Discrimination Reversal Facilitates Contextual Conditioning in Rats' Appetitive conditioning

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

Associations among different stimuli are not always stable in nature. The environment changes, and what it was certain at a given point may not

be true later. Organisms have to deal with these changes by adjusting their behaviour to the new environmental conditions. These natural situations are mimicked within the laboratory by using experimental procedures in which cue-outcome relationships change across different phases of learning. This is the case of extinction, discrimination reversal or counterconditioning, among others. For instance, in a standard discrimination reversal design, two conditioned stimuli (CSs) are followed by different unconditioned stimuli (USs) in the initial stages of training (i.e., CS1-US, CS2-NoUS), and these relationships are reversed at a given point (i.e., CS1-NoUS, CS2-US) leading the organism to adapt its behaviour to the new environmental conditions (e.g., Bouton & Brooks, 1993; Üngör & Lachnit, 2006).

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

To explain susceptibility of second-learned information to context-changes, Bouton (1997) sustains that the change in the learning conditions raises the organism`s attention to the context where such change takes place, so that retrieval of second-learned, interfering information, becomes context dependent. The idea of interference leading to attentional changes is not new in the literature. Pearce and Hall (1980) suggested that when the

learning conditions become ambiguous, animals tend to attend more to stimuli with uncertain outcomes. In agreement with this idea, Kaye and Pearce (1984) found that orienting responses in rats increase to both, extinguished stimuli and stimuli that underwent partial reinforcement, with respect to stimuli that were consistent predictors of their outcomes. Similar results have been reported in humans by using eye tracking devices, finding that participants spend more time looking at stimuli with uncertain outcomes than looking at stimuli with consistent outcomes (Beesley, Nguyen, Pearson, & Le Pelley, 2015; Hogarth, Dickinson, Austin, Brown, & Duka, 2008).

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

Lamoureux, & León, 2013) and context-conditioning in human participants (Lamoureux, Dunstan, Fabiano, & Nelson, 2017).

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

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

Thus, previous research suggests that uncertainty may increase attention to both, ambiguous CSs (e.g., Kaye & Pearce, 1984), and redundant contexts (Bernal-Gamboa et al. 2014; Rosas & Callejas-Aguilera, 2006, 2007; see also Darby & Pearce, 1995). Taking these two findings together suggests that the interference treatments might lead to a more general increase on attention than the one so far discussed. Larrauri and Schmajuk, (2008; also see Schmajuk and Larrauri, 2006) suggest that the organism's attention to the stimuli increases in the presence of novelty,

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

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

(Beesley, et al., 2015). These apparently conflicting results may be understood is we consider that predictiveness is related with the capacity of attracting attention, while holding attention may be more influenced by the uncertainty of the cues (Koenig, Uengoer, & Lachnit, 2017).

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

EXPERIMENT 1

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

conditioning is expected to be at least partially overshadowed by CS conditioning.

METHOD

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

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

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

Three 10 sec. stimuli were used as CSs: A 2850-Hz 85 dB tone presented through a module placed 22 cm above the floor level in the top right corner of the rear wall; an 80 dB white noise presented through a

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

Procedure.

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

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

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

Table 1. Experimental Design

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

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

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

RESULTS

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

Mean magazine entries during the Pre-CS period in Phase I were 2.07 (SD = 2.79) and 1.50 (SD = 2.12) for CS1, and 1.77 (SD = 1.49) and 1.40 (SD = 1.39) for CS2 in Groups R and D, respectively. A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 8 Session found a significant main effect of

Session, $F(7, 98) = 14.78$, MSe $= 3.11$, p $< .001$, $\eta_p^2 = .51$, and a significant CS x Session interaction, $F(7, 98) = 7.57$, MSe $= 1.15$, p $< .001$, $\eta_p^2 = .35$. No other effect main effect of interaction were significant, largest $F(1, 14) = 3.68$, MSe $= 1.49$, p $=.076$, $\eta_p^2 = .20$ for the main effect of CS. Given that no differences on Pre-CS were expected, subsequent analyses were conducted to determine the importance of the CS x Session interaction. These analyses found that the simple effect of CS was significant only in Sessions 1, $F(1, 14) = 6.84$, Mse $= .02$, p $= .02$, $\eta_p^2 = .33$, and 2, $F(1,14) = 9.96$, Mse $= 6.35$, p $=.007$, $\eta_p^2 = .42$, with higher Pre-CS magazine entries in CS2 than in CS1 in Session 1, and vice versa in Session 2. Pre-CS differences seem to be localized at the very early sessions of training and did not show a regular pattern. Thus, they should not condition the interpretation of differences on the CS entries that appeared later.
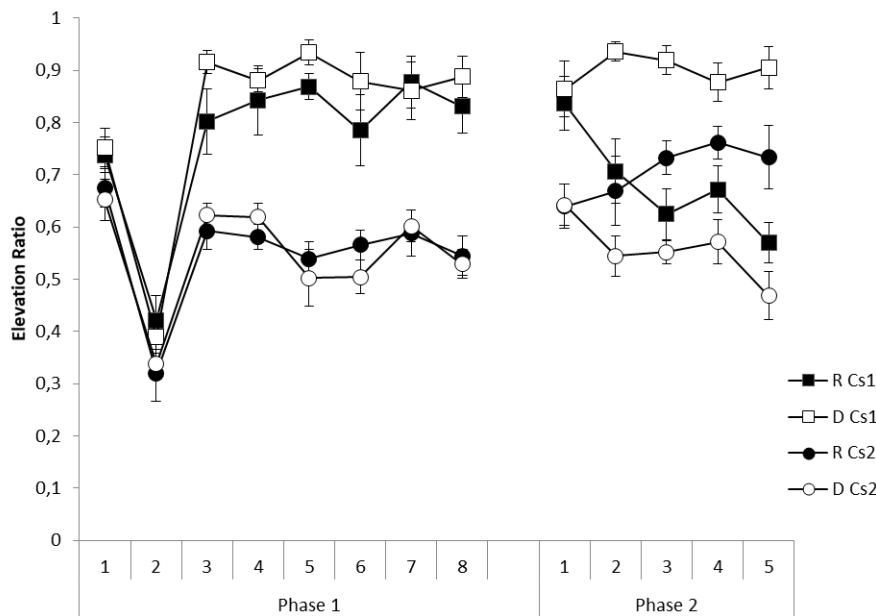
Figure 1. Mean elevation ratios to CS1 and CS2 throughout the 8 sessions of Phase I, and the 5 sessions of Phase II in groups Reversal and Discrimination. Error bars denote standard error of the mean.

A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 5 Session ANOVA conducted with elevation ratios from the 5 sessions of training of Phase II found a significant main effect of CS, $F(1,14) = 31.37$, MSe $= .03$, $p < .001$, $\eta_p^2 = .69$, and significant Group x CS, $F(1,14) = 42.11$, MSe $=.03$, p

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

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

Figure 2 presents the elevation ratios obtained with CS3 during the five sessions of Phase II training in groups R and D. Acquisition of new

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

Mean Pre-CS scores to CS3 were 2.57 (SD = 2.42) and 1.13 (SD = 1.27) for groups R and D, respectively. As it was found with the Pre-CS of CS1 and CS2, responding during the Pre-CS was higher in Group R than in Group D. However, a 2 (Group) x 5 (Session) ANOVA conducted with Pre-Cs entries did not find significant effects, largest F for the main effect of Group, $F(1,14) = 3.11$, MSe = 13.51, $p = .10$, $\eta_p^2 = .18$.
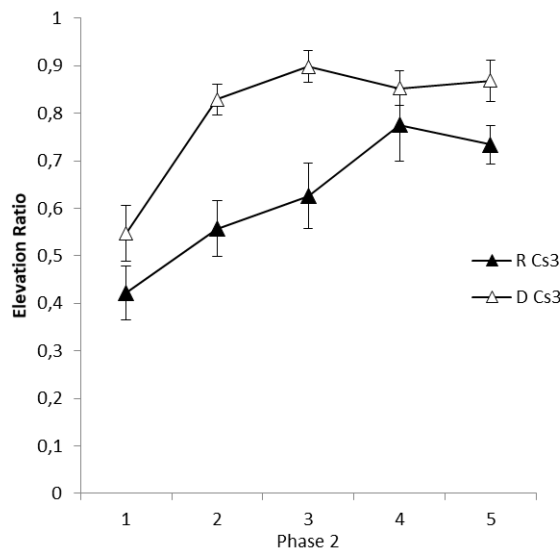
Figure 2. Mean elevation ratios to CS3 throughout the 5 sessions of Phase II training in groups Reversal and Discrimination. Error bars denote standard error of the mean.

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

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

In summary, the results of Experiment 1 suggest that the experience of associative interference does not improve concurrent conditioning of a new CS, though there was a trend that suggests that it might facilitate context conditioning. Facilitation of context conditioning is not clear

though, as numerical differences in magazine entries between groups R and D did not reach clear statistical significance, probably due to the potential weakness of the expected effect, given that contextual conditioning was expected to be partially blocked by CSs conditioning. Experiment 2 was conducted with the goal of exploring further the potential effect of associative interference upon context-conditioning by simplifying the testing situation and increasing the statistical power of the test by an increase of the sample.

EXPERIMENT 2

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

METHOD

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

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

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

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

RESULTS AND DISCUSSION

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

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

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

A 2 Group (R vs. D) x 2 CS (CS1 vs. CS2) x 5 Session x 2 Replication ANOVA conducted with the magazine entries to CS1 and CS2 during Phase II found significant main effects of CS, $F(1, 60)$ = 28.82 , MSe = 95.84, $p < .001$, η_p^2 = .32, and Session, $F(4, 240)$ = 5. 45, MSe = 5.64, $p < .001$, η_p^2 = .08. The interactions Group x CS, $F(1, 60)$ = 94.51 , MSe = 95.84, $p < .001$, η_p^2 = .61, and Group x Session, $F(4, 240)$ = 3.40 , MSe = 7.74, $p < = .001$, η_p^2 = .05, were also significant. Most importantly, the Group x CS x Session interaction was also significant, $F(4, 240)$ = 42.50, MSe = 7.74, $p < .001$, η_p^2 = .41. Further analyses to explore the 3-way interaction found that the CS x Session interaction was significant in Group R, $F(4, 120)$ = 52.05, MSe = 11.94, $p < .001$, η_p^2 = .63, but it was not significant in group D, $F < 1$. Similar to what it was obtained in Experiment 1, this pattern of results shows that reversal training was effective, with group R adapting its behavior to the new circumstances while group D kept its behavior constant. More relevant for the goals of this experiment, a similar analysis conducted with Pre-CS scores during Phase II found a significant main effect of group, $F(1, 60)$ = 15.92 , MSe = 24.92, $p < .001$, η_p^2 = .21. No other main effect or interaction was significant, largest $F(4, 240)$ = 1.41, MSe= 3.54, p = .22, η_p^2 = 02.
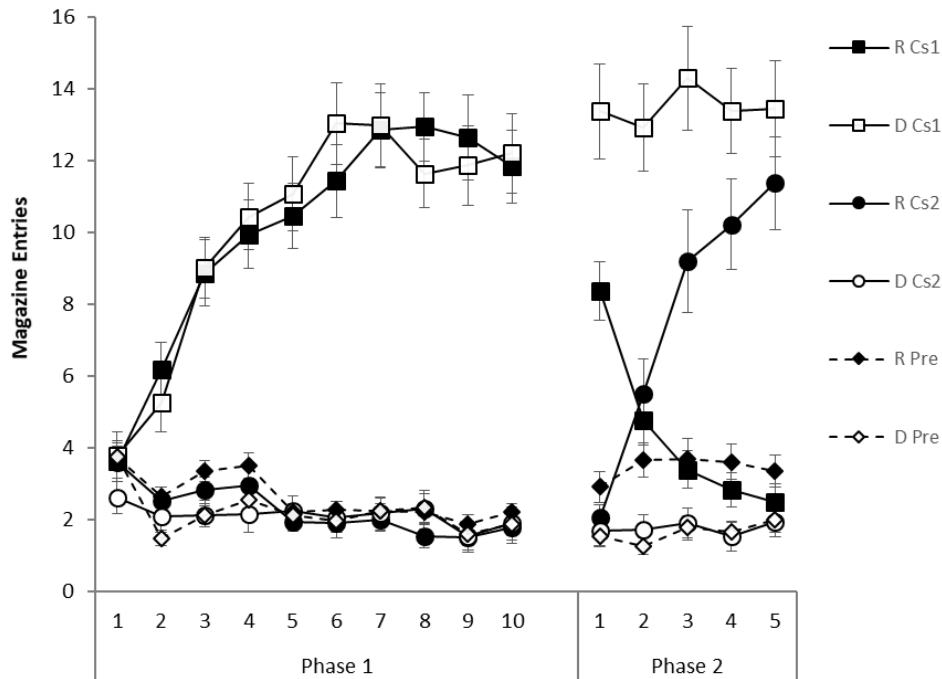
Figure 3. Mean magazine entries to CS1 and CS2 in groups Reversal and Discrimination across the 10 sessions of Phase I and the 5 sessions of Phase 2 in Experiment 2. Pre-CS entries are presented collapsed across CSs. Error bars denote standard error of the mean.

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

In summary, the simplification of the design and the increase of the statistical power of Experiment 2 allowed for finding a clearer evidence of the differential effect of associative interference upon context conditioning. Reversing the discrimination increased responding during magazine training

in the absence of the CS in Group R with respect to Group D. This difference only appeared in Phase 2, when the interference treatment was given to group R, but not to group D, and the difference did not disappear with the training parameters used here.

GENERAL DISCUSSION

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

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

Retardation of CS conditioning after reversal training comes in to conflict with previous results in the literature showing that associative interference improves subsequent learning. For instance, Alcalá, Callejas-Aguilera, Lamoureux et al. (2017) found that temporal discrimination under a fixed time reinforcement schedule developed faster in rats that had previously experienced discrimination reversal than in rats that did not have the discrimination reversal experience. However, rats trained under a variable time reinforcing schedule did not show any evidence for better context conditioning after discrimination reversal (see also Bouton & Peck, 1993). It should be noted that these authors tested the influence of discrimination reversal upon new learning after the reversal phase had ended (see also Alcalá, Callejas-Aguilera, Nelson et al., 2017). In this experiment, the effect of reversing the training conditions was tested during the reversal training phase under the assumption that any effect of associative interference on new learning should be greater the closer the new learning experience is to the associative interference experience. This

manipulation was aimed to favour detection an improvement in context conditioning in this experiment. According to Beesley et al. (2015), interference or uncertainty could enhance an exploration pattern of behaviour. They found that participants' attention to stimuli with uncertain outcomes was kept high, while it decreased when the stimuli outcome was certain. The idea underlying this exploration pattern is that participants would engage in a search for other sources of information in the absence of reliable predictors. In a reversal training situation such as the one used in these experiments, the outcomes of the CSs became uncertain at the start of Phase II, and that should have facilitated the engagement of the rats on exploratory behaviours that would increase context and new CSs attention in group reversal, favouring learning about context and cues when the evaluation is conducted concurrently to the associative interference treatment (see also Bouton, 1997; Ogállar et al., 2017; Rosas et al., 2006).

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

Taking in account all the results reported so far in the literature, the most reasonable conclusion will be that there are some boundaries to the facilitation effects upon new learning that discrimination reversal has. In general, it can be concluded that changes in the conditions of learning may facilitate subsequent learning about contexts and cues. However, this facilitation effect is not a strong one, and detecting one or the other may depend on parametric variables that should be studied both, to better understand the phenomenon, and to establish the boundaries for the effects of uncertainty upon new learning. Further research will need to solve the conflicting results that have been reported in the literature. For instance, it needs to be understood why the effect of associative interference upon subsequent learning is specific to the stimulus that receives the interference

treatment in some situations (Pearce & Hall, 1980; Hall & Pearce, 1982), while in some others, such as in this study, is not (Alcalá, Callejas-Aguilera, Lamoureux, et al. 2017; Alcalá, Callejas-Aguilera, Nelson et al. 2017; Lamoureux, et al. 2017).

RESUMEN

LA INVERSIÓN DE LA DISCRIMINACIÓN FACILITA EL CONDICIONAMIENTO CONTEXTUAL EN UNA PREPARACIÓN DE CONDICIONAMIENTO APETITIVO CON RATAS

Se realizaron dos experimentos con el objetivo de explorar el efecto de experimentar una interferencia asociativa sobre el aprendizaje concurrente acerca de estímulos condicionados y contextos en condicionamiento apetitivo con ratas. Durante la primera fase de entrenamiento, dos grupos de ratas recibieron un estímulo condicionado (CS1) seguido de comida, mientras otro (CS2) se presentaba solo. Durante la segunda fase de entrenamiento, la discriminación se invirtió en el grupo R, mientras se mantuvo constante en el grupo D. Durante esta segunda fase, un estímulo condicionado nuevo (CS3) fue presentado seguido de comida (Experimento 1). La inversión de la discriminación no facilitó el aprendizaje concurrente acerca del nuevo estímulo, pero sí hubo una tendencia hacia la facilitación del condicionamiento contextual, medido a partir de la respuesta de entrada en el comedero en ausencia de estimulación, que se confirmó en el Experimento 2. Estos resultados sugieren que los tratamientos de interferencia pueden facilitar el condicionamiento contextual en circunstancias y con limitaciones que están aún por determinarse.

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