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Context switch effects and Context Experience in Rats' Conditioned Taste Aversion

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Context specificity of rats' conditioned taste aversion as a function of context experience was assessed in two experiments. Rats received a single pairing between a flavor X and a LiCl injection in a distinctive context (context A) being subsequently tested either in the same context or in a different but equally familiar context (context B). Experiment 1 found that the context change attenuated aversion to X when contexts were new at the time of conditioning. No effect of context change was found when rats had experience with the contexts before conditioning. Experiment 2 found that consumption was lower in the context of conditioning than in the alternative context, regardless of whether the stimulus was conditioned or not, suggesting that contexts exert their control through direct context-outcome associations in this situation.

It is well known that changes in the background contextual cues in which the target cues are embedded may influence retrieval of information in different situations both in human (e.g., Hamid, Wendemuth, & Braun, 2010; Hermans, Craske, Mineka, & Lovibond, 2006; Pineño & Miller, 2004; Rosas, Vila, Lugo, & López, 2001; Smith, 2001) and nonhuman animals (Bouton, 1993; Bouton, Nelson, & Rosas, 1999; Riccio, Richardson, & Ebner, 1984; Spear & Riccio, 1994). The cues that have been shown to be part of the background contextual cues in the literature are quite varied (see Bouton, 2010). For instance, it is generally assumed that external stimuli such as the apparatus or the room where learning takes

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place may play the role of contextual cues (e.g., Fanselow, 2007); but this role has also be claimed to be played by cognitive instructions (e.g., Rosas & Callejas-Aguilera, 2006), and by different internal states such as hormonal (e.g., Ahlers & Richardson, 1985), mood (e.g., Eich, 2007), or deprivation (e.g., Davidson, 1993); it has been also suggested that internal states produced by the ingestion of drugs such as alcohol (e.g., Lattal, 2007) or Benzodiazepines (e.g., Bouton, Kenney, & Rosengard, 1990) may play the role of contexts.

A key question that flies over context studies is the mechanisms through which contexts exert their control of behavior. In many occasions, contexts are assumed to allow for a flexible expression of the information learned within them, so that they exert their control as modulators of cue-outcome associations (e.g., Bouton, 1993, 2007; Bouton & Swartzentruber, 1986). However, the change in background contextual cues may control expression of cue-outcome associations through different mechanisms. For instance, context-switches may lead to a decrease in performance by producing a generalization decrement. That is, changing subjects' perception of the cues so that the cues end being perceptually different from the trained cues (see, for instance, Pearce, 1987). Finally, the decrease in performance produced by context changes may compete for target stimuli for the prediction of the outcomes, so that when target cues are tested outside the learning context, expectative of the outcome decreases because one of the predictors is not longer present (e.g., Rescorla & Wagner, 1972; Wagner, 1981). Impairment of performance after the context change may be due to any of the mechanisms outlined above, and many reports in the literature are unclear with respect to which one is in effect in a specific experimental situation (see Nelson, Sanjuan, Vadillo-Ruiz, Pérez, & León, 2011).

In the present experimental series we are going to focus on context-switch effects after simple acquisition of taste aversion learning in rats. Specifically, we are going to try to isolate some of the factors that determine context-specificity of taste aversion learning, and the mechanism underlying such context-specificity of performance.

The first fact that captures our attention in context-specificity literature is that not all the information seems to be equally context-specific. Bouton's (1993) review of the literature on context-switch effects in animal associative conditioning found that information about extinction is more context specific than information about simple acquisition. This assertion also seems to hold true for human predictive learning (e.g., Nelson et al., 2011; Paredes-Olay & Rosas, 1999; Rosas et al., 2001; Vervliet, Vansteenwegen, & Hermans, 2010; Vila & Rosas, 2001). These results have led Bouton (1993, 1994, 1997) to suggest that background contexts are ignored by the organism when the target cue has a reliable meaning (i.e., during simple acquisition). Only when the meaning of the target cue is changed as it is the case in extinction and other forms of interference, contexts are assumed to be used to disambiguate the meaning of the cue (e.g., Bouton, 1993, 1994).

While the differential effect of context switches on acquisition and extinction is well established within the literature (for a review see Bouton 1993), the idea that retrieval of information about simple acquisition is not context specific has to deal with an increasing number of conflicting results. For instance, Rosas and Callejas-Aguilera (2006, 2007) found that retrieval of information about a reliable cue may be context-specific when it is learned within a context in which a different cue has been extinguished (see also, Nelson & Callejas-Aguilera, 2007; Rosas, García-Gutiérrez, & Callejas-Aguilera, 2006). Similarly, Preston, Dickinson, and Mackintosh (1986) found that conditioned responding (CR) to a conditioned stimulus (CS) that is a reliable predictor of the unconditioned stimulus (US) becomes context dependent when the CS-US relationship is learned within a context that has been made informative by training animals in a discrimination that is reversed across contexts (see also Darby & Pearce, 1995; León, Abad, & Rosas, 2008, 2010a). Context-specificity of cue-outcome relationships has been also reported when they are learned within a context in which ambiguous information is presented by conducting pseudo-discrimination training (Callejas-Aguilera & Rosas, 2010). In all of these studies context-specificity of reliable information is found after different manipulations of non target information (i.e., extinction, discrimination reversal, pseudo-discrimination). However, the literature also shows examples of context-specificity of information after simple acquisition, without additional manipulations involved (e.g., Hall & Honey, 1990; León, Abad, & Rosas, 2010b; Sjödén & Archer, 1989).

Focusing on conditioned taste aversion studies, context specificity of CS-US relationships has been reported in different experimental series of the literature. For instance, Loy, Álvarez, Rey, and López (1993) report contextual control of taste aversion learning after a discriminative training in which the CS-US relationship was in effect in one of the contexts used, but not in the other, so that contexts ended playing the role of occasion setters. More relevant for the present purposes, context-specificity of conditioned taste aversion has also been found in the absence of explicit discriminative training, when a taste-illness pairing is conducted in one context, and tested in a different one (e.g., Archer, Sjödén, & Nilsson, 1985; Archer, Sjödèn, Nilsson, & Carter, 1979; Chelonis, Calton, Hart, &

Schachtman, 1999; Sjödén & Archer, 1989). Although it has been claimed that these results could have been the consequence of flavor variations due to the use of different types of bottles (plastic versus glass), or different spouts (with or without a ball) across different contexts (Holder, 1988a, 1988b; but see Sjödén & Archer, 1988a, 1988b), the possibility of contexts controlling the CS-US relationships cannot be ruled out. Another factor that has been used to explain context-specificity of conditioned taste aversion in these experiments is that rats had no previous experience with the testing context before the test; accordingly, context-switch effects could be just caused by novelty, rather than by a failure to transfer learning across contexts (see Rosas & Bouton, 1997). In agreement with this idea, when context experience is equated before the test, a null effect of context-switch upon simple conditioning has been repeatedly reported in taste aversion literature (see for instance, Rosas & Bouton, 1997, 1998; Rosas, García-Gutiérrez, & Callejas-Aguilera, 2007). However, this is not always the case. Bonardi, Honey, and Hall (1990) equated familiarity across contexts in conditioned taste aversion and reported a null effect of a context switch after a single acquisition trial, but a deleterious effect of context change when a multi-trial acquisition procedure was used (c.f., Hall & Honey, 1990). Although conclusions regarding the effect of the number of training trials in this experimental series are tenuous at best, as they rely on a cross-experiment comparison that involved changes in the US used across experiments, results with respect to context-specificity of conditioned taste aversion are unequivocal. In fact, a closer look to their results reveals a clear (though not reliable) tendency to weaker aversion in context different also after a single conditioning trial (Bonardi et al., 1990, Experiment 1).

Summarizing these conflicting results, simple acquisition of conditioned taste aversion may or may not be context-specific, and the factors that lead to context specificity of conditioned taste aversion are all but clear in the literature. Context-specificity (or not) of conditioned taste aversion has been found both after a single conditioning trial (compare for instance Sjödén & Archer, 1989, with Rosas & Bouton, 1997), and after a multi-trial procedure (Bonardi et al., 1990, Experiment 2). Whether the test context is familiar at the time of testing does not seem to be a key factor on context specificity either, given that context switch effects on taste aversion learning have been reported with familiar contexts in some occasions (e.g., Bonardi et al., 1990) but not in others (e.g., Rosas & Bouton, 1997, 1998; Rosas et al., 2007). An obvious explanation of these differences across reports in terms of context salience is readily discarded, as most of the reports that show perfect transfer of conditioned taste aversion across contexts, they subsequently report context specificity of extinction within the same experimental setting (e.g., Rosas & Bouton, 1997; 1998; Rosas et al., 2007).

So, a question that remains to be solved in taste aversion literature is what makes simple acquisition context-specific in some situations and not in others. A tentative answer to this question may be provided by the theoretical analysis conducted by Rosas, Callejas-Aguilera, Ramos-Álvarez, and Abad (2006). These authors suggest that when human and nonhuman animals are confronting a task for the first time, they pay attention to all the cues available in the environment. Contexts will play a role on retrieval of the information during those early stages of learning either because they enter into direct associations with the outcome (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972; see also Willner, 1978), because they are perceived as part of the configure that forms the target stimulus (e.g., Pearce, 1987, 1994), or because they modulate retrieval of cue-outcome relationships through a high-order relationship (e.g, Bouton & Swartzentruber, 1986; Holland 1983, 1992). Following the ideas of attentional theories of associative learning, it is assumed that attention to the contexts decreases as predictive value of the cues increases because the organism has the opportunity to learn that contexts are irrelevant to solve the task (e.g., Kruschke, 2001; Mackintosh, 1975; Myers & Gluck, 1994; but see Pearce & Hall, 1980). Simple experience with the contexts before receiving CS-US pairings should have nominally the same effects that multiple CS-US trials within a context. In both cases, the treatment should facilitate contexts to be considered irrelevant to the task, so that context-switch effects should not be observed. In fact, if we take a close look to the design of the studies in the taste aversion literature that report a null effect of context change upon acquisition, all of them include at least two sessions of context exposure prior conditioning (e.g., Rosas & Bouton, 1997, 1998; Rosas et al., 2007). Alternatively, those studies reporting context-switch effects after simple acquisition of conditioned taste aversion either did not use context-exposure (e.g., Archer et al., 1985; Sjödén & Archer, 1989), or they used a single exposure to the contexts before conditioning (Bonardi et al., 1990). Context exposure and context familiarity has been shown to play an important role on both, context-US and CS-US associations within taste aversion learning (Bills, Smith, Myers, & Schachtman, 2003; see also Kurz & Levitsky, 1982; Loy et al., 1993; Nakajima, Kobayashi, & Imada, 1995), as well as within some other conditioning methods such as fear conditioning (see for instance, Balaz, Capra, Kasprow, & Miller, 1982). Within taste aversion learning, McLaren, Bennett, Plaisted, Aitken, and Mackintosh (1994) found that context-specificity of latent inhibition could be abolished by giving rats prior exposure to the context of stimulus pre-exposure before the start of the latent inhibition training. Thus, it seems reasonable to suggest that context-exposure before, during, or after conditioning may play an important role on the differential effects of context-switches that are reported in the literature, integrating them within the same theoretical framework (Rosas, Callejas-Aguilera, et al., 2006).

The goal of the present experiments was to test the influence of experience with the contexts prior conditioning on context specificity of conditioned performance, and to begin the analysis of the mechanism underlying context specificity of taste aversion learning. Rats received a single conditioning trial in which flavor X was followed by the US in context A. Testing was conducted in extinction either in context A or in context B. Context-switch effects on taste aversion should appear as higher consumption of X in context B than in context A during the test. Experiment 1 manipulated contexts' experience. Experiment 2 explored the possibility of an explanation of context switch effects in this situation in terms of contexts entering into direct association with the US.

EXPERIMENT 1

Our analysis of the conflicting reports of context-switch effects in the taste aversion literature suggests that they may be due to differential exposure to the contexts prior conditioning across experimental reports. The role of contexts as predictors may be reduced as animals have more experience with contexts and cues over training (e.g., Kruschke, 2001; Mackintosh, 1975; Myers & Gluck, 1994; Rosas, Callejas-Aguilera et al., 2006). Accordingly, the main goal of Experiment 1 was to test the effect of the experience with the contexts in context-specificity of conditioned taste aversion.

Design of Experiment 1 is presented in the top panel of Table 1. Four groups of rats received conditioning with a saccharine solution (X) in a distinctive context (A). Half of the groups were then tested in extinction in context A (groups S) while the other half were tested in a different but equally familiar context (context B, groups D). Procedure in groups PS and PD was identical to the one used by Rosas and his colleagues, except that animals were exposed to the two contexts in the three last days of deprivation prior conditioning, rather than in the last two (e.g., Rosas & Bouton, 1997, 1998; Rosas et al., 2007). Accordingly, no context-switch effect upon conditioned taste aversion was expected in those groups. However, groups S and D received an identical treatment with the exception that contexts were new at the time of conditioning in a situation more akin to that used by Archer and his colleagues (see Archer et al., 1985; Sjödén & Archer, 1989). So, if context experience were the key factor on the differential effect of context change reported in the literature, then a deleterious effect of context change should be found in group D with respect to group S. Note that this experiment uses a procedure that usually leads to no effects of context change on simple conditioned taste aversion (see Rosas & Bouton, 1997, 1998; Rosas et al., 2007).

Table 1. Experimental designs

Exp.	Group	Context Exposure	Conditioning	Test
1	S		A: 1X+ / B: 1W	A: 6X- / B: 6W
	D		A: 1X+ / B: 1W	A: 6W- / B: 6X-
	PS	A: 3W / B: 3W	A: 1X+ / B: 1W	A: 6X- / B: 6W
	PD	A: 3W / B: 3W	A: 1X+ / B: 1W	A: 6W- / B: 6X-
2	S		A: 1X+ / B: 1Y-	A: 6X- / B: 6Y-
	D		A: 1X+ / B: 1Y-	A: 6Y- / B: 6X-

***Note:* A & B were two different boxes and times of day, counterbalanced. X was 0.05% saccharine solution in Experiment 1; in Experiment 2 X and Y were 0.05% saccharine and 0.4% salt solutions, counterbalanced. W stands for water. "+" was LiCl injection (0.15 molar, 2% body weight). "–" means no injection.**

METHOD

Animals. A total of 32 female Wistar rats were used in the experiment. Rats were about two months old with a mean weight of 160.46 g at the beginning of the experiment. They 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 beginning at 7 a.m. 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 two daily 15-min sessions of free access to fluid. The first session took place at 9:00 a.m., and the second session began at 7:00 p.m.

Apparatus. A solution of 0.05% Sacharine (Sigma Chemical Co.) diluted in distilled water was used as conditioned stimulus X. Illness was induced by a 2% body-weight intraperitoneal injection of 0.15M LiCl. Two different sets of Plexiglas cages (14 x 23 x 23 cm, height x width x depth) were combined with the daily sessions (morning or evening) to be used as experimental contexts (A or B), counterbalanced between subjects. In one 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 fiber 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. The design of the Experiment is presented in the top panel of Table 1.

Days 1-5 (Water deprivation). Rats received distilled water in the two daily sessions during the water deprivation phase. All rats received their sessions in the colony room on Days 1 and 2. Rats were then divided in two squads matched in their water consumption on Days 1 and 2. One of the squads was selected as group P (Pre-exposed) and received water in the experimental contexts during Days 3, 4, and 5. The other squad continued receiving water in the colony room. At the end of Day 5, group P was divided in two groups (PS and PD) matched on Day 5 consumption. Similarly, non pre-exposed rats were assigned to groups S and D matched on Day 5 water consumption.

Days 6 (Conditioning). All rats received free access to X in Context A and water in Context B. Half of the rats within each group received the treatment in Context A during the morning, and water in context B during the afternoon, while the contrary was true for the other half of the rats. X was followed by an injection of LiCl in Context A. Immediately after the LiCl injection, rats were returned to Context A for 15 minutes, before being taken to their home cages.

Day 7. Rats received distilled water in their home cages.

Days 8-13 (Test). Rats in groups same (PS and S) received 6 trials with flavor X in extinction in Context A, while rats in groups different (PD and D) received the test in Context B. All rats received water in the other context.

Dependent variable and data analysis. Fluid consumption was recorded throughout the experiment by weighing the bottles before and after each session. Consumption was evaluated with an analysis of variance (ANOVA). The rejection criterion was set at $p < .05$.

RESULTS AND DISCUSSION

Mean saccharine (X) consumption during the conditioning trial was 4.94 (.45), 4.94 (.44), 6.44 (.79), and 6.19 (.34) in groups S, P, PS and PD respectively (standard errors of the mean are presented within brackets). A 2 (Pre-exposure) x 2 (Test context) found a significant main effect of Pre-exposure, F (1, 28) = 6.65 (MSe = 2.27). Neither the main effect of Test context, nor the Pre-exposure by Test context interaction, were significant, $F < 1$. Consumption was higher in groups PS and PD than in groups S and D. This result is not surprising. This lower consumption when animals are placed in the contexts for the first time is a consistently repeated result in our laboratory, likely due to rats in groups S and D spending part of their drinking time exploring the new contexts. This difference should not compromise the conclusions of this experiment, as no interaction with Test context was found, an interaction that will be the key result of the test. It would be yet possible that the difference in consumption would lead to differential levels of conditioning between pre-exposed and non pre-exposed groups. However, as the critical test was conducted in extinction, it would allow for detecting differences in consumption across contexts regardless of the hypothetical level of conditioning, though differential conditioning could make that differences would not appear in the same extinction trials in groups pre-exposed and non pre-exposed.

Figure 1 presents the mean consumption of X (saccharine) across the three 2-Trial blocks of extinction in groups S, D, PS, and PD. Consumption of X, low in the first block increased as extinction progressed. Consumption of X was higher in group D than in group S, while no differences in consumption across extinction seem to appear between groups PS and PD. Statistical analyses confirmed these impressions. A 2 (Pre-exposure) x 2 (Test Context) x 3 (Block) ANOVA found a significant main effect of Block, F (2, 56) = 171.31 (MSe = 0.71). Pre-exposure x Block interaction was significant, F (2, 56) = 4.31 (MSe = 0.71). Most important, the Pre-exposure x Test context x Block interaction was also significant, F (2, 56) = 3.62 (MSe = 0.71). No other main effect or interaction was significant, largest F (1, 28) = 2.08 (MSe = 0.68).

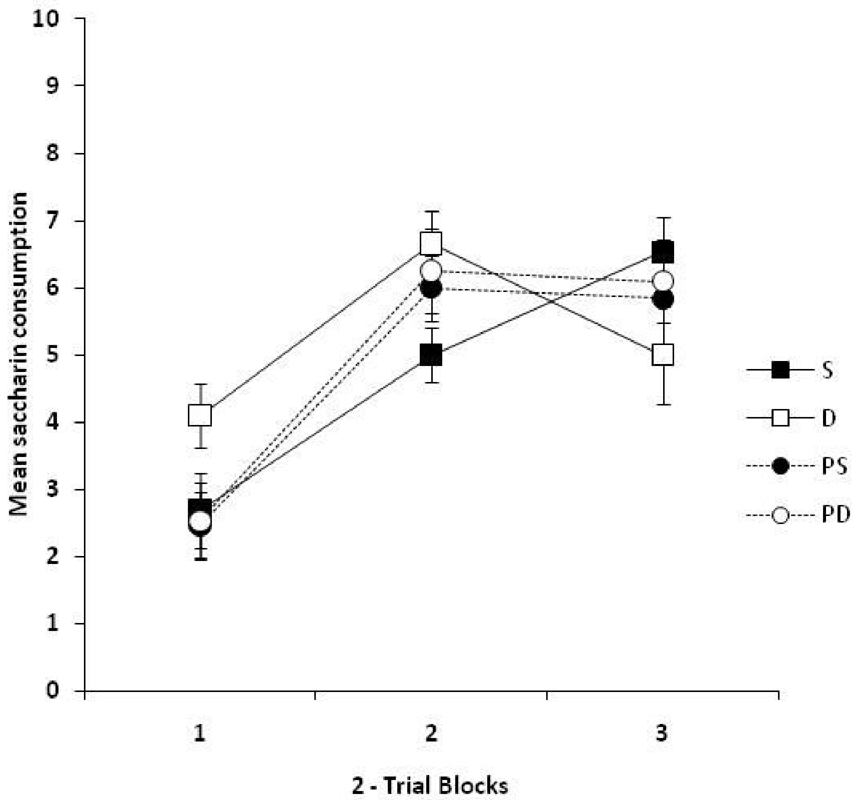

Figure 1. Mean saccharine consumption across the three 2-Trial blocks of the extinction test for groups S, D, PS and PD in Experiment 1. Groups P received exposure to the context before conditioning. Groups S were tested in the conditioning context. Groups D were tested in a different but equally familiar context. Error bars denote standard errors of the mean.

Subsequent analysis conducted to explore the three-way interaction found that the Test context x Block interaction was significant in the absence of context pre-exposure (groups S and D), F (2, 28) = 4.40 (MSe = 0.61). However, when contexts were pre-exposed (groups PS and PD), neither the simple main effect of Test context, nor the Test context x Block interaction were significant, $Fs < 1$. Finally, analyses conducted to explore the Test context x Block interaction in non pre-exposed groups (S and D) found that the simple effect of context was close to being significant in Block 1, F (1, 14) = 3.65 (MSe = 2.16), $p = .07$, it was significant in Block

2, F (1, 14) = 6.71 (MSe = 1.63), and it was not significant in Block 3, $F < 1$. Thus, greater consumption was found in context Different than in context Same in non pre-exposed groups. The differences reached statistical significance only in Block 2, though they were close to significance in Block 1. This is not surprising though, as statistical differences should be hidden by floor and ceiling effects in consumption at the beginning and the end of the testing period.

Mean water consumption in the alternative context (B for groups PS and S, and A for groups PD and D) during the three 2-Trial blocks of the extinction test was between 6.39 (.50) and 4.90 (.54) (standard errors are presented between brackets). A 2 (Pre-exposure) x 2 (Test Context) x 3 (Block) ANOVA only found a significant main effect of block, F (2, 56) = 8.23 (MSe = 1.56). No other main effect or interaction were significant, largest F (2, 56) = 1.88 (MSe = 1.56), suggesting that differences in CS consumption in the test context did not affect consumption of water in the alternative context.

Results in groups pre-exposed replicated the usual lack of effect of context change upon acquisition across different levels of extinction that we usually find in our taste aversion experiments in which rats are familiarized with the contexts before conditioning the flavor (Rosas & Bouton, 1997, 1998; Rosas et al., 2007). However, when contexts were not pre-exposed before conditioning, taste aversion was context specific. Aversion was weaker when the test was conducted in a different but equally familiar context than when it was conducted in the conditioning context. This result is in agreement with the idea of contexts playing a role early in training that may disappear with exposure to the contexts and the task (e.g., Rosas, Callejas-Aguilera et al., 2006). Accordingly, the amount of context experience before conditioning may explain the conflicting results about conditioned taste aversion that are reported in the literature, as there seems to be a negative relationship between the amount of context experience and the likelihood of finding a context-switch effect on acquisition of a conditioned taste aversion (compare for instance, Archer et al., 1985 and Bonardi et al., 1990 with Rosas & Bouton, 1997, 1998).

Once context-specificity of taste aversion learning has been found when contexts are new at the time of conditioning, our next step was to explore the mechanism that underlies such a context-switch effect in this situation. Bouton (1993) suggested that context-switch effects on extinction are based on a modulator role of the context with respect to the extinction information (see Holland, 1983, 1992). Alternatively, contexts may enter into direct associations with the outcome (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972; Pearce, 1987). At first sight, it might be considered that the results obtained in this experiment could favor the interpretation in terms of contexts playing the role of modulators: If contexts specificity would be due to context A been associated with the US in groups S and D during conditioning, leading to an increase in saccharine consumption in context B with respect to the consumption in the allegedly excitatory context A, then consumption of water in context A in the alternative session of the day should have been reduced with respect to consumption of water in context B, a result that was not obtained in this experiment. However, we should be cautious before reaching this conclusion. Animals have been exposed to water followed by the positive outcome of reducing their thirst. Consequently, it would be reasonably to hypothesize that water consumption would be very difficult to be changed in a thirsty animal. Accordingly, using water consumption might not be the most sensitive test of the strength of a context aversion that may be weak. Experiment 2 conducted a test of strength of the aversion to the context by using a fluid that it is not familiar to the animal before the beginning of the experiment.

EXPERIMENT 2

Experiment 1 suggests that experience with the contexts prior conditioning could be a key factor on finding context-specificity of conditioned taste aversion. However, it did not allow for a clear conclusion about which mechanism underlies context-specificity in this situation. Traditionally, contexts have been assumed to play a modulating role akin to the one played by occasion setters (e.g., Holland, 1983, 1992). Under this idea, contexts need not establishing direct associations with the US, but set the occasion in which the CS is going (or not going) to be followed by the US (e.g., Bouton, 1993, 1994; Bouton & Swartzentruber, 1986). Alternatively, contexts may control behavior by entering into direct associations with the outcome either by themselves (e.g., Mackintosh, 1975; Rescorla & Wagner, 1972; Willner, 1978) or in configuration with the CSs (e.g. Pearce, 1987; 1994). Experiments on context-specificity of conditioned taste aversion are in agreement with contexts entering into direct associations with the US (e.g., Loy et al., 1993), with contexts modulating CS-US relationships (e.g., Bonardi et al., 1990; Puente, Cannon, Best, & Carrell, 1988), or even with the idea that both roles may be played at the same time (e.g., Nakajima et al., 1995). The results of groups S and D of Experiment 1 may be explained by either of these mechanisms. From the hierarchical point of view, context A would set the occasion for X to become associated with the US, so that when X is tested in the absence of context A, X-US relationship is not shown (or it is weakened). Rescorla and Wagner (1972) predict the same results with respect to the differential performance in S and D from a different approach. Context A is assumed to enter into an association with the US competing with X for gaining associative strength. So, associative strength of X will be partially overshadowed by context A. Then, when X is tested in context B, the joint associative strength of the incompletely conditioned X and the neutral context B will be lower than the joint associative strength of X and the excitatory context A (see also Mackintosh, 1975; Pearce, 1987, 1994).

Experiment 2 was designed as a test for an explanation of the context-switch effect on simple acquisition of conditioned taste aversion in terms of direct associations between the context and the US during conditioning (see bottom panel of Table 1). Two groups of rats were conditioned with flavor X in context A while exposed to flavor Y in the absence of the US in context B. During the test, Group S (context Same) received extinction with X in context A while Y was presented in context B. However, group D (context Different) received extinction with X in context B while Y was presented in context A. According to the results obtained in Experiment 1 with the non pre-exposed groups, a deleterious effect of context switch on conditioned responding to X was expected when extinguished in context B with respect to when it is extinguished in context A. If this effect was due to context A becoming associated with the US during conditioning, then consumption of Y should be lower in the allegedly excitatory context A than in the neutral context B. Alternatively, if context A would have became an occasion setter, occasion setting properties should not transfer to Y, as occasion setters only have shown to transfer to target stimuli that have been trained with other occasion setters (see Holland, 1992).

METHOD

Animals. A total of 16 female Wistar rats were used in this experiment. Rats were about 5 months old at the beginning of the experiment, with a mean weight of 229.13 g. They were kept under the same conditions than those in Experiment 1.

Apparatus and procedure. Apparatus was the same as in Experiment 1, except for what follows. A solution of 0.4% salt diluted in distilled water was used as a second flavor. Salt and saccharine were counterbalanced as stimuli X and Y.

The design of the experiment is presented in the bottom panel of Table 1. Procedure was identical to the one used in groups S and D in

Experiment 1 except for what follows. Two flavors were presented during conditioning, X followed by the outcome in context A, and Y alone in context B. To guaranty consumption of Y in context B in those cases in which rats were exposed to context A during the first session of the day, conditioning was conducted in two days. During Day 1 the morning session was conducted in context A for half of the rats, and in context B for the other half. Rats in context A received X followed by the US. During the afternoon session of Day 1, and the morning session of Day 2 rats received water in the colony room. Finally, during the afternoon session of Day 2 rats were returned to their respective contexts, and those receiving the session in context A were conditioned with X, while those receiving their session in context B (that had been conditioned in the morning of Day 1) received simple exposure to Y in that context.

A 6-trial extinction test was conducted with flavors X and Y. In group S (Same), flavor X was presented in context A, while flavor Y was presented in context B, the same contexts in which they were presented during the conditioning phase. In group D (Different) contexts were changed with respect to conditioning, with flavor X being tested in context B while flavor Y was tested in context A.

RESULTS AND DISCUSSION

Mean consumption during the conditioning day for groups S and D was 6.38 (.71) and 6.63 (.85) in the case of flavor X (the conditioned flavor), and 5.38 (.92) and 5.50 (1.13) in the case of flavor Y (the non conditioned flavor). A 2 (Test context) x 2 (Stimulus) ANOVA found no significant main effects or interaction between them, $F < 1$. So, no differences as a function of the stimulus or the test context were present during the conditioning day.

Figure 2 presents consumption of X (left panel) and consumption of Y (right panel) across the three 2-Trial blocks of extinction during the test in groups S and D. Conditioned responding to X did not transfer well to context B, as consumption of X seems consistently higher in group D than in group S. The opposite result was found with the non conditioned stimulus. Consumption of Y decreased when tested in context A (group D) with respect to the reference consumption in context B (group S). A 2 (Test context) x 2 (Stimulus) x 3 (Block) found a significant main effect of block, $F\,(2, 28) = 4.45$ (MSe = 1.68). Test context x Stimulus interaction, $F\,(2, 28) = 17.67$ (MSe = 10.90) and Test context x Stimulus x Block interaction, $F\,(2, 28) = 5.04$ (MSe = 2.37) were also significant. No other main effect or interaction were significant, largest $F\,(2, 28) = 2.00$ (MSe = 1.68).

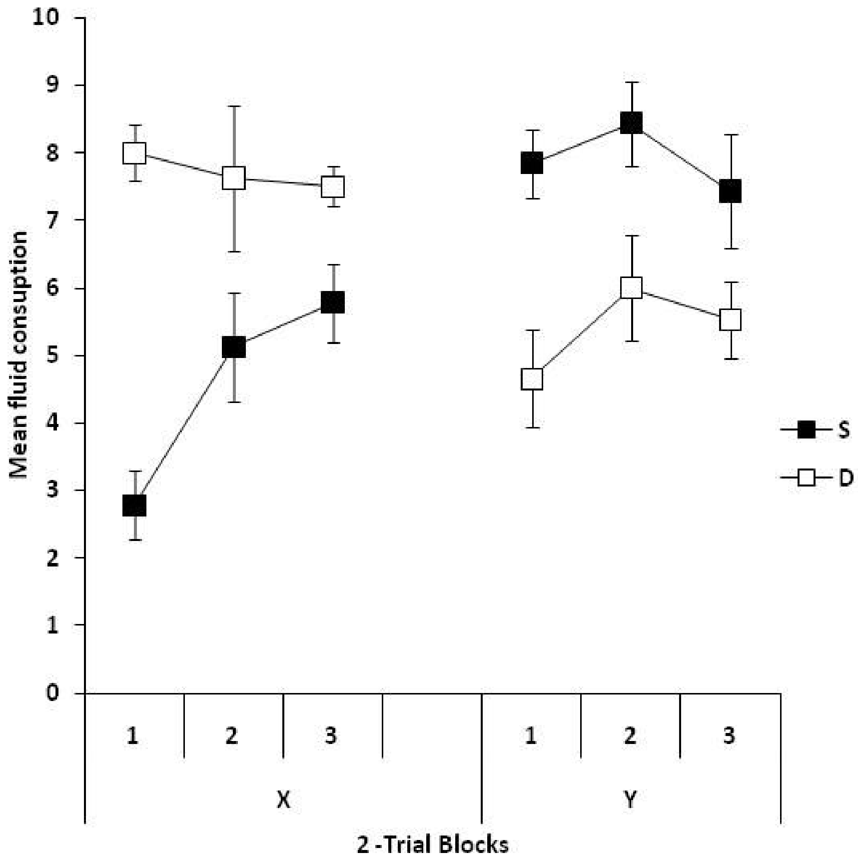

Figure 2. Mean consumption of flavors X (conditioned) and Y (not conditioned) across the three 2-Trial blocks of the extinction test in groups S and D of Experiment 2. Group S received the flavors in the same contexts in which they were presented during the conditioned day, while group S received the flavors in the alternative contexts. Error bars denote standard errors of the mean.

Subsequent analysis conducted to explored the three way interaction found that the Test context x Stimulus interaction was significant in every block of trials, smallest *F* (1, 14) = 6.42 (MSe = 7.77). As the Test context x Stimulus interaction was significant in all the blocks, subsequent analyses explored the simple main effect of context at each level of the variable stimulus, regardless of the block, finding that it was significant in both, flavor X, *F* (1, 14) = 17.38 (MSe = 6.92), and flavor Y, *F* (1, 14) = 9.37 (MSe = 8.00).

The results of this experiment are easily summarized. Regardless of the flavor, consumption was lower in context A (the context in which conditioning took place) than in context B (the context in which the US was never presented). At first sight, differences found in consumption of flavor Y could be explained if rats would regulate their consumption of Y based on their consumption of flavor X so that they could reach the overall daily amount of liquid consumption they need. In other words, consumption of Y could be understood as mirroring consumption of X, so that when the latest is low the animal would increase consumption of the first and vice versa. If this interpretation were true, differences in consumption of X in groups S and D during the first session of the day would explain differences on consumption of Y during the second session of the day. Note that this interpretation would not apply to the animals that were tested with Y during the morning, due to contexts' counterbalancing. So, this interpretation predicts that results should interact with test order. However, a complementary ANOVA 2 (Test context) x 2 (Stimuli) x 3 (Block) x 2 (Test order) conducted with the extinction data found that the 4-way interaction was not significant, $F < 1$, revealing that the 3-way interaction reported above did not depend on the test order. Additionally, note that the same type of differences would have been expected with water consumption in the alternative context between groups S and D of Experiment 1. As stated above, no differences in consumption of water were obtained at testing in Experiment 1. Thus, it seems reasonably safe to interpret these results is in terms of contexts competing with the CS for the prediction of the US conditioning (e.g., Mackintosh, 1975; Pearce, 1987; Rescorla & Wagner, 1972; see also Loy et al., 1993; Willner, 1978), rather than modulating flavor-US relationships (e.g., Bouton & Swartzentruber, 1986; see also Puente et al., 1988). Note that this kind of result implies that to detect context-specificity of the information after simple acquisition it is needed that the outcome is presented only in one of the contexts involved. If the outcome were presented in both contexts, no context-switch effect would be found as the target cue would be tested in a context similarly associated with the outcome as the context in which it was trained (see León, Abad, & Rosas, 2011).

The design of this experiment included the presentation of a new flavor (Y) without an outcome in context B. Note that this procedure could be considered explicit discrimination training between contexts in Experiment 2 that seemingly did not take place in Experiment 1. The question then is whether the conclusions of Experiment 2 can be applied to Experiment 1 and to other situations in which context discrimination training is not conducted. However, note that any procedure that equates context-experience prior the test involves that form of discrimination training. In Experiment 1, the cue-outcome relationship is presented in context A, while water is presented in context B. The only difference between Experiments 1 and 2 on this respect is that Experiment 1 uses a familiar fluid in context B, while in Experiment 2 a novel flavor is presented. If anything, the use of a familiar fluid in Experiment 1 should have facilitated contextual discrimination, as generalization across fluids should have been smaller in Experiment 1 (between saccharine and water) than in Experiment 2 (between saccharine and salt), suggesting that results of Experiment 2 may be extended to situations that equate animals' experience with the contexts before the test. These results cannot be directly applied to situations in which experience with the contexts is not equated during acquisition given that, in those situations, any context effect based on either hierarchical or binary associations would be confounded with the role that may be played by the novelty of the context.

GENERAL DISCUSSION

The goal of the experiments reported in this paper was to explore the factors and mechanisms underlying context-specificity of simple acquisition of conditioned taste aversion. Experiment 1 found that taste aversion was context specific when contexts were new for the rats at the time of conditioning. However, taste aversion transferred perfectly across contexts when they were made familiar to the animals before conditioning. Experiment 2 found that consumption in the conditioning context was lower than in the alternative context regardless of whether the flavor underwent conditioning or not, suggesting that part of the aversion was controlled by the conditioning context, rather than by the CS only.

The role of context experience on context-specificity of taste aversion learning helps to understand the differential results reported in the literature. As stated in the introduction, those reports that inform of a context-switch effect on simple acquisition of conditioned taste aversion in the literature coincide on conducting conditioning within either new (e.g., Archer et al., 1985) or barely familiar contexts (Bonardi et al., 1990). However, reports of perfect transfer of taste aversion across contexts typically conduct conditioning within familiar contexts (e.g., Rosas & Bouton, 1997, 1998; Rosas et al., 2007). The results of Experiment 1 are in agreement with the idea that animals do not seem to use familiar contexts to control simple acquisition (e.g., Kruschke, 2001; Mackintosh, 1975; Myers & Gluck, 1994; Rosas, Callejas-Aguilera et al., 2006).

The finding of context-specificity of simple acquisition establishes some boundaries on the explanation of context-switch effects proposed by Bouton (1993). According to Bouton (1993, 1994, 1997) contexts are assumed not to play a role on retrieval of the information before extinction or some other interference treatment takes place. Bouton (1997) assumes that contexts are not attended during the initial phases of learning, and only when information becomes ambiguous (i.e., because the meaning of the cue has been changed through extinction) contexts become attended and ambiguous information becomes context specific. While this explanation seems to fit most of the results obtained in the literature when extinction procedures are used (but see Rosas & Callejas-Aguilera, 2006, 2007), is not able to explain context-specificity of simple acquisition. Rosas, Callejas-Aguilera et al. (2006) extension of Bouton's (1993) retrieval theory of forgetting introduces a plausible role of attention that allows for explaining context-specificity both in extinction and in acquisition. According to this theory, context specificity in both cases would depend on whether rats pay attention to the contexts during learning. However, the factors that modulate attention to the contexts are assumed to be different during acquisition and during extinction. During acquisition, attention to the contexts it is assumed to occur because animals did not have the opportunity of separating contextual cues from the target information. However, attention to the contexts during extinction is assumed to be raised by the ambiguity on the meaning of the cues that makes the entire information context-specific (see Rosas & Callejas-Aguilera, 2006; Rosas, García-Gutiérrez et al., 2006; c. f. Bouton, 1997).

One important difference between these two theories is that Bouton (1993) specifically assumes that contexts exert their control on behavior by modulating CS-US relationships, rather than by establishing direct relationships with the outcome. However, Rosas and his colleagues (e.g., Callejas-Aguilera & Rosas, 2010; Rosas, Callejas-Aguilera et al., 2006) assume that once the organism pays attention to the context, contexts will exert contextual control on performance, but they do not specify the type of mechanism that will be in effect. In fact, the same contextual cues have shown to exert contextual control of behavior through hierarchical modulation (e.g., Callejas-Aguilera & Rosas, 2010) and through direct context-outcome associations (e.g., León et al., 2011).

Experiment 2 suggests that contexts here control behavior through direct associations with the US. Results of Experiment 2 may be explained by a variety of associative learning models such as Rescorla and Wagner (1972) and Pearce (1987) models of associative learning, just to mention the most representative ones. Applied to the design of Experiment 2, Rescorla and Wagner (1972) model assumes that context A competes with cue X for the associative strength. During this competition part of the associative strength is gained by A. When X is tested in B responding will be lower than when tested in A because part of the response observed in AX comes from the associative strength of A. Conversely, responding to Y will be higher when tested in A, given that A will produce some aversion because of its direct association with the US. Pearce (1987) reaches the same conclusion but for a different reason. His model assumes that configure AX is associated with the US during conditioning. Responding during the test will depend on the similarity between the test compounds and the training configure. Accordingly, responding to BX and AY will be lower than responding to AX, but in both cases should be higher than responding to BY. Results observed in Figure 2 approach this pattern, but do not fit it. It could be argued that differences in BY could have been hidden by a ceiling effect in consumption. However, neither an explanation in terms of competition between cues and contexts, nor an explanation in terms of generalization decrements by context-switches could account for the results obtained in Experiment 1, as both approaches predict the same results regardless of context exposure before conditioning.

To explain the combined results of Experiments 1 and 2 it will be necessary to count with an additional mechanism that allows for discarding the role of irrelevant contexts on performance when rats receive context exposure before conditioning. The idea that attention to irrelevant contexts is attenuated with context experience proposed by Rosas, Callejas-Aguilera et al. (2006) is a possible candidate. However, in this specific situation the same idea was already implemented by Mackintosh (1975) attentional theory of learning. According to this theory, associability of contextual cues will be reduced during contexts pre-exposure, as they are not better predictors of the US than other stimuli present in the situation, so that it will be unlikely that they enter into association with the US at the time of conditioning (see also Pearce & Hall, 1980). Thus, combined results of the two experiments reported above are consistent with the idea that contexts may enter into direct associations with the US in taste aversion learning, and that these direct associations may be attenuated by context pre-exposure, probably because contexts underwent a process of latent inhibition (Lubow, 1973).

Note that contexts seemed to play the role of cues within these two experiments. However, renewal experiments in taste aversion that used the same contexts we used here are better explained if contexts play the role of modulating cue-no outcome associations (Rosas et al., 2007). This idea of different roles for the same type of contexts within taste aversion learning studies comes from a cross-experiment comparison. However, it is in agreement with recent results in the literature showing that contexts may play different roles depending on parametric variations such as the spacing of trials within Pavlovian fear conditioning (Urcelay & Miller, 2010). Future research should focus on specifying the roles contexts play in different experimental settings. Understanding the different roles contexts may play and the variables that establish through which mechanism contexts control behavior in a specific situation should lead to create a definition of context that is all but clear in the literature.

RESUMEN

Efecto de cambio de contexto y experiencia con el contexto en aversión condicionada al sabor en ratas. Dos experimentos evaluaron la especificidad contextual de la aversión condicionada al sabor en ratas en función de la experiencia con el contexto. Las ratas recibieron un único emparejamiento entre un sabor X y una inyección de LiCl en un contexto distintivo (contexto A) recibiendo posteriormente una prueba bien en el mismo contexto o en un contexto diferente pero igualmente familiar (contexto B). El experimento 1 encontró que el cambio de contexto atenuó la aversión a X cuando los contextos eran nuevos en el momento del condicionamiento. No se encontró un efecto de cambio de contexto cuando las ratas tuvieron experiencia con los contextos antes del condicionamiento. El experimento 2 encontró que el consumo fue más bajo en el contexto de condicionamiento que en el contexto alternativo, independientemente de que el estímulo fuera condicionado o no lo fuera, sugiriendo que en esta situación los contextos ejercen su control a través de asociaciones directas contexto-consecuencia.

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