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SHORT ARTICLE

Acquisition of a Conditioned Taste Aversion becomes Context Dependent when it is learned after Extinction

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Abstract

A conditioned taste aversion experiment tested context-switch effects on retrieval of CS-US acquisition performance in rats. A context switch impaired performance when the target flavour was trained in a context where a different flavour underwent extinction. Conditioned taste aversion in the absence of previous extinction of the alternate flavour was not context dependent. It is suggested that the ambiguity in the meaning of the extinguished cue leads animals to pay attention to the context, so that the information learned in that context becomes context dependent.

Acquisition of a Conditioned Taste Aversion becomes Context Dependent when it is learned after Extinction

The role of context in learning and retrieval of the information has been extensively explored in animal conditioning during the last few decades (see Bouton, 1993; Bouton, Nelson, & Rosas, 1999 for review). This research has shown that contexts play only a small role at best in retrieval of simple conditioned stimulus- unconditioned stimulus (CS-US) relationships. In most cases, retrieval of the CS-US relationships seems to be identical when tested in the training context or in a different but equally familiar context (see Bouton, 1993). Alternatively, when the CS-US association is extinguished by the presentation of the CS without the US, extinction seems to become context dependent in a phenomenon that has been called renewal (e.g., Bouton & Bolles, 1979).

In a typical renewal situation, a CS-US association is established in a context (Context A); that association is then extinguished in a different context (Context B); and finally the association is tested again in Context A. Acquisition performance is usually renewed compared to a group that received acquisition, extinction, and testing in Context A (e.g., Rosas & Bouton, 1998). Similar results have been found when acquisition and extinction are conducted in the same context, and the context is changed during the test (AAB renewal, e.g., Bouton & Ricker, 1994; Tamai & Nakajima, 2000). Renewal has been also reported when acquisition, extinction, and testing are conducted in three different contexts (ABC renewal, e.g., Bouton & Swartzentruber, 1986; Thomas, Larsen, & Ayres, 2003). Similar results have been recently reported in human causal/predictive learning (e.g., Rosas, Vila, Lugo, & López, 2001).

The differential effect of context changes on acquisition and extinction has become a key feature for the explanations of renewal. In situations where context changes affect acquisition performance (e.g., Archer, Sjödén, & Nilsson, 1985; Sjödén & Archer, 1989), renewal may be explained as recovery of a non extinguished CS-US association. This explanation is difficult to defend in the absence of a context switch effect on acquisition, or in AAB, and ABC renewal situations.

An interesting issue within this area of research is why extinction seems to be more context dependent than acquisition. An answer to this question is provided by Bouton (1993). According to this author, both inhibitory and second-learned information about a CS are more context-dependent than excitatory or first learned information about the CS. Extinction learning is both, inhibitory (e.g., Bouton, 1993; Konorsky, 1948; Pearce & Hall, 1980) and the second learning the animal establishes about the CS. In trying to separate whether contextual dependency depends on the information being inhibitory or second-learned, Nelson (2002) found that the context switch effect only appeared when the information was learned in the second place, regardless of whether such information is inhibitory or excitatory. For example, when rats received excitatory conditioning with a tone paired with food pellets, responding to the tone was similar whether the tone was tested in the context in which it was conditioned or in a different context. However, excitatory conditioning was highly sensitive to the context when the tone had been previously trained to signal the absence of food (inhibitory conditioning). According to this analysis, context specificity of information may depend on a feature of the information (being second-learned).

Bouton (1997) gives an alternative response to the question of why second-learned information becomes context specific. According to this author, second-learned information becomes context specific because extinction makes the meaning of the CS ambiguous. When the CS becomes ambiguous during the interference treatment, animals begin to pay attention to the context so that the ambiguity in the meaning of the cue can be resolved. Once the animal pays attention to the context during extinction, information becomes context specific (see also, Darby & Pearce, 1995; Nelson, 2002).

Rosas and Callejas-Aguilera (2006) developed this idea of ambiguity in a human predictive learning situation. According to these authors, if contextual dependency of extinction appears because the ambiguity on the meaning of the cue leads participants' attention to the context, then any information learned within an ambiguous situation should become context specific, regardless of whether that information is inhibitory or excitatory, first- or second-learned. On testing this implication of Bouton's (1997) proposal, Rosas and Callejas-Aguilera (2006) found that cue-outcome relationships learned either concurrently, or after extinction became context specific (see also Rosas, García-Gutiérrez, & Callejas-Aguilera, 2006).

The results reported by Rosas and Callejas-Aguilera (2006) suggest that contextual dependency does not depend on a feature of the information, but on a characteristic of the situation that makes participants to pay attention to the context where the information is learned (see also Rosas et al., 2006). However, these results were obtained in a human predictive learning situation. Results in human causal/predictive learning tasks have shown to be quite similar to the results obtained in animal conditioning with respect to the effects of context switches on extinction and other forms of interference –compare for instance the results reported by Rosas and Bouton (1998) with the results reported by Rosas et al. (2001).The goal of this type of research has been to test whether effects reported in nonhuman animal research could be replicated in humans. From the evolutionary perspective, human and nonhuman animals share basic mechanisms of learning and memory. Accordingly, basic learning and memory effects found in animal learning are expected to be replicated in humans.

However, when the effect is reported in human predictive learning, as it is the case of the attentional effect of interference on context processing reported by Rosas and Callejas-Aguilera (2006), the inference about the presence of that effect in nonhuman animals might not be so straightforward. Though attentional processes have been reported to play an important role in animal learning (e.g., Mackintosh, 1975; Pearce & Hall, 1980), the attentional effect of interference on context processing could be restricted to humans, or even to human predictive learning. To conclude that this is a basic memory mechanism it would be necessary to show this effect in nonhuman animals.

The goal of this experiment was to test whether context dependency of a CS-US relationship depends on the ambiguity produced by extinction of a different CS, as a way to evaluate if the attentional mechanism proposed by Rosas and Callejas-Aguilera (2006) is a basic retrieval mechanism that may be shared by other animal species, besides humans.

The design of the experiment is presented in Table 1. A 2 (X treatment: Unpaired versus Extinguished) x 2 (Test context: Context A versus Context B) factorial design was used in the experiment. All the rats received pairings between a flavour (Y) and the gastric malaise produced by an intra-peritoneal injection of LiCl in Context A. An extinction test with Y was then conducted. Groups EA and UA received the test in Context A (the conditioning context) while groups EB and UB received the test in Context B (a different, but equally familiar context). Extinction (EA and EB) and unpaired (UA and UB) groups differed in the previous experience with an alternate flavour (X). Extinction groups were sequentially exposed to conditioning and extinction of X. Unpaired groups received the same exposure to flavour X and the US, but X and the US where presented unpaired.

According to the results reported by Rosas and Callejas-Aguilera (2006; Rosas et al., 2006) in human predictive learning, aversion to Y should be weaker in the alternate context (group EB) than in the acquisition context (group EA) in the extinction groups, while no differences were expected in the control groups.

Method

Animals

Thirty two female Wistar rats were used in the experiment. Rats were about 70 days old with a mean weight of 183.72 grams at the beginning of the experiment. They were individually housed in standard Plexiglass cages inside a room maintained on a 12-12 hrs. light-dark cycle with the light part of the cycle beginning at 7 am. Rats were water deprived 24 hr. before the beginning of the experiment. Throughout the experiment rats were maintained on a water-deprivation schedule that included 2 daily 15-min sessions of free access to fluid. The first session took place at 9:00 am, and the second session begun at 7:00 pm.

Aparatus

Two flavours (a solution of 0.05 % saccharine “Sigma Chemical Co.” and a solution of 0.4% salt, both diluted in distilled water) were counterbalanced as conditioned stimuli X and Y. Illness was induced by a 2% body-weight intraperitoneal injection of 0.15 Molar LiCl. Two different sets of Plexiglass cages (14x23x23cm, HxWxD) were used as experimental contexts (A or B), counterbalanced between subjects. In one of set the walls of the cages were covered with squared pattern paper (red and white squares –7 mm. side). In the other set, cage walls were covered with dark green paper, and the floor of the cages was covered by standard two-and-a-half dozen recycled fibre paper egg trays adapted to the floor of the cage. Cages were wiped up, and egg trays were changed after each daily session. For half of the rats in each group, red squared boxes in the morning were context A, and green boxes in the evening were context B, while the opposite was true for the other half. Fluids were administered in 150 ml. bottles with a standard spout.

Procedure

Days 1-3. Rats received distilled water in the two daily sessions in the colony room. On day 3, rats were assigned to groups EA, EB, UA and UB matched on water consumption during the three prior days.

Days 4-5. All rats received distilled water in their two daily intakes in the experimental contexts.

Day 6. All the rats received free access to X in Context A. In groups EA and EB, X was followed by an injection of LiCl. Immediately after the LiCl injection, rats were left in Context A for 15 minutes, before taking them to their home cages. Post-injection procedure was always the same. Rats received distilled water in context B during their other session on this day.

Day 7. It was identical to days 4-5 with the exception that groups UA and UB received an injection of LiCl after their water consumption in context A.

Day 8. Rats received distilled water in their home cages.

Days 9-11. Rats in all groups received 3 sessions of exposure to X in context A while they received water in Context B.

Day 12 (Conditioning of Y). All the rats received free access to flavour Y followed by an injection of LiCl in context A. They received water in Context B.

Day 13. Rats received distilled water in their home cages.

Day 14-16 (Test). All the rats received free access to Y in one of the two daily sessions while receiving water in the alternate session for a total of 3 extinction trials. Rats in groups EB and UB received Y in context B (a context different from the conditioning context), and rats in EA and UA groups received Y in context A (the conditioning context).

Dependent variable and data analysis

Fluid consumption was recorded throughout the experiment by weighing the bottles before and after the sessions. Consumption was evaluated with an analysis of variance (ANOVA). Planned comparisons were made by using the methods discussed by Howell (1987, pp. 431-443). The rejection criterion was set at $p < .05$.

Results

Figure 1 presents the mean consumption of flavour X during the conditioning day, and the three days of exposure to the flavour in groups EA, EB, UA and UB. A 2 (X treatment) x 2 (Test context) ANOVA conducted with data from the conditioning day found no significant main effects or interaction between them, $F < 1$. A 2 (X treatment) x 2 (Test context) x 3 (Day) ANOVA conducted with data from the three days of exposure to X found a significant X treatment x Day interaction, $F(2, 56) = 19.77$ (MSe=1.98). Subsequent analysis conducted to explore the X treatment x Day interaction found that the simple effect of day was significant in groups extinguished (E), $F(2, 56) = 59.22$ (MSe=1.98), while it was not significant in groups unpaired (U), $F(2, 56) = 2.92$ (MSe=1.98), reflecting the effect of the differential treatment received by X in groups E and U. Consumption of X in paired groups increased as a consequence of extinction, while consumption of X in the unpaired groups remained unchanged across trials. This increase of consumption of X in groups E did not reach the level of consumption shown by groups U, as the simple effect of treatment was still significant in the last extinction trial, $F(1, 45) = 5.01$ (MSe = 5.61).

Figure 2 presents the mean consumption of flavour Y in the conditioning day, and in the 3 days of testing in groups EA, EB, UA, and UB. A 2 (X treatment) x 2 (Test context) ANOVA conducted with data from the conditioning day found no significant main effects or interaction between them, $Fs < 1$.

However, a 2 (X treatment) x 2 (Test context) x 3 (Day) ANOVA conducted with data from the three days of testing with Y found a significant 3-way interaction, $F(2, 56) = 3.31$ (MSe=2.83). Subsequent analysis conducted to explore the 3-way interaction found that the Test context x Day interaction was significant in groups E, $F(2, 56) = 3.40$ (MSe=2.83), but it was not significant in groups U, $F<1$. Exploration of Test context x Day interaction in groups E revealed that the simple effect of Test Context was significant in Days 1 and 2, *Fs*(1, 52) = 5.30 and 4.85, respectively (MSe=6.24).

Thus, the deleterious effect of context change on Y appeared only when the animals underwent extinction with a different flavour. In the absence of extinction of X, aversion to Y was similar across contexts regardless of the extinction trial.

Discussion

The reported experiment explored the influence of extinction of a flavour on context dependency of a different flavour that was subsequently followed by the US. Retrieval of conditioning of a flavour-US association was found to be context dependent when the flavour-US training followed conditioning and extinction of a different flavour, while no effect of context change on conditioning was found in the absence of previous extinction of the alternate flavour.

Context dependency in this experiment was found on a CS that had no mixed history of reinforcement. Thus, this CS was neither ambiguous, nor a conditioned inhibitor. This result is not expected from the explanations of the context switch effects in terms of differentially affecting different types of information (second-learned or inhibitory; Bouton, 1993; Nelson, 2002). However, it is consistent with Bouton's (1997) proposal that ambiguity in the meaning of the cues prompts attention to the contexts, if we accept that such attention generally affect to all the CS-US associations that are learned within the extinction context.

This inference was drawn by Rosas and Callejas-Aguilera (2006; see also Rosas et al., 2006) and, in agreement with the results obtained in this experiment, these authors found that all the information learned after extinction became context specific, regardless of the kind of information or the context where it was learned (see Rosas & Bouton 1998, for the effect of context switches on extinction in conditioned taste aversion). To explain their results in human predictive learning, Rosas and Callejas-Aguilera (2006) suggested that the ambiguity in the meaning of the cue that extinction produces led participants to pay attention to the context, so that all the information learned after extinction begun became context dependent. The results obtained in this experiment are in agreement with that interpretation of the effects of context change.

It should be noted that this results were reached in a situation where consumption of X in groups E did not reach the same level shown by consumption of the same flavour in groups U by the end of the extinction treatment. This result is not surprising, given that Rosas and Bouton (1996, Experiment 4) have reported that the asymptote of extinction in taste aversion is reached below the level of consumption of unpaired groups. However, it does raise the question of whether context specificity of unambiguous information would be obtained if extinction is extended beyond the asymptote. Thought there is nothing in the reported data that allow answering this question, some results in the animal literature indicate that the effect of context change on extinction weakens when the level of extinction increases (e.g., Rosas, García-Gutiérrez, & Callejas-Aguilera, submitted; Thomas et al., 2003). Accordingly, it might be expected that the attentional effect of extinction on context processing may disappear when the number of extinction trials is increased. At any rate, this possibility does not preclude the conclusion that, under the present circumstances, extinction of a conditioned flavour makes conditioning of an alternate flavour context specific.

Additionally, this experiment found context-specificity of an unambiguous CS after extinction in nonhuman animals. Finding this result in animal conditioning suggest that the attentional mechanism of context processing suggested by Rosas and Callejas-Aguilera (2006) in their human predictive learning studies is a basic mechanism of memory retrieval that can be found in other animal species, the laboratory rat in this case. Additional research should explore whether inhibition and second-learned information's context dependency is independent of the effect of attention that seem to be aroused when they are acquired.

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Table 1

Experimental design

Group	Conditioning of X	Extinction of X	Conditioning of Y	Test with Y
EA	A: X+ / B: W	A: X- / B: W	A: Y+/ B: W	A: Y-/ B: W
EB	A: X+ / B: W	A: X- / B: W	A: Y+/ B: W	A: W / B: Y-
UA	A: X-/+ / B: W	A: X- / B: W	A: Y+/ B: W	A: Y-/ B: W
UB	A: X-/+ / B: W	A: X- / B: W	A: Y+/ B: W	A: W / B: Y-

Note: The first letter in the group's label reflects the treatment received by X (Extinguished or Unpaired). The second letter reflects the Test context with Y (A, Conditioning context or B, a different context). A & B were two different boxes and times of day, counterbalanced. 0.05% saccharine and 0.4% salt solutions were counterbalanced as X and Y. W: Water. "+": LiCl injection (0.15 molar, 2% body weight). "–": No injection.

Figure legends

Figure 1. Mean consumption of flavor X in the conditioning day, and in the 3 days of flavor exposure in Context A in groups EA, EB, UA, and UB. The first letter in the group's label represents the treatment received by X (E, extinguished or U, unpaired). Error bars denote standard errors of the mean.

Figure 2. Mean consumption of flavor Y in the conditioning day, and in the 3 days of testing in groups EA, EB, UA, and UB. The first letter in the group's label represents the treatment received by X (E, extinguished or U, unpaired). The second letter represents the Context where the test with Y took place. Conditioning of Y took place in Context A for all the groups. Error bars denote standard errors of the mean.

Figure 1

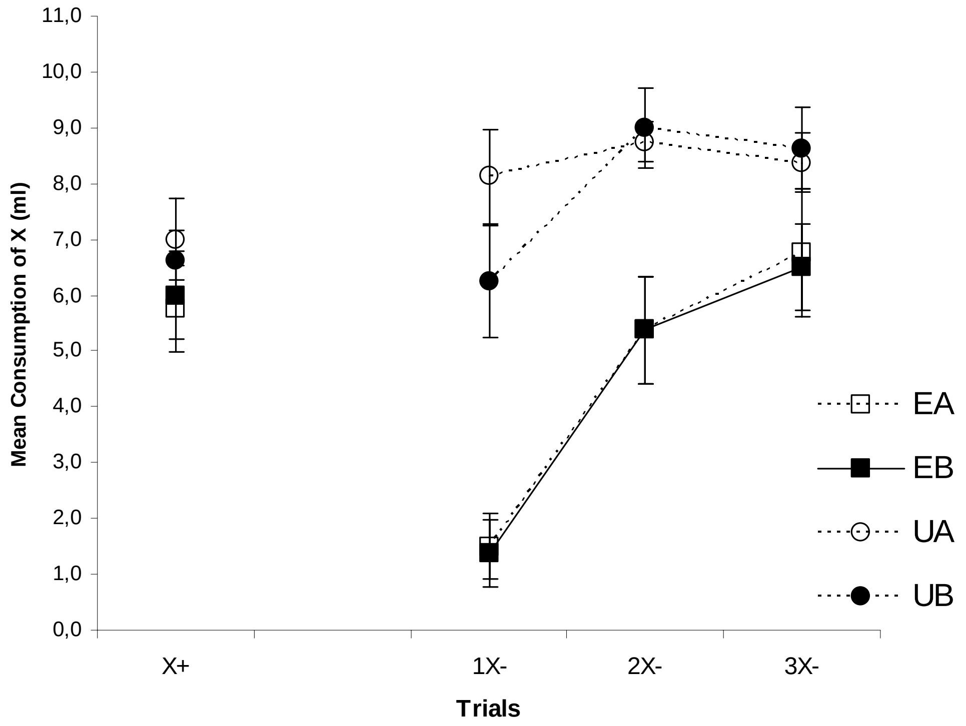
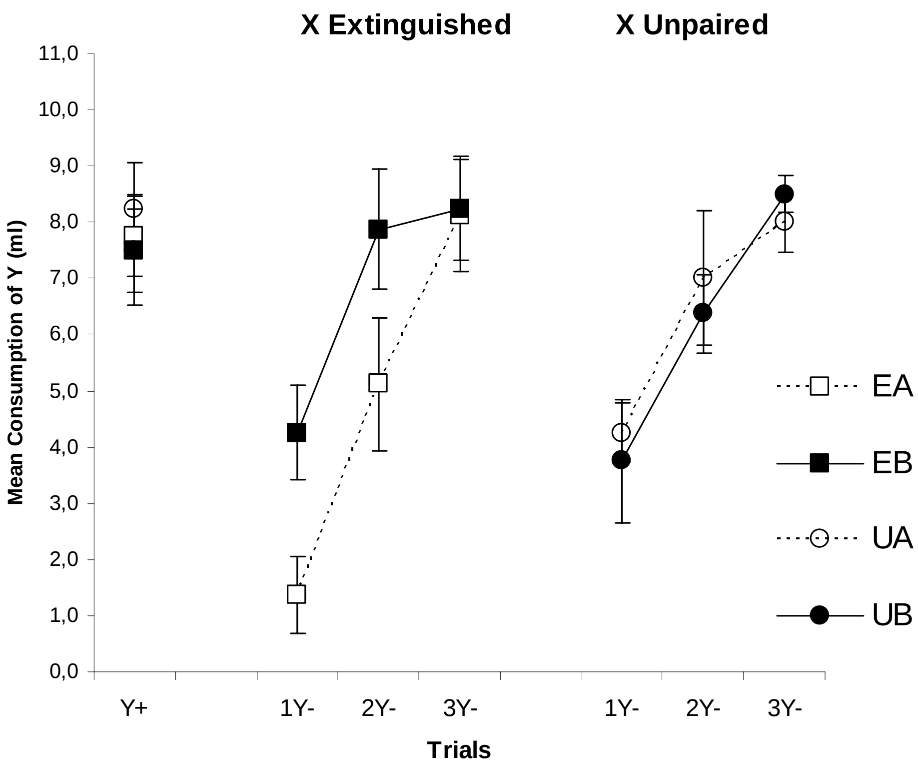

11,0
10,0
9,0
8,0
7,0
6,0
5,0
4,0
3,0
2,0
1,0
0,0
Mean Consumption of X (ml)
X+
1X-
2X-
3X-
Trials
EA
EB
UA
UB

Figure 2


X Extinguished
X Unpaired
11,0
10,0
9,0
8,0
7,0
6,0
5,0
4,0
3,0
2,0
1,0
0,0
Mean Consumption of Y (ml)
Y+
1Y-
2Y-
3Y-
1Y-
2Y-
3Y-
Trials
EA
EB
UA
UB