Wagner, Logan, Haberlandt, & Price, 1968) are three hallmark effects of associative learning. These effects have come to be collectively referred to as "cue-competition" effects. They are all examples where stimuli appear to compete with each other to become predictors of upcoming events. These effects were fundamental in the development of the Rescorla-Wagner (1972) model, which brought them together into a single theoretical framework, and predicting these phenomena has become a required basis for any following theory.

The blocking experiment, as reported by Kamin (1969), consisted of two critical groups of rats that received training in which different conditioned stimuli (CSs) were paired with a shock unconditioned stimulus (US) while barpressing for food. The result of that training was that the rats suppressed their barpressing in the presence of the CSs that predicted the shock. One group received LN+ trials, where a light (L) was compounded with a Noise (N) and paired with the US (+). These rats showed a very strong suppression response when tested with just L during the test. Though there was likely some effect of conditioning L in compound with N, simply conditioning L in compound with another stimulus did not prevent the animals learning about L and the shock. The data of most interest are from the other group. There, the animals first received parings of N with the shock, and then parings of L and N with the shock in the same manner as the previous group. Even though they had more experience with shock, very little conditioned response to L was observed. At the time LN was paired with shock, N was already a good predictor of shock, and it is said to have "blocked" learning about L.

In Overshadowing, two stimuli, often differing in salience, are combined and paired with a US (as in the groups above). The result is that stimuli tend to show less conditioning when tested individually than if they had been conditioned alone. Moreover, when they differ in salience, the less salient stimulus shows weaker conditioning than the more salient stimulus. In theory, the more salient stimulus conditions faster (e.g., Kamin & Schaub, 1963) and becomes a good predictor of the upcoming US. Thus, it also blocks further learning about the less salient stimulus. For example, Mackintosh (1976) combined a salient 85db noise and a light and paired that compound with shock. The data were converted to standard "suppression ratios" where responding in the CS is expressed as a percentage of overall responding in the trial. Small numbers indicate strong suppression, and numbers near .5 indicate no suppression whatsoever. When tested with those stimuli, the resulting suppression ratios for the noise and light were .18 and .39, respectively. Clearly, the intense noise elicited much greater suppression than the light. The rats also showed less conditioning to the light than a group that was conditioned to the light alone (suppression ratio= .14).

Relative validity is a similar phenomenon coming from a more complicated design. Here, animals receive multiple trials with a cue (X) embedded in compounds with different cues (AX, BX). The trials are arranged so that the correlation of cues A and B with the outcome is either perfect (e.g., AX+/BX-) or imperfect (AX+/AX-/BX+/BX-), while the relationship of X with the outcome is the same in each condition. The animals are subsequently tested with X. Cue X elicits greater conditioned responding in the imperfect condition (e.g., Wagner *et alii*, 1968). The idea here (as embodied in the Rescorla-Wagner [1972] model) is that in the perfect condition, A and B are strongly associated with the outcome, which can only support a limited amount of learning, and they thus block learning about X. Such blocking does not occur in the imperfect condition where A and B are not so strongly associated with the outcome.

Each of these hallmark associative learning effects has been demonstrated in humans. Blocking can be clearly seen in the work of Arcediano, Miller, and Matute (1997). Participants played a video game ("Martians") where a baseline of key pressing on a keyboard was established by firing lasers at invading Martians. On this baseline, CSs in the form of colored flickers of the screen or tones played through headphones, signaled that the Martians were protected by a reflective screen and could not be destroyed. During that time participants had to suppress their rate of firing; otherwise, their firing would reflect back to them and thousands of Martians would invade the planet. Within the design, two groups received conditioning with a compound AX, and a test with X. In the Blocking group, A had been established as a predictor that the Martians could not be destroyed in an earlier phase, while in the Control group A had simply been pre-exposed. On test, there was greater suppression to X in the Control group (.27) than in the Blocking group (.39). Though clear in this experiment and several others (e.g., Siegel & Allan, 1985; Shanks, 1985), the effects of blocking are not always so clear in humans. Sometimes the effect has not been obtained when it would ordinarily be expected based on the design (e.g., Davey & Singh, 1988; Lovibond, Siddel, & Bond, 1988), though it is also true that blocking is not always reliably observed in animals

(Maes *et alii*, 2016). Moreover, some results suggest that humans are sensitive to the phasic nature of experiments. That is, they sometimes may treat the separate phases as if they were unrelated, preventing the conditioning in the prior phase from blocking learning in the later phase (see Hinchy, Lovibond, & Ter Hoost, 1995). It is safe to say, however, that in the absence of the elicitation of other processes which might prevent or obscure it, blocking is fundamental in human associative learning.

Overshadowing has likewise been clearly demonstrated with humans (e.g., Baetu & Baker, 2010; Le Pelley & McLaren, 2001; Okifuji & Friedman, 1992; Spetch, 1995). For example, Baetu and Baker (2010), trained participants on a computer in a predictive-learning task where foods were paired with changes in hormone levels in fictitious people. Later, participants were presented with the food cues and asked to rate whether hormone levels would increase, decrease, or remain the same. Larger numbers are associated with a predicted increase in hormone levels. Within the design, two cues, I and J occurred together and predicted an increase in hormone levels. Another cue, N, also predicted a hormone increase. When tested with these stimuli, ratings for N (82.64) were higher than to either I (26.21) or J (30.57). When conditioned in compound, the stimuli overshadowed each other resulting in less associative strength accruing to the individual stimuli than to one conditioned alone.

A clear demonstration of the relative validity effect comes from the work of Baker, Mercier, Vallee-Tourangeau, Frank, and Pan (1993). In that study participants observed a tank crossing a field and the tank was either destroyed, or not. There were two cues that participants could use to try to determine whether the tank would be destroyed. In two conditions, the tank could be camouflaged, and a plane could appear on the screen. The camouflage was not necessarily a good predictor of the outcome; 50% of the time the tank was destroyed when the camouflage was present, and the tank was destroyed 50% of the time when the camouflage was not present. In one condition the plane was a perfect predictor of the outcome. In another condition the plane was an imperfect predictor. It predicted the outcome no better than the camouflage. When participants were asked to judge the contingency between the camouflage and the tank exploding, participants from the condition where the plane was no better at predicting the explosion ranked the contingency as higher than in the condition where the plane was the better predictor (see also Matute, Arcediano, & Miller, 1996).

Blocking and overshadowing have received extensive study in humans, in large part, due to the ease at which they lend themselves to "retrospective revaluation" (for a recent review see Miller & Witnauer, 2016). After learning about the stimuli, further experience with one of the stimuli affects how participants respond to the other. In general, after conditioning a compound, additional treatment with one of the stimuli tends to have the opposite effect on the other. To illustrate, consider a study by Wasserman and Berglan (1998). Here participants were presented with food cues that were paired with allergic symptoms in fictitious patients. Within-subject, participants received compound cues AW, CY, and BX. Each was paired separately with an allergic reaction over trials. Then, they received additional trials where A was presented and continued to be paired with the allergic reaction, while C was presented alone without the reaction. Presenting A with the outcome following AW trials is what is referred to as a "Backward Blocking" design as it is functionally the reverse of the blocking design presented earlier. When tested with cues W and X participants should rate these cues as equally predictive of the allergic reaction because they were all trained in the same way in compound with another cue.

On test, responding to W was less than responding to X. Presenting A with the outcome after the AW trials led subjects to retrospectively re-evaluate the association between W and the outcome. When tested with Y, responding to Y was greater than responding to X. The presentations of C, previously conditioned in compound with Y, were without the outcome, and they had the opposite effect on Y. It appeared that as C underwent extinction, participants re-evaluated the association between Y and the outcome, treating Y more like the cause than they would have without the additional C- trials. When the CY compound was conditioned, C and Y should have mutually overshadowed each other. Additional presentations of C without the outcome increased responding to Y. That is, Y retrospectively recovered from overshadowing. Further representative demonstrations of these types of effects can be found in Arcediano, Escobar, and Matute (2001), Dickinson and Burke (1996), Shanks (1985) and Van Hamme & Wasserman (1994).

Although backward blocking appears reliably in humans, it either does not occur in animals (e.g., Miller, Hallam, & Graham, 1990; Schweitzer & Green, 1982) or only in special circumstances (Denniston, Miller, & Matute, 1996; Miller & Matute, 1996). The situations where it appears with animals seem to be those where the stimuli involved are not “biologically significant” (Denniston, Miller, & Matute, 1996; Miller & Matute, 1996), a term used by Miller and Matute to refer to the ability of a stimulus to elicit a response. Because the predicted outcomes in a typical animal study are significant in some way (e.g., food, electric shock), as opposed to the innocuous stimuli used in predictive learning tasks, the associations established during compound conditioning are assumed to be somehow protected from further change as might be induced by retrospective revaluation techniques. Interestingly, backward blocking has been obtained in humans using electric shock as an outcome (Mitchell & Lovibond, 2002), which would contradict the idea presented by Miller and his colleagues. The effect, however, was dependent on the instructions used.

Unlike backward blocking, recovery from overshadowing-type effects have been reported more extensively in the animal literature, beginning with Kaufman and Bolles (1981), and subsequently (e.g., Blaisdell, Gunther, & Miller, 1999; Matzel, Schachtman, & Miller 1998; Miller, Barnet, & Grahame 1992). However, these types of effects are not universally found when they are sought (Holland, 1984; 1999; Rahut, McPhee, DiPietro, & Ayres, 2000).

In summary, basic associative effects involving blocking and overshadowing that occur in rats also occur in humans, although in the latter case other processes may be involved that make people more sensitive to manipulations such as retrospective revaluation. Tasks with humans have been shown to be sensitive to the wording of instructions and test questions (Matute *et alii*, 1996; Matute, Vegas, De Marez, 1992; Mitchell & Lovibond, 2002). Nevertheless, the fundamentals of the phenomena appear to be largely the same between man and animal.

The contents of learning

In the previous section we showed that the study of competition between stimuli has played a core role both in determining the conditions governing associative learning and in the evaluation of the mechanisms that underlie the formation of associations between events. Although there are cases where humans exhibit phenomena, such as retrospective evaluation, where animals do not, the opposite is far less true. Conditions which affect associative learning in animals also affect that learning in humans in similar ways. In this section we will focus on the comparative analysis of the contents of learning during acquisition and extinction in both classical conditioning and instrumental conditioning.

Contents of acquisition in classical conditioning

When a CS is repeatedly paired with a US the CS comes to elicit a conditioned response that is used as an indication that an association has been formed. In the conditioning literature there are two general theories about the type of associations that are established in classical conditioning. S-R theories consider that an association is established between a stimulus and response (S-R), so that the CS directly elicits a version of the unconditioned response (UR) with which it was paired. The US simply acts as a catalyst for the formation of the S-R association, but is not part of it (e.g., Hull, 1943). Alternatively, S-S theories assume that classical conditioning results in an association between two stimuli, the CS and the US, so that the presentation of the CS evokes the representation of the US. The conditioned response (CR) appears as an effect of eliciting the US representation (e.g., Pavlov, 1927; Tolman, 1932; Wagner, 1981; Wagner & Brandon, 1989).

Animal studies have distinguished between these two types of learning by modifying the value of the outcome after conditioning in "outcome revaluation" procedures. A manipulation is used to change how the animal would respond to the US itself. A food-US might be paired with lithium chloride so that an aversion is conditioned to it and animals subsequently avoid the food. A loud frightening noise US might be presented over and over so that the animal's fear of it habituates. Because the US is not involved in response generation according to S-R learning, the CR should not be affected by post-conditioning modifications of the US. On the other hand, if the CR is a function of an evoked representation of the US, and that representation has been changed, then the response evoked by S should also change as it serves to evoke the modified US representation. In general, the results are consistent with the idea that S-S learning takes place in classical conditioning. Post-conditioning changes of the outcome produce changes in the CR (e.g., Rescorla, 1973; Rescorla & Freberg, 1978). Similar results have been found using the outcome revaluation procedure in human predictive learning (Gámez, Martos, Abad, & Rosas, 2013). After learning to respond to a cue predicting attacking vessels (e.g., planes, ships) participants were simply told that the vessel was now indestructible. Attaching that new information to the predicted outcome led to a suppression of responding to the cue. Participants had not learned to simply respond to the cue, rather, they had detailed knowledge as to what event the cue predicted and the impact of their actions on that event.

Using a different approach, Paredes Olay, Abad, Gámez, and Rosas, (2002) adapted the Pavlovian-to-Instrumental Transfer (PIT) task to the study of the contents of learning in humans. The PIT procedure has proved useful for analyzing the contents of learning in animals (e.g., Colwill, 1993; Delamater, 1996). In this procedure the association between a stimulus and an outcome is measured through the influence this association has on an instrumental response that has been associated with the same outcome. For example, in rats a CS that predicts a food pellet will energize lever pressing when that pressing leads to the delivery of food (e.g., Corbit & Balleine, 2011; Overmier & Lawry, 1979; Trapold & Overmier, 1972). In dogs, a CS that predicts a shock will increase runway shuttling to avoid that shock (e.g., Rescorla & Solomon, 1967).

Paredes Olay *et alii* (2002) first trained participants in a video game in which they had to defend Andalusia from attacks by destroying planes and ships (O1 and O2, counterbalanced) by performing two responses, R1 and R2, on the keyboard of a computer (e.g., an orange key destroyed the ships and a green key destroyed the planes). While looking at an image of a city and beach with a sky overhead, a ship or a plane would appear on the screen and remain until the relevant key had been pressed enough times on a variable interval 5-s schedule at which time the ship or plane was shown exploding. In a second phase, a Pavlovian association was established between two cues, C1 and C2 (colored drawings representing the logos of fictitious Defense Companies), and each of the outcomes previously associated with R1 and R2. During this phase, participants were told that they were observing the results from another participant. Logos (e.g., C1) appeared on the screen along with targets (e.g. O1) and the participant was told to guess which weapon the hidden participant was using. After they guessed, and independently of what they guessed, the ship or plane was destroyed. During the test, participants were given the opportunity to perform R1 and R2 in the presence and absence of C1 and C2. Participants preferably performed the instrumental response that matched the outcome signaled by the logo (R1 in the presence of C1 and R2 in the presence of C2) showing that an S-S association was established during the Pavlovian conditioning of C1 and C2.

In a task involving food rewards, Lovibond and Colagiuri (2013) instrumentally trained people to press a button on a variable-ratio 10 schedule for M&M chocolates. Then, the option to respond was removed and they received Pavlovian conditioning of a red or blue light, one of which (counterbalanced) was always followed with the delivery of an M&M (e.g., R+/B-). Following the Pavlovian conditioning of one of the colors, the participants were allowed to respond on the button again for the chocolate. Presentations of the colored lights selectively increased responding. That is, if the light had been paired with chocolate, it increased instrumental responding for chocolate (see also Colagiuri & Lovibond, 2015; Lovibond, Satkunaraja, & Colagiuri, 2015). Results of studies that revalue the outcome or assess the impact of a predicted outcome on instrumental responding in humans both concur with the findings from animal research. Classical conditioning results in the formation of strong S-S associations.

Contents of extinction learning in classical conditioning

Extinction consists of repeated presentation of the CS without the US, which leads to a decrease in the CR (Pavlov, 1927). In the simplest approach, extinction may eliminate the associations established during the acquisition training (e.g., Rescorla & Wagner, 1972). However, as we will see in a later section, manipulations such as the simple passage of time or a change of context after extinction produce a recovery of the extinguished response. Such a recovery would be impossible if extinction erased the original learning. Thus, extinction is widely regarded as being a new form of inhibitory learning that competes with the expression of the original association learned during acquisition (e.g., Bouton, 1993; Konorski, 1948; Wagner & Brandon, 1989). Animal research reveals that extinction involves new learning that, minimally, affects how the CS is represented (Pavlov, 1927; Robbins, 1990), leads to the formation of inhibitory stimulus-response (S-noCR) associations (e.g., Rescorla, 1993), and recent evidence indicates that extinction involves inhibition of the US representation as advocated by the theories cited above (Laurent, Chieng, & Balleine, 2016; see also Schachtman, Threlkeld, & Meyer, 2000).

Though evidence for each of these mechanisms exists, less is known about the exact way these mechanisms operate and interact. For example, using the PIT procedure with rats, Delamater (1996) found that the PIT transfer effect described earlier remained unchanged across a variety of different extinction manipulations. That finding is not wholly compatible with the idea that the US representation is suppressed. Rather, it suggests that a CR is inhibited leaving the US representation intact and able to affect other US-related responses. Research with humans has not investigated the mechanisms of extinction as extensively as they have been investigated in animals. Yet, where those mechanisms have been investigated, parallel results have been found. Rosas, Paredes Olay, García Gutiérrez, Espinosa, and Abad (2010) obtained an identical result to that obtained by Delamater (1996) in humans using the Paredes Olay *et alii* (2002) procedure described above. Hogarth *et alii* (2014) also found that PIT survives simple extinction treatments.

Contents of learning in instrumental conditioning

In a typical instrumental conditioning situation, a target response (R) is followed by a rewarding outcome (O) when performed in the presence of a discriminative stimulus (S^D). Studies regarding the contents of instrumental conditioning have found evidence of the formation of R-O, S^D-O, S^D-R, and S^D-(R-O) associations in both animals and humans.

R-O. A procedure often used to demonstrate the R-O association is the outcome revaluation procedure described above. After training a response using a food reward, the food is made unappealing by paring it with lithium chloride. Using this procedure, Colwill and Rescorla (1985) found that rats showed a clear preference for a response whose reinforcer had not been devalued after conditioning. This selective decrease in a response whose reinforcer has been devalued, compared to one that has not, has been also reported in human instrumental conditioning (e.g., Gámez & Rosas, 2007; Vega, Vila, & Rosas, 2004). A recent report of this effect in humans also comes from Morris, Quail, Griffiths, Green, and Balleine (2015). In their task, participants shook a virtual vending machine to obtain a preferred snack. Then, participants viewed a video showing their favorite snack infested with cockroaches. Viewing the video decreased their rate of subsequent machine tilting, clearly showing that their behavior was not simply elicited by the stimulus, but was "goal directed" and controlled by knowledge of the outcome produced by the response.

S^D-R. Showing that R-O associations are established in instrumental conditioning does not imply that no other associations are involved in this type of learning. Colwill (1994) presents evidence she interprets as S^D-R associations in rats. She used a complex transfer procedure in which a group of rats was rewarded with food (O1) in the presence of two discriminative stimuli (A and B) if they performed two instrumental responses (i.e., A:R1-O1 and B:R2-O1). Next, two new responses were trained with two new reinforcers in the absence of the S^D's (R3-O2 and R4-O3). In a third phase, the original responses R1 and R2 were followed by outcomes O2 and O3, also in the absence of the S^D (R1-O2 and R2-O3). Finally, during the extinction test, responding to R3 and R4 was recorded in the presence of discriminative stimuli A and B. The idea behind the experiment is that the S^D's would selectively affect other responses trained with the same outcome by way of the expression of an associative chain that begins with an S-R association (e.g., A-R1-O1). Colwill found that the S^D's selectively affected performance to R3 and R4. When the S^D had been paired with the response that shared

an outcome, it depressed responding. The S^D produced transfer (in this case a negative transfer) through an S-R-O chain, which depends upon establishing an S-R association. The A-R1 association evoked representations of both O1 and O2, creating interference with other responses that shared one of those outcomes. S^D A, however, had no effect on R4, for which the response associated with the S^D did not share an outcome.

Gámez and Rosas (2007) have reported results in human instrumental conditioning that reach the same conclusions as Colwill (1994), but with a more direct evaluation that would be difficult to implement in animals. Using the Andalusia-defense video game described earlier participants learned to destroy an enemy (e.g., a ship) in the presence of particular S^Ds (a red or blue oval near the top of screen) by pressing keys. The relevant response key depended on the S^D. Then, on test, participants viewed the beach scene, but a new outcome (e.g., a plane) was present. Despite having no knowledge of the correct response for that stimulus, the chosen response was determined by the S^D with which the response had been previously associated. This result is evidence of the direct involvement of the S^D-R association in human instrumental conditioning (see also Gámez, León, & Rosas, 2016).

S^D-O. Instrumental conditioning also produces associations between the discriminative stimulus and the outcome (S^D-O association) comparable to that established between the CS and the US in classical conditioning in both human (Gámez & Rosas, 2005, 2007) and non-human animals (Colwill & Rescorla, 1986, 1988). Using a transfer procedure analogous to that used by Colwill and Rescorla (1988), Gámez and Rosas (2007) trained participants to perform a response that was followed by a specific outcome in the presence of a given S^D [i.e., S^D-(R1-O1)]. Then, participants learned two new responses that were trained in the absence of any S^D, one of which produced the outcome from the earlier phase (i.e., R3-O1 and R4-O2). When presented with the phase-1 S^D, participants preferentially chose to respond on the alternative that had been reinforced with the outcome that was paired with SD in the earlier phase (R3 in the example).

S^D-(R-O). In addition to the R-O, S^D-R and S^D-O binary associations, hierarchical [S^D -(R-O)] associations have been found where the S^D signals an entire response-outcome unit (Colwill & Rescorla, 1990; Gámez & Rosas, 2007; Skinner, 1938). Colwill and Rescorla (1990) trained rats in a discrimination in which the outcomes of two responses, R1 and R2, were reversed depending on the S^D present [e.g., A-R1-O1), A-(R2-O2), B-(R1-O2), B-(R2-O1)]. After devaluating one of the outcomes, they tested the rats' performance in the two response alternatives in the presence of each discriminative stimulus. Rats preferentially chose the response alternative that was followed by the non-devalued outcome, so that the specific response chosen changed depending on the S^D presented. In this design, the binary associations discussed earlier would lead to an indistinct choice between the two response alternatives. Thus, the result demonstrates that they had formed hierarchical S^D-(R-O) associations. Using an analogous design, Gámez and Rosas (2007) found similar results in human instrumental conditioning. Using the Andalusia-defense task participants were trained in a task where A signaled that R1 led to O1 and R2 led to O2. The assignment of outcomes to responses was reversed in the presence of B. Then, O1 was devalued by instructing the participants that the enemy was now indestructible. In the presence of A, participants performed R2 more than R1, in the presence of B that pattern was reversed (the opposite occurred when O2 was devalued). Like the results of Colwill and Rescorla (1990), these findings show that the SD's A and B were associated with entire R-O units.

Recent reports by Gámez *et alii* (2016) and Thrailkill and Bouton (2015) invited further comparisons that have not yet been made. Gámez *et alii* (2016) showed that instrumental learning also involves associations between the context where training takes place and each of the aforementioned elements. These authors used the Andalusia-defense game and found that context-O, context-S^D, and context-R associations were established after just three conditioning trials within the same training paradigm. In animals, evidence for these types of associations with context in instrumental learning has not yet been sought. In rats, a context switch tends to cause a loss of the portion of responding maintained by habit (Thrailkill & Bouton, 2015). The role of habit in responding in instrumental learning tasks has yet to be investigated.

Contents of extinction learning in instrumental conditioning

Extinction of instrumental responding occurs when a response is no longer followed by its outcome leading to a decrease in response strength. To determine the fate of the R-O association during extinction, Rescorla (1993) devaluated the reinforcer after extinction. He found that responses that had been associated with that outcome were depressed, even when that response-outcome association had undergone extinction. Such a finding suggests that the association between the response and the outcome survives extinction. The mechanism responsible for the response decrease during extinction seems to be relatively independent of the state of the R-O association. Something similar happens with the S^D-O association. Using a transfer technique where S^D‘s selectively increase responding on a response alternative with which they had shared outcomes, Rescorla (1992) observed transfer regardless of whether the response had been extinguished or not. The S^D-O association appeared to also survive instrumental extinction. The results of those, and related, experiments further ruled out the possibility that S^D-noO or R-noO inhibitory associations are established during extinction. Those findings are similar to what had been found during classical conditioning and suggest an inhibitory association between the S^D and the response (S^D-noR) as the most likely candidate to explain the learning during the instrumental extinction (e.g., Rescorla, 1991).

Results in humans are not so clear. The only study analyzing the contents of instrumental extinction in humans, as far as we know, reports results that differ from those found in animals (Gámez & Rosas, 2005). These authors designed an experiment based on a transfer procedure similar to that used by Rescorla (1992) in order to test whether the S^D-O association was affected by extinction. After an acquisition phase in which participants were trained to perform two instrumental responses for two different outcomes (R1-O1 and R2-O2), new training was conducted in which two new responses were followed by the same outcomes in the presence of two discriminative stimuli (S^D1-(R3-O1) and S^D2–(R4-O2)). Finally, after one of those responses was extinguished, a test was performed in which the S^D’s that had been previously associated with R3 and R4 were presented, but only R1 and R2 were available. Extinction abolished the normal transfer effect. That is, if R3 had been extinguished, S^D1 would no longer affect R1. That result suggests that, unlike in rats, extinction of instrumental responses led to the formation of S^D-noO associations in the human task. The generality of this divergence is still to be determined as it is the result of a single experiment and it questions the uniformity of what has been otherwise parallel conclusions between human and nonhuman animals in terms of the contents of associative learning (see also Hogarth *et alii*, 2014). As with the cue-competition phenomena discussed earlier, knowledge gained from animal research as to the mechanisms involved in learning continues to be confirmed in humans.

Basic conditions of retrieval

As with studies of cue competition and the contents of learning, studies examining basic conditions of memory retrieval have also revealed striking similarities in how it is accomplished in human and nonhuman animals. In the following paragraphs, we will focus on a brief analysis of spontaneous forgetting and retrieval failures that occur with manipulations of the contexts in which learning and testing takes place.

Spontaneous forgetting

One important issue within the experimental studies of memory has been to establish the conditions in which forgetting occurs. From a layperson point of view, forgetting of information is understood as an erasure of the learned information and seems unavoidable. Much of what is learned seems to be condemned to be forgotten and the only issue is how long it will take. However, the literature in this field suggests that while some information seems to be easily forgotten, other information is very resilient and difficult to forget. Rosas and Bouton (1996) found that, in rats, a single experience with a taste paired with gastric distress is similarly remembered 5 or 21 days after the experience took place. Hoffman, Selekman, and Jensen (1966) found that pigeons were able to retain information acquired in a fear-conditioning situation for over 30 months. Gleitman and Holmes (1967), using a conditioned suppression procedure in rats, found that rats showed the same level of fear either one day or three months after training (see also Hendersen, 1978, 1985; Thomas, 1979), even if that training was pre-asymptotic. In another line of work, Revusky (1968) found that when one-month old rats consumed two solutions (coffee and vinegar), one when they were thirsty and the other when they were sated, they developed a preference for the solution ingested while they were thirsty. This preference remained even when they were tested 60 days after the original experience. Similar results were found in appetitive conditioning in crickets (*Gryllus bimaculatus*) in which a peppermint odor was paired with access to water. The crickets retained appetitive and differential conditioning for up to 4 days, although aversive conditioning seemed to disappear after 24 hours (Matsumoto & Mizunami, 2002).

Our own anecdotal experience suggests that humans are no exception, and that is confirmed in the laboratory. Enright, Rovee-Collier, Fagen, and Caniglia (1983) instrumentally trained three-month old infants to kick in order to activate a mobile in a single session, and that learning was retained for up to two weeks. Conditioned eye-blink response in 20- and 30-day old infants has been also shown to be retained when tested 10 days after conditioning (Little, Lipsitt, & Rovee-Collier, 1984; see also Sullivan, Rovee-Collier, & Tynes, 1979). In similar lines, Schugens and Daum (1999) found that eyelid conditioning remains practically intact two months after training in patients with amnesia produced by different factors (brain injury, alcohol abuse or early Alzheimer's disease), and in their respective controls. Analogous results have been found within human causal and predictive learning studies. Vila and Rosas (2001) found that the relationship between a fictitious drug and an imaginary disease remained intact 48 hours after the end of training (see also Romero, Vila, & Rosas, 2003). Schiller *et alii* (2010) have produced evidence of the persistence of memory that a colored square predicts a shock after one year in college-aged participants. Taken together, these results suggest that in species ranging from insects to humans, information about simple relationships between two events can be retained for long periods of time, showing little evidence of forgetting by the simple passage of time.

Other instances of learning are clearly more affected by the simple passage of time. For example, Sahley, Martin, and Gelperin (1990) trained slugs (*Limax maximus*) in a differential conditioning task in which an aversive odor was paired with an attractive taste (CS1+), while another odor was presented alone, without the taste (CS2-). The preference for CS1 developed rapidly. However, this preference was attenuated when slugs received the test 48 hours after conditioning. These results are consistent with the idea that forgetting of specific details may occur with the passage of time, and that the organisms subsequently confuse CS+ and CS-. In a classic experiment, Thomas and Riccio (1979) trained rats in a conditioned suppression task using a blocking design. A noise was first paired with an electric shock, and then a compound formed by a different noise and a light was paired with the same shock either 1 or 21 days after the initial training with the noise. These authors found that blocking of the light was greater after the 21-day interval than after the 1-day retention interval, suggesting that rats had increasing difficulty discriminating between the original sound and the new sound as time passed (see Riccio, Richardson, & Ebner, 1984). This forgetting of the precise attributes of the stimulus and situation has also been observed in humans (Bahrick, Clarck, & Bahrick, 1967; for a review see Bouton, Nelson, & Rosas, 1999).

The combination of the results reported in the two previous paragraphs suggests that not all information is equally likely to be affected by the retention interval. For example, Thomas (1979) found, in pigeons, that conditioned inhibition, in which one learns that a stimulus signals the absence of an outcome, can be forgotten after a 21-day retention interval. Such forgetting did not occur with excitatory conditioning (Gleitman, 1967; but see Sissons & Miller, 2009).

Perhaps the most obvious cases of differential retrieval of different types of information are the multiple examples of extinction and interference that appear in the literature. When an animal, whether human or not, learns a relationship between two stimuli or between a response and an outcome, and this relationship is later changed, the initially acquired information is very resistant to the effects of a retention interval. However, information about the change is clearly deteriorated by different manipulations which we will briefly describe below, including the passage of time (for a review see Bouton, 1993).

Spontaneous recovery from extinction

Spontaneous recovery is defined as the recovery of an extinguished response that is observed with the passage of time between the end of the extinction and the test. This phenomenon, initially described by Pavlov (1927), is found in many different animal species and with a variety of different procedures, showing that recovery of information learned in extinction is more affected by the passage of time than information about acquisition. For example, Rosas and Bouton (1996) found that when a sweet taste was paired with gastrointestinal discomfort in rats, rats avoid subsequent consumption of the flavored solution. However, if the rat is forced to drink the sweet taste again (because it has no other liquid alternatives) and the taste is not followed by the discomfort, the aversion eventually extinguishes and the rat no longer rejects the sweet taste. In a well-controlled situation, these authors found that when rats were tested 18 days after extinction ended, they showed spontaneous recovery of the original aversion to the sweet taste. Analogous results have been found among a diverse set of species and tasks, such as autoshaping in pigeons (e.g., Robbins, 1990), instrumental conditioning in rats (e.g., Rescorla, 1997), salivary conditioning in dogs (e.g., Pavlov, 1927), gustatory aversive conditioning in goats (Kimball & Billings, 2007) and in the conditioning of the proboscis extension response after odor-sugar access pairings in bees (Sandoz & Pham-Delègue, 2004). Spontaneous recovery is not limited to simple extinction, but also occurs after counterconditioning. When a CS is first associated with shock or food, and then later associated with the US not used in the first phase, a retention interval causes a loss of performance associated with phase 2 and a recovery of that associated with the earlier phase (e.g., Bouton & Peck, 1992).

In humans, this phenomenon is also easily observed. Schiller *et alii* (2008) used a fear conditioning paradigm in which a stimulus (a colored image of a snake) was paired with a moderate shock in the wrist in 33% of the trials (CS1+) while another stimulus was presented without shock (CS2-); twenty-four hours after extinguishing CS1, spontaneous recovery was observed measuring the galvanic skin response as a CR. Likewise, spontaneous recovery from such retroactive inhibition has been found when participants learn two successive paired associated lists so that the same words were presented in both lists but paired with different associates in each case (A-B, A-C). Recall of associates from the first list increased over time while recall of associates in the second list decreased over time (between 1 min and 48 hours: Underwood, 1948; for a review see Brown, 1976). Similar results have been shown in eye blink conditioning (Franks, 1963; Hartman & Grant, 1962) and verbal expectations (e.g., Humphreys, Miller, & Ellson, 1940). Spontaneous recovery of both extinction (e.g., Vila and Rosas, 2001) and other treatments where later learning interferes with initial learning (e.g., Alvarado, Jara, Vila, & Rosas, 2006; Rosas, Vila, Lugo, & López, 2001) has been found in human causal and predictive learning, as well as instrumental preparations (e.g., Vila, Romero, & Rosas, 2002).

Renewal from extinction

Bouton and Bolles (1979) found that when rats received fear conditioning in a context (i.e., context “A”) and then received extinction in a different context, context “B”, subsequent testing of the CS in context A produced a renewal of the extinguished CR, compared to a control group in which acquisition, extinction and testing took place in the same context. Such an effect has been termed “ABA renewal”, where the letters indicate the contexts where acquisition, extinction, and testing phases take place. Renewal is also found when acquisition and extinction take place in one context and the test takes place in a different context (AAB renewal, e.g., Bouton & Ricker, 1994; Tamai & Nakajima, 2000; Rosas, García Gutiérrez, & Callejas Aguilera, 2007), as well as in the ABC case when acquisition, extinction and testing take place in three different contexts (e.g., Bouton & Swartzentruber, 1986; Thomas, Larsen, & Ayres, 2003). These latter findings, AAB and ABC Renewal, suggest that retrieval of information about extinction depends on the similarity between the context in which extinction takes place and the context of testing. Testing in the context of acquisition is not necessary to observe renewal. AAB and ABC renewal experiments clearly show that retrieval of the learning that occurs during extinction is more likely to be affected by a context change than learning that occurs during acquisition.

Renewal also occurs after counterconditioning. For example, rather than undergo extinction, a tone that predicts food might be now paired with shock. However, the performance elicited by the tone, either food- or fear-related performance, depends on the context of testing (e.g., Peck & Bouton, 1990). Renewal might be best viewed as an example of a more general phenomenon by which new conflicting information learned about a stimulus comes to be controlled by the context in which it occurs (Nelson, 2002; Nelson & Callejas Aguilera, 2007).

Renewal in humans has received considerable attention in the last two decades, particularly because it is viewed as a factor contributing to relapse after the treatment of phobias (e.g., Mineka, Mystkowski, Hladek, & Rodríguez, 1999), aversive conditioning (e.g., Effting & Kindt, 2007, Neumann, Lipp, & Cory, 2007), and addictions such as alcoholism (e.g., Stasiewicz, Brandom, & Bradizza, 2007), or smoking (e.g., Thewissen, Snijders, Havermans, Van den Hout, & Jansen, 2006). Renewal is also found after extinction or interference treatments in predictive learning tasks (e.g., Paredes Olay & Rosas, 1999; Rosas & Callejas Aguilera, 2006; Rosas, García Gutierrez, & Callejas Aguilera, 2006), and in conditioning using videogames (e.g., Havermans, Keuker, Lataster, & Jansen, 2005; Nelson, Sanjuan, Vadillo Ruiz, Pérez, & León, 2011; Neumann, 2006).

Reinstatement

The reinstatement effect is the recovery of an extinguished response that occurs when the organism is exposed to the outcome after extinction and before the test. The CS and US do not need to be paired again. The organism simply needs to re-experience the US in the context where the CS will be tested. This phenomenon has been shown in aversive (e.g., Rescorla & Heth, 1975) and appetitive conditioning (e.g., Delamater, 1997) with rats. It is also shown in counterconditioning (e.g., Brooks, Hale, Nelson, & Bouton, 1995). The effect is found in humans both after extinction in causal learning (Vila & Rosas, 2001) and after interference (counterconditioning) in human predictive learning (e.g., García Gutiérrez & Rosas, 2003a, 2003b; García Gutiérrez, Rosas, & Nelson, 2005).

In studies of reinstatement after counterconditioning we find a potential divergence between nonhuman and human animal studies. While evaluating explanations for the reinstatement effect, García Gutiérrez and Rosas (2003a), sequentially paired the same cue with two different outcomes (A-O1 and then A-O2) and then evaluated the relationship between the cue and the two outcomes. Before conducting the test, during the reinstatement phase, either the original outcome (O1), the phase 2 outcome (O2), or a third outcome that had not appeared before was presented. Reinstatement occurred regardless of which outcome was presented during the reinstatement phase. That result is consistent with an explanation offered by Bouton (1993) suggesting that reinstatement occurs because of what could be characterized as a change in the subjective perception of the context by the participant as a consequence of the context-outcome pairings. Unlike in humans, Delamater (1997) reports outcome-specific reinstatement both in classical and instrumental conditioning in rats. These divergent results in animals and humans should make us cautious when considering that the effect of reinstatement, behaviorally identical in the rat and the human being, is due to the same mechanism in both species. Nevertheless, the divergence must also be accepted with equal caution because while García Gutiérrez and Rosas (2003a) used a counter-conditioning procedure to reduce the initial response, Delamater (1997) used simple extinction. The use of multiple different outcomes, as opposed to the outcomes presence vs. absence, could have served to promote generalization between them, rendering them both effective in producing reinstatement.

Effects of context change on simple acquisition

Earlier we pointed out that simple acquisition seemed to be a phenomenon resistant to forgetting with the simple passage of time. The same appears to be the case with context change. Generally speaking, information about a consistent relationship between a cue and an outcome, a CS and a US, transfers well across different contexts in both animals and humans. However, this general characteristic also has exceptions (for a review see Rosas, Todd, & Bouton, 2013). For example, Hall and Honey (1990), using a single paring of a CS with an intense footshock in rats, found that the conditioned response did not transfer well between different contexts. However, transfer was basically perfect after 5 conditioning trials. In contrast, Bonardi, Hall, and Honey (1990) found good transfer of taste aversion between contexts with a single conditioning trial, and poor transfer between contexts after 5 conditioning trials. León, Callejas Aguilera, and Rosas (2012) noted that procedural aspects such as the experience animals have with the contexts may modulate context-switch effects after acquisition in some situations. They reported that a taste aversion acquired after a single trial transferred well across contexts only if the contexts were familiar at the time of conditioning. This aspect cannot necessarily account for the contradictory results summarized above, as in both studies animals had experience with the contexts before conditioning started. In humans, research suggests that context changes deteriorate performance after simple acquisition in the initial stages of training, but not when training is more extended (León, Abad, & Rosas, 2010), analogous to what was reported by Hall and Honey (1990). Similar losses of performance with context-switch effects have been also reported in animal (e.g., Bouton & Todd, 2014) and human instrumental conditioning (León, Abad, & Rosas, 2010).

Additionally, some studies show that simple acquisition may be found to be context dependent, even after training reaches an asymptote (see Rosas *et alii*, 2013). For instance, in a predictive learning task Rosas and Callejas Aguilera (2006) found that retrieval of a consistent relationship between a cue and an outcome was deteriorated by a change of context when it was learned in a situation in which another cue received extinction. That effect led the authors to propose that extinction results in attention to the contexts, and that contextual attention leads to information being learned coming under the control of that context. Nevertheless, in a behavioral video-game task, Nelson and Lamoureux (2015) found that extinction of a cue had no effect on contextual control of simple acquisition, even though attention to contexts was maintained. In animals, similar contradictory results have been found. Rosas and Callejas Aguilera (2007) showed that a simple conditioned aversion to one flavor is forgotten with a change in context when it is learned after the extinction of an aversion conditioned to a different flavor. However, Nelson, Lombas, and León (2011), using an appetitive conditioning procedure in rats, found that extinction of a CS that predicts food, if anything, increased the transfer of another CS to a different context. The mechanisms that underlie these divergent effects are presently not fully understood, but the parallel investigations with both animals and humans will undoubtedly facilitate the understanding of those mechanisms.

CONCLUSIONS

Though clearly not exhaustive, we have presented a general review of many parallels and a few divergences between animal and human associative learning with regard to cue competition, the contents of learning, and conditions affecting retrieval processes. Overall, we have shown considerable parallels in the associative learning processes between animals and man. Competition phenomena such as blocking, overshadowing, and relative validity are largely analogous. When examining the associative structures formed in classical and instrumental conditioning, additional parallels are observed. Finally, forgetting and retrieval seem to be affected by many of the same factors in human and nonhuman animals. Human and nonhuman animals share a significant number of simple predictive and retrieval mechanisms that are essential to their successful interaction with the world. For guiding their actions, associative processes in humans could be elaborated by seemingly more complex cognitive processes (e.g., reasoning). But much can still be learned about human behavior and its mechanisms from the study of animals where such complexity need not be inferred.

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