ABA, AAB and ABC renewal with Pavlovian Conditioning of Tentacle Lowering procedure in the snail *Cornu aspersum*

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ABSTRACT

This study assesses the recovery of the conditioned response (CR) due to a contextual change (renewal effect) in the *Cornu aspersum*, using the appetitive Pavlovian Conditioning of Tentacle Lowering procedure. Snails experienced an odorous conditioned stimulus (CS) paired with food (conditioning), followed by the exposition to the CS without any consequence (extinction). Then, they were exposed to the CS in a different context from the extinction one (renewal test). The contexts were three types of illumination. In Experiment 1a, the conditioning was performed in context A, the extinction was conducted in context B and the renewal test was performed in context A. For Experiment 1b, the conditioning and extinction were conducted in context A and renewal was performed in context B. In Experiment 1c, three dissimilar contexts were used for each experimental phase: context A for the conditioning, context B for the extinction and context C for the renewal. In Experiment 2, the renewal magnitude was compared among the three paradigms (ABA, AAB and ABC). Experiments 1a, 1b and 1c showed a recovery of the CR when subjects experienced a contextual change and Experiment 2 showed equivalent levels of renewal in the three paradigms. Learning processes and theories involved are discussed.

1. Introduction

After pairing a CS and an US, animals can learn to produce a conditioned response (CR) in the presence of the CS alone (Pavlovian Conditioning). Then, a decrease of the CR has been observed when the exposition to CS occurs in the absence of the unconditioned stimulus (US), named extinction phenomenon (Pavlov, 1927/, 1970). This phenomenon exhibits context specificity (Bouton, 1993, 2004) and several elements play the role of context such as external cues, internal states, recent events or time (Bouton, 2000). Several learning phenomena which are related to extinction show a recovery of the extinguished response, such as spontaneous recovery, when a long period of time elapses between the extinction training and the test; reinstatement, in which a re-exposition of the US is presented after the extinction; and renewal, in which the extinction phase takes place in a different context from the recovery test one (see Bouton, 2004). In renewal, there are three different paradigms according to where the contextual change takes place: when the contextual change occurs in the extinction phase (ABA, e.g., Anderson and Petrovich, 2015; Chaudhri et al., 2008; Khoo

et al., 2020; Mesich et al., 2022), when the contextual change occurs during the recovery test (AAB, e.g., Bouton and Ricker, 1994) and when three different contexts are employed for each experimental phase (ABC, e.g., Khoo et al., 2020).

Several learning theories may be used to explain the renewal phenomenon. On the one hand, Acquisition theories explain the extinction based on changes in the association that has been initially acquired (e.g., Rescorla and Wagner, 1972; Mackintosh, 1975; Pearce and Hall, 1980; Wagner, 1978, 1981). During the training, the conditioning context acquired an excitatory strength whereas during the extinction, the extinction context acquired an inhibitory strength. Thus, this associative strength would be involved in the renewal effect. An alternative explanation is offered by Retrieval theories, which predict that a new learning takes place during the extinction and this new learning interferes in the previous one (see Bouton, 2004). This interference is modulated by the context, so as long as the renewal test is performed in a different context from the extinction one, the interference of the new learning does not occur and the recovery of the extinguished response will be observed (Bouton, 2004).

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In addition, according to Retrieval theories (Bouton, 1993, 2004), the magnitude of the three renewal paradigms would be equal (see Bernal-Gamboa et al., 2012). In this sense, some studies are congruent with this claim. For example, Todd (2013) –using Operant Conditioning and two different responses (lever press and chain pull) in rats– showed the three renewal paradigms. Moreover, Experiment 2 provided equivalent levels of renewal between ABA and AAB. In Todd et al.'s (2012) study with rats and a Free-Operant Conditioning procedure it was observed that ABA and ABC renewal were strengthened by the increase of the acquisition trials and that there were no differences between both renewal paradigms. Another example is the work of Bernal-Gamboa et al. (2012), in which a Pavlovian Conditioning procedure of Taste Aversion Learning was employed in rats and ABA, AAB and ABC were compared together. The results showed equivalent levels of renewal among them.

Nevertheless, there are experimental works that provide differences among the three paradigms. The most frequent result is that the renewal effect is stronger in ABA than AAB. For example, Experiment 1 of Bouton et al. (2011) using Operant Conditioning in rats showed ABA and AAB renewal but the magnitude of the renewal was higher in ABA than AAB. However, in this study the increase in the number of extinction trials did not affect AAB renewal, in contrast with the study of Rosas et al. (2007) using a Conditioning Taste Aversion Learning procedure (CTA) in rats, in which the increase in the number of extinction trials eliminated the AAB. Thomas et al. (2003), using fear conditioned in rats and lever pressing conditioned suppression, showed a higher renewal magnitude in ABA than AAB. Also, Rescorla (2008), with a sign-tracking procedure in pigeons, provided evidence of renewal in the three paradigms but only ABA and AAB were explicitly compared, showing a lower renewal effect in the latter. Finally, Üngör and Lachnit (2008) compared the three renewal paradigms in humans with a predictive learning experiment and the renewal effect was equivalent in ABA and ABC, whereas AAB renewal was not observed. Other investigations provide differences in the magnitude of renewal between ABA and ABC paradigms. Effting and Kindt (2007), using a differential fear conditioning in humans, provided a higher recovery of the extinguished response in ABA than in ABC. In another study of fear conditioning in humans (Neumann and Kitlertsirivatana, 2010), a higher renewal effect was observed in ABA. Also, Harris et al. (2000) provided the same effect in rats with an Operant Conditioning procedure. The study of Balooch et al. (2012) in humans, with self-reported expectancy of shock and startle blink responses, showed that ABC renewal is attenuated when extinction was carried out in multiple contexts. In a similar direction, Bustamante et al. (2016) working with predictive-learning experiments in humans observed that an extinction in multiple contexts cancelled ABC renewal, but not ABA renewal. The same results were provided by Bernal-Gamboa et al. (2017) in rats, with a lever pressing Operant Conditioning procedure. Finally, the study of Bernal-Gamboa et al. (2014) with Operant Conditioning in rats showed that ABA paradigm had a higher level of renewal than AAB and ABC.

The differences in the renewal magnitude observed in the studies mentioned above can be explained by three mechanisms: in the first one (the excitatory strength of the conditioning context), the conditioning context acquires excitatory strength during training; in the second one (the inhibitory strength of the extinction context), the extinction context acquires an inhibitory strength during extinction phase; and finally, in the third mechanism (the conditioning context control of the CS-US association), the CS-US association acquired in the conditioning phase is controlled by the conditioning context during the extinction (Rosas et al., 2006). The conditioning context plays the role as the retrieval cue for the CS-US excitatory association whereas, the extinction context is considered as a retrieval cue for the CS-US inhibitory association, which develops during the extinction phase, for ABA and ABC renewal paradigms. In addition, the CS-US inhibitory association is retrieved only in the extinction context but, the CS-US excitatory association is generalized to new contexts. Thus, taken into account that in ABC and AAB

renewal paradigms the test contexts do not have experience with the US, the renewal effect can only be attributed to the priority retrieval of the excitatory association (the conditioning context control of the CS-US association) instead of the actual predictive value for the contextual cues (see Rosas et al., 2006, for a review).

The three mechanisms would be involved in ABA renewal, whereas inhibitory strength of the extinction context and the conditioning context control of the CS-US association would be involved in ABC and AAB renewal and AAB renewal should most effectively isolate the last one (Rosas et al., 2006). This claim offers an explanation in which both theoretical accounts (Acquisition and Retrieval theories) are involved for the renewal understanding. However, taking into account the existing literature on the subject, there is no conclusive evidence confirming the explanation of the mechanisms, nor the explanation of the Retrieval theories. Therefore, the debate about this issue is still open.

Renewal effect has been broadly studied in vertebrates such as humans (e.g., Effting et al., 2013; Krypotos et al., 2014; Lipp et al., 2021; Ritchey et al., 2021), rodents (e.g., Bernal-Gamboa et al., 2022; Bouton and King, 1983, 1986; Tamai and Nakajima, 2000), dogs (e.g., Chia, 2020), pigeons (e.g., Donoso et al., 2021; Packheiser et al., 2021; Packheiser et al., 2019), fire-bellied toad (e.g., Mesich et al., 2022) or zebrafish (e.g., Kuroda et al., 2017, Kuroda et al., 2020; Kuroda et al., 2021). However, there are only two studies of renewal in invertebrates (Loy et al., 2020; McComb et al., 2002). In the study of McComb et al. (2002) ABA renewal was observed in the snail *Lymnaea stagnalis,* using an Operant Conditioning procedure and food or no food odorant as context. In contrast, Loy et al. (2020) showed ABA renewal in the snail *Cornu aspersum*, using the Pavlovian Conditioning of Tentacle Lowering procedure with odours (Experiment 1) or the photoperiod, defined by the hour of the day and the lighting (Experiment 2), as contexts. Moreover, there are not previous demonstrations of AAB and ABC renewal in invertebrates, neither studies which compare the renewal magnitude among the three paradigms in these species. Thus, the aim of this work is to assess the terrestrial snails *Cornu aspersum* in the three types of renewal, showing whether the three paradigms can be observed and, in that case, to compare the magnitude of renewal among them. Experiment 1a was designed to replicate the results shown in Loy et al. (2020), using illumination as context instead of the photoperiod to simplify the procedure. Then, Experiments 1b and 1c were conducted to study AAB and ABC renewal paradigms, respectively, using illumination as context. Finally, the last experiment (Experiment 2) was carried out to compare the magnitude of the recovery in the three renewal paradigms.

2. Method

2.1. Subjects and housing

The subjects used in this study were the common snails *Cornu aspersum*, which were collected from the wild in a garden from Noreña (Asturias). They lived grouped among the garden stones and their food was the green leaves of the ferns present in their habitat. They were manually collected from their habitat and taken directly to the laboratory, where they were maintained and prepared for each experiment.

In Experiment 1a (ABA renewal), 24 adult snails were employed with a mean shell diameter of 28.08 mm (range 24–32 mm). In Experiment 1b (AAB renewal) there were 36 adult snails with a mean shell diameter of 28.5 mm (range 24–34 mm). Firstly, for Experiment 1c (ABC renewal), there were 20 adult snails with a mean shell diameter of 24.85 mm (range 20–33 mm). Then, two replicas (BCA and CAB) were conducted with 10 adult snails per replica. The mean shell diameter for BCA renewal was 27.7 mm (range 21–31 mm) and the mean shell diameter for CAB renewal was 27.7 mm too (range 25–35 mm). Finally, in Experiment 2 (magnitude of the renewal effect among the three paradigms) there were 63 adult snails with a mean shell diameter of 24.69 mm (range 17–34 mm). Snails were individually housed in plastic cages (50 ×50×100 mm) with air holes. The house boxes were placed in a

room with a constant temperature of 22ºC and a reversed 12 light/dark cycle, starting at 06:00 am. They were given access to a small amount of water and ad libitum food, which was composed of corn grains for poultry and, prior to the start of the experiment, they were food-deprived for 10 days, in which they did not receive any kind of food. At the end of each experiment, snails were given food ad libitum (corn grains) and placed back into the wild, but in a different garden 50 km away from the place where they were collected in order to avoid their recapture.

2.2. Apparatus and stimuli

The experimental set was a perforated plastic surface (390 ×360 mm; 5.5 mm diameter holes, roughly 2 mm apart from one to another) placed 65 mm above the surface of a table. The experimental room was maintained at 22ºC and lights were used as illumination context: two white lights of LED 5.5 W and LED 7 W were used as the brilliant-light and the dim-light contexts, respectively, and a red light of LED 3 W was used as the dark context. These lights were chosen given that prior research had established the snail's spectral sensitivity range between 390 and 580 nm (Barker, 2006), which is lower than the red light range (620 and 750 nm), but not for the brilliant and dim light range, so although the red light cannot be perceived by snails, they can perceive the brilliant and the dim light (Zieger and Meyer-Rochow, 2008). By contrast, the red light is perceived by humans and its use allows us to observe the response of the subject properly. The dimensions of the bulbs for the dark and brilliant-light contexts were 60 × 118 mm and for the bulb of the dim-light context 50 × 100 mm. They were located over the surface at 700 mm height. The luxes for each light was: brilliant-light 11.182,34 lux, red light 5.804,84 lux and dim-light 1.994,30 lux.

The stimuli employed were a mango solution (oil brand *La Casa de Los Aromas*, 2 ml/L of distilled water) as the CS and carrot as the US. The pieces of carrot had a mean diameter of 27 mm (range 22–29 mm) and were 1 mm thick.

2.3. Procedure

Tentacle lowering was measured as the CR by one observer, who was not aware of the group to which each subject belonged. This measure consisted of counting in real time the number of times the left tentacle descended below an imaginary line, drawn horizontally just above the head of the snail (Ungless, 1998, 2001).

The experimental design is summarized in Table 1. In Experiments 1a, 1b and 1c, snails were randomly assigned to two groups according to the contextual change during extinction. In the Experiments 1a, during

the conditioning, subjects from "ABA group" were exposed to the CS paired with the US in context A. Then, in the extinction phase, they were exposed to the CS alone in a different context (context B). Finally, during the renewal test, they were exposed to the CS in the same context as the conditioning phase (context A). However, subjects from "AAA group" received all the experimental phases in the same context. In Experiment 1b, subjects from "AAB group" received the conditioning and the extinction in context A but, during the renewal test, they were exposed to the CS in a different context (context B). As in Experiment 1a, subjects from "AAA group" were exposed to all experiment phases in the same context. For these experiments, two illuminations were used as contexts: the brilliant-light context and the dark context. In addition, both contexts were counterbalanced so, for half of the subjects in each group, the conditioning was performed in the light context and, for the other half, it was performed in the dark context. In Experiment 1c, for the conditioning phase, subjects from "ABC group" were exposed to the CS paired with the US in context A. Then, in extinction, subjects were exposed to the CS alone in context B. Finally, during the renewal test, they were exposed to the CS in a third different context (context C). For subjects from "ABB group" the conditioning was carried out in context A, but the extinction and the renewal test were conducted in context B. Besides the contexts used in the previous experiments the dim-light context was included as the third one. Taking into account that there are multiple possible counterbalances for the ABC design, three one were chosen at random, based on a Latin square criterion, for experimental and control groups (ABC, BCA and CAB; ABB, ACC and CAA, respectively). In addition, the BCA-ACC counterbalance allows us to know if the snails discriminate between the two types of light context used in this work: brilliant-light and dim-light context.

In Experiment 2, snails were randomly assigned to four groups according to the renewal paradigm. Subjects from the "ABA renewal group" received the contextual change during extinction, subjects from the "AAB renewal group" received the contextual change during renewal test, subjects from the "ABC renewal group" received three different contexts for each experimental phase, and the "AAA renewal or control group" received the same context throughout all experimental phases. "AAA group" was used as control because it was employed in the study of Bernal-Gamboa et al. (2012), which we take as a reference for the design of Experiment 2. The role of the contexts was not counterbalanced.

At the beginning of each trial, snails were sprayed with fresh water to induce activity and at the end of each trial they were returned to their home boxes without any access to the stimuli used throughout the experimental phases. Then, the experimental setting was cleaned. The experimental phases were carried out in different days and always they

Table 1
Design for each experiment.

Exp.	Groups	Pre-Test	Conditioning	Conditioning Test	Extinction	Extinction Test	Renewal Test
1a	ABA	(A)CS	(A)CS+US	(A)CS	(B)CS	(B)CS	(A)CS
	AAA				(A)CS	(A)CS	
1b	AAB	(A)CS	(A)CS+US	(A)CS	(A)CS	(A)CS	(B)CS
	AAA						(A)CS
1c	ABC	(A)CS	(A)CS+US	(A)CS	(B)CS	(B)CS	(C)CS
	ABB						(B)CS
	BCA	(B)CS	(B)CS+US	(B)CS	(C)CS	(C)CS	(A)CS
	ACC	(A)CS	(A)CS+US	(A)CS			(C)CS
	CAB	(C)CS	(C)CS+US	(C)CS	(A)CS	(A)CS	(B)CS
	CAA						(A)CS
2	ABA	(A)CS	(A)CS+US	(A)CS	(B)CS	(B)CS	(A)CS
	AAB				(A)CS	(A)CS	(B)CS
	ABC				(B)CS	(B)CS	(C)CS
	AAA				(A)CS	(A)CS	(A)CS

*Note: Exp. = Experiment. The CS employed was a solution of mango and the US was a piece of carrot. In Experiments 1a and 1b, A and B were counterbalanced as the brilliant-light or dark context. In Experiments 1c the three replicas with different counterbalance of the contexts were showed. Experiment 2 the contexts were not counterbalanced. Always in Experiments 1c and 2, A was the brilliant-light context, B was the dark context and C was the dim-light context. The symbol "+" indicates that stimuli were paired.

started at 8:00 a.m.

2.3.1. Pre-test

On the first day of the experiments, tentacle lowering was measured for each subject individually, during all the time that the CS was presented. Snails were exposed to the odour (CS) for 2 min in the same context as conditioning. This odour was placed below the perforated surface in a dish containing four cotton pads and each one was impregnated with 2 ml of the solution.

2.3.2. Conditioning and conditioning test

On the following day, subjects were exposed to CS paired with access to food (US) for 2 min. A piece of carrot was placed in front of snail whereas the odour was placed in the same way as the previous phase. The conditioning was conducted in groups, with 6 trials per session and an ITI of 58 min. On the next day of one conditioning session, the conditioning test was carried out at the same time that the first conditioning trial began. In this test, tentacle lowering was measured with the same procedure used during the pre-test and in the same context as the conditioning training. For experiments 1a, 1c and 2 (ABA, ABC with its three counterbalances and the magnitude of the renewal comparison, respectively), one session and one test of conditioning were conducted whereas, for experiment 1b (AAB renewal), two sessions and two tests of conditioning were carried out. Fig. 1.

2.3.3. Extinction and the Extinction test

On the following day after finishing the conditioning treatment (training and test), snails were exposed to the CS for 2 min in each extinction trial, but they did not have access to the US. Snails from the control groups were exposed to the CS in the conditioning context, whereas snails from the renewal groups were exposed to the CS in a different context from the conditioning one. As during the conditioning, the extinction was carried out in groups, with 6 trials per session and an ITI of 58 min. On the next day of one extinction session, at the same time that the first extinction trial began, tentacle lowering was measured in the same way as previous tests, considering the different contexts used for each group during the extinction. For experiments 1a, 1c and 2 (ABA, ABC with its three counterbalances and the magnitude of the renewal comparison, respectively), one session and one test of extinction were conducted while, in experiment 1b (AAB renewal), two sessions and two tests of extinction were carried out.

2.3.4. Renewal test

On the next day after finishing the extinction treatment (extinction phase and extinction test), the renewal test was conducted using the same procedure as previous tests, but subjects from the renewal groups were exposed to a different context for the extinction one, whereas subjects from the control groups were exposed to the extinction context.

2.4. Statistical analysis

The number of times which the subjects lowered the left tentacle was measured during the experimental tests. A repeated-measures analyses of variance (ANOVAs) and the analyses of the interactions with the Bonferroni corrected pairwise comparisons were carried out. The level of significance used was $\alpha = 0.05$ and the effect sizes for ANOVAs were reported as partial Eta-square (η_p^2). Moreover, in Experiment 1a comparisons among pre-test, conditioning test and extinction test conducted by Bonferroni were included, proving that the conditioning and extinction phases were efficient. They were carried out in the rest of experiments but they were omitted to simplify the text. These analyses were run using SPSS v21 (SPSS Inc., Chicago, IL, U.S.A.).

3. Results

3.1. Results of experiment 1a (ABA renewal)

Fig. 2 shows the tentacle lowering mean in both groups throughout all the experimental tests. It can be observed that both groups showed equivalent levels of conditioning and extinction. However, during renewal test, subjects which had received the extinction in a different context from the conditioning one showed an increase in the number of
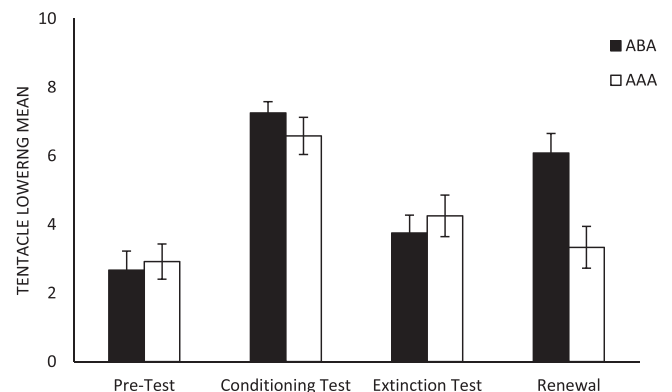

Fig. 2. *Results of Experiment 1a (ABA renewal). *Note.* Tentacle lowering mean is shown for ABA group, represented by the dark bars, and AAA group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.
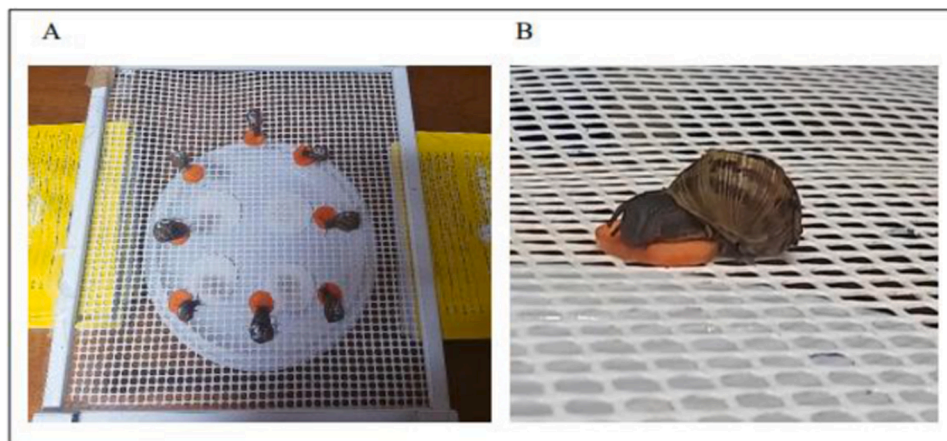

Fig. 1. Conditioning. Panel A shows the experimental setting and how the conditioning was performed in groups. Panel B shows a snail eating during the conditioning (This picture has been obtained from Muñiz-Moreno and Loy, 2022, p.3).

CRs than subjects which had received the extinction and the conditioning in the same context. The description of the results was confirmed by the statistical analyses.

Firstly, the analyses of the context counterbalancing (role of the context) were conducted, in which half of the subjects received the conditioning in the brilliant-light context and the other half in the dark context. A repeated-measures ANOVA was conducted with the tests as the within-subjects factor, and the groups (AAA and ABA groups) and the role of the context as the between-subjects factors. The effect of the context and the effect of the test were significant [ANOVA: $F_{1, 20} = 7.034$, $P = 0.015$, $\eta_p^2 = 0.260$; $F_{3, 60} = 23.217$, $P < 0.001$, $\eta_p^2 = 0.537$, respectively], but not the effect of the group (ABA and AAA) [ANOVA: $F_{1, 20} = 2.664$, $P = 0.118$, $\eta_p^2 = 0.188$]. In addition, there were not significant interactions between the context and the groups [ANOVA: $F_{1, 20} = 0.260$, $P = 0.616$, $\eta_p^2 = 0.013$] and the context with the test [ANOVA: $F_{3, 60} = 0.474$, $P = 0.701$, $\eta_p^2 = 0.023$], while the interaction of the groups with the test was significant [ANOVA: $F_{3, 60} = 4.215$, $P = 0.009$, $\eta_p^2 = 0.174$]. The second-degree interaction was not significant [ANOVA: $F_{3, 60} = 0.523$, $P = 0.668$, $\eta_p^2 = 0.26$]. In all the experimental phases, the mean response of snails was higher when the context was dark in contrast with the brilliant-light context [the brilliant-light context: the pre-test 1.91 ± 0.39, the conditioning test 6.33 ± 0.46, the extinction test 3.66 ± 0.63 and the renewal test 4.33 ± 0.68; the dark context: the pre-test 3.66 ± 0.527, the conditioning test 7.50 ± 0.37, the extinction test 4.33 ± 0.48 and the renewal test 5.08 ± 0.73]. This effect happens because under the circadian cycles of darkness the locomotor activity of snails is greater (Attia, 2004), but since they are counterbalanced, the effect was offset. Thus, the data were collapsed.

The data showed in Fig. 2 were analysed with the repeated-measures ANOVA, with the tests as the within-subjects factor and the groups (AAA and ABA groups) as the between-subjects factors. It showed a significant effect of the test [ANOVA: $F_{3, 66} = 24.325$, $P < 0.001$, $\eta_p^2 = 0.525$], but not a significant effect of the groups [ANOVA: $F_{1, 22} = 2.147$, $P = 0.157$, $\eta_p^2 = 0.089$]. The interaction between the groups and the test was significant [ANOVA: $F_{3, 66} = 4.416$, $P = 0.007$, $\eta_p^2 = 0.167$] so, Bonferroni corrected pairwise comparisons were carried out to analyse this interaction.

Firstly, to provide that conditioning was effective it was compare the pre-test with the conditioning test and there were significant differences between them in both groups [ABA and AAA $P < 0.001$ in both cases]. Then, to observe that extinction treatment has been effective to reduce the CR it was compared the conditioning test with the extinction test and significant differences were shown [ABA $P < 0.001$; AAA $P = 0.007$]. Finally, to show that the CS exposure alone during the extinction training results in a return to the pre-conditioning basal level, the pre-test with the extinction test were compared and there was not differences between them [ABA $P = 1.000$; AAA $P = 0.733$].

Then, the Bonferroni revealed significant differences between groups only in the renewal test (AAA group 3.33 ± 0.60, ABA group 6.08 ± 0.57, $P = 0.003$). Thus, in both groups, equivalent levels of conditioning and extinction were observed. However, subjects which received the extinction in a different context from the conditioning one presented a significant recovery of the extinguished response when they return to the conditioning context during the renewal test in contrast with subjects which received all the experimental phases in the same context, which maintained a low level of the response in the renewal test.

These results showed ABA renewal and corroborated the observations in Loy et al. (2020) with the same invertebrate species. In addition, it is shown that the illumination is an effective context as the photoperiod used in Loy et al. (2020), but the illumination use offers a simpler procedure for the study of this phenomenon in this species. The renewal effect has three paradigms according to the experimental phase in which the contextual change is made: ABA, AAB and ABC. In invertebrates, only ABA renewal has been observed, so the study of the other two renewal paradigms would be a great novelty in the study of the

phenomenon in these species, focusing to understand the role of the context as a predictive value or as an occasion setter. For this reason, in the next experiments (Experiment 1b and Experiment 1c) AAB and ABC paradigms were examined, respectively.

3.2. Results of experiment 1b (AAB renewal)

Fig. 3 presents the tentacle lowering mean in both groups throughout the pre-test, the second conditioning test, the second extinction test and the renewal. It is observed that both groups showed equivalent levels of conditioning and extinction. However, subjects which received the renewal test in a different context from the one of the other experimental phases showed an increment of the CR in contrast with subjects which received all the experimental phases in the same context. This was confirmed by the statistical analyses.

As in the previous study, the analysis of the context counterbalancing was carried out. A repeated-measures ANOVA was conducted, with the tests as the within-subjects factor and the groups (AAA and AAB groups) and the role of the context as the between-subjects factors. There were not significant effect of the context [ANOVA: $F_{1, 32} = 4.045$, $P = 0.053$, $\eta_p^2 = 0.112$] and effect of the group [ANOVA: $F_{1, 32} = 1.404$, $P = 0.245$, $\eta_p^2 = 0.042$], but there was a significant effect of the test [ANOVA: $F_{3, 96} = 31.914$, $P < 0.001$, $\eta_p^2 = 0.499$]. The interactions of the test with the context and the groups were significant [ANOVA: $F_{3, 96} = 3.516$, $P = 0.018$, $\eta_p^2 = 0.099$; $F_{3, 96} = 7.873$, $P < 0.001$, $\eta_p^2 = 0.197$, respectively], but not the interaction between the context and the groups [ANOVA: $F_{1, 32} = 2.283$, $P = 0.141$, $\eta_p^2 = 0.067$] and the second-degree interaction [ANOVA: $F_{3,96} = 1.019$, $P = 0.388$, $\eta_p^2 = 0.031$]. The significant effect of the interaction between the context and the test is not based on the role of the brilliant-light and dark contexts. The effect of the counterbalance, its interaction with the groups and the second-degree one were not significant, so the data were collapsed.

The analyses of the data depicted in Fig. 3 were carried out with the repeated-measures ANOVA, employing the tests as the within-subjects factor and the groups as the between-subjects factors. It showed a significant effect of the test [ANOVA: $F_{3, 102} = 29.826$, $P < 0.001$, $\eta_p^2 = 0.467$], but not a significant effect of the groups [ANOVA: $F_{1, 34} = 1.644$, $P = 0.208$, $\eta_p^2 = 0.046$]. The interaction of the groups with the test was significant [ANOVA: $F_{3, 102} = 7.978$, $P < 0.001$, $\eta_p^2 = 0.190$].

The Bonferroni corrected pairwise comparisons was made to analyse this interaction and it showed significant differences between groups only in the renewal test (AAA group 2.72 ± 0.34, AAB 5.44 ± 0.36, $P < 0.001$), showing that the AAB group differs from the other one during renewal test.

Results of Experiment 1b (depicted in Fig. 3) and the statistical analyses showed equivalent levels of conditioning and extinction in both groups. Furthermore, during renewal test, subjects which had been
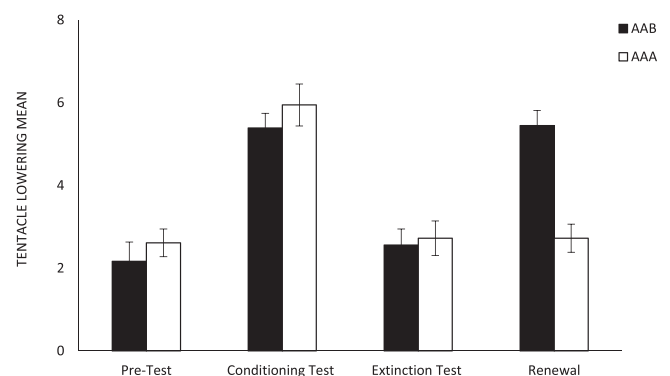

Fig. 3. *Results of Experiment 1b (AAB renewal). *Note. Tentacle lowering mean is shown for AAB group, represented by the dark bars, and AAA group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.*

exposed to the CS in a different context from the other experimental phases, showed a recovery of the extinguished response in comparison with subjects which had been exposed to the CS in the same context for all the experimental phases, consistent with AAB renewal effect. Thus, it is the first evidence of renewal with this paradigm in invertebrates. So, in Experiment 1c ABC paradigm was conducted to complete all the renewal paradigms in the snail *Cornu aspersum* This experiment was carried out in three replicas (ABC-ABB, BCA-ACC and CAB-CAA), providing a counterbalance of the role of the context based on a Latin square criterion. Furthermore, the BCA-ACC counterbalance allows us to know if the snails discriminate between the brilliant-light and the dim-light contexts.

3.3. Results of experiment 1c (ABC renewal)

In Fig. 4, the tentacle lowering mean is shown in both groups throughout all the experimental tests. The results of the three replicas were included in this Figure. We can observe that both groups have equivalent levels of conditioning and extinction, but during the renewal test, subjects which received this test in a third different context present an increment of the CR in contrast with subjects which received the renewal test in the same context as the extinction one, which was confirmed by the statistical analyses.

Firstly, the analysis of the replicas ABC, BCA and CAB renewal was carried out. A repeated-measures ANOVA was conducted, with the tests as the within-subjects factor and the replicas as the between-subjects factors. The effect of the replicas was not significant [ANOVA: $F_{1,38} = 4.107$, $P = 0.050$, $\eta_p^2 = 0.164$], but there was a significant effect of the test [ANOVA: $F_{3114} = 23.912$, $P < 0.001$, $\eta_p^2 = 0.386$]. The interaction of the replicas with the test was not significant [ANOVA: $F_{3114} = 1.822$, $P = 0.147$, $\eta_p^2 = 0.084$]. Therefore, the data were collapsed.

The repeated-measures ANOVA was conducted with the tests as the within-subjects factor and the groups ABB and ABC as the between-subjects factors. It showed a significant effect of the test [ANOVA: $F_{3, 114} = 28.142$, $P < 0.001$, $\eta_p^2 = 0.425$], but not a significant effect of the groups [ANOVA: $F_{1, 38} = 4.107$, $P = 0.050$, $\eta_p^2 = 0.098$]. However, there was a significant effect of the interaction of the groups with the test [ANOVA: $F_{3, 114} = 8.865$, $P < 0.001$, $\eta_p^2 = 0.189$].

The Bonferroni corrected pairwise comparisons was made to analyse this interaction and it showed significant differences between groups only in the renewal test (ABB group 2.45 ± 0.42, ABC group 5.7 ± 0.43, $P < 0.001$). Thus, there are significant differences between ABC and ABB groups during the renewal test.

The data in Fig. 4 indicate that subjects from both groups showed an equivalent level of conditioning and extinction. Nevertheless, in renewal test, subjects which had been exposed to the CS in a third different context showed a recovery of the tentacle lowering response in contrast with subjects which had been exposed to the CS in the same context from the extinction one. Therefore, these results stand for the first evidence of ABC renewal effect in the snail *Cornu aspersum*.

In these three experiments, the three renewal paradigms have been observed. However, through these experiments it has not been proven whether there are differences in the magnitude of the renewal among the three paradigms or not. For this reason, Experiment 2 was carried out to test experimentally this issue.

3.4. Results of experiment 2 (the renewal magnitude)

In Fig. 5 the tentacle lowering mean is shown for each group throughout all the experimental tests. All the groups have equivalent levels of conditioning and extinction. Then, at a first glance, the renewal groups show an increase in CR regardless the paradigm during the renewal test, in contrast with subjects from the control group that received all the experimental phases in the same context. This description was confirmed by the statistical analyses.

The repeated-measures ANOVA was conducted, with the tests as the within-subjects factor and the groups as the between-subjects factors. It showed a significant effect of the test [ANOVA: $F_{3, 177} = 36.077$, $P < 0.001$, $\eta_p^2 = 0.379$], but not a significant effect of the groups [ANOVA: $F_{1, 59} = 1.082$, $P = 0.364$, $\eta_p^2 = 0.052$]. The interaction of the groups with the test was significant [ANOVA: $F_{9, 177} = 2.826$, $P = 0.004$, $\eta_p^2 = 0.126$].

The Bonferroni corrected pairwise comparisons was made to analyse this interaction and it showed significant differences between the renewal groups with the control group only in the renewal test, but there were no significant differences among the renewal groups (the "ABA renewal group" 3.62 ± 0.49 the "AAA renewal group" 1.12 ± 0.45, $P = 0.002$; the "ABA renewal group" 3.87 ± 0.59 the "AAA renewal group" 1.12 ± 0.45, $P = 0.012$; and the "ABC renewal group" 3.75 ± 0.87 the "AAA renewal group" 1.12 ± 0.45, $P = 0.003$). Taking into account these statistical analyses, the four groups showed an equivalent level of conditioning and extinction. However, in the renewal test, all the renewal groups differ from the AAA group. This experiment replicates the results observed in experiments 1a, 1b and 1c. Moreover, the renewal groups do not differ among them.

The data shown in Fig. 5 and the statistics corroborated that subject which received the renewal test in a different context from the extinction one (the ABA, AAB and ABC renewal groups) showed a recovery of the CR in contrast with subjects which received all the experimental phases in the same context (the control group). In addition, it was observed that there were no differences in the magnitude of the renewal effect among the three paradigms.
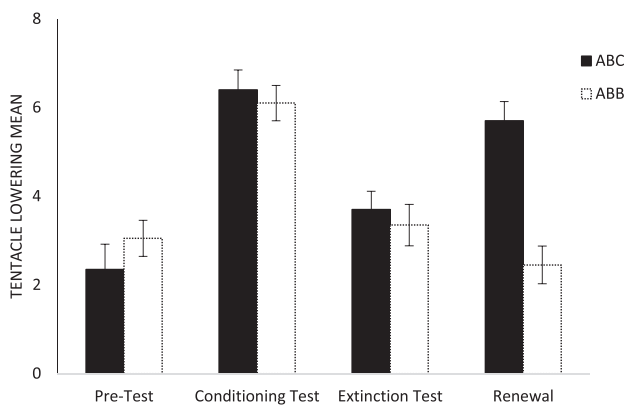

Fig. 4. *Results of Experiment 1c (ABC renewal).* *Note.* Tentacle lowering mean for ABC group, represented by the dark bars, and ABB group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.
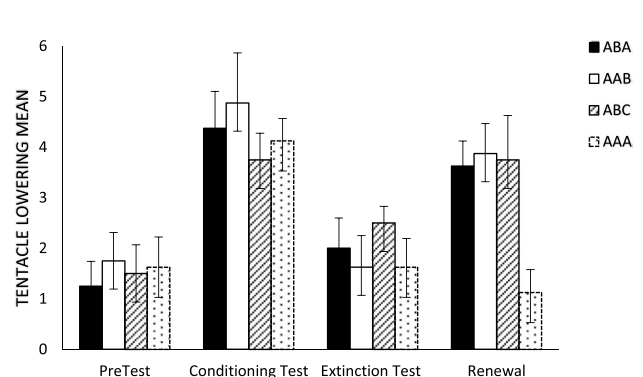

Fig. 5. *Results of Experiment 2 (Renewal magnitude).* *Note.* Tentacle lowering mean is shown for ABA group, represented by the dark bars; AAB group, represented by the white bars; ABC group, represented by the striped bars; and AAA group, represented by the bars with points, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.

4. General discussion

The purpose of the current experimental research was to replicate and extend the previous results of the renewal phenomenon reported by Loy et al. (2020) in the snail *Cornu aspersum,* using the Pavlovian Conditioning of Tentacle Lowering procedure with different contextual cues and different renewal paradigms. Experiment 1a showed ABA renewal using the illumination instead of the photoperiod as context, which is congruent with the results of Loy et al. (2020). Experiments 1b and 1c showed AAB and ABC renewal, respectively, providing the first evidence of these paradigms, as far as we know, in invertebrates. Finally, in Experiment 2 the magnitude of the renewal effect among the three paradigms was compared, showing equivalent levels of renewal.

This phenomenon has been explained by two theoretical approaches: on the one hand, Acquisition theories explain the extinction as a change in the acquired association which is explain in terms of excitatory and inhibitory associations between the context and the US during the conditioning and the extinction, respectively. On the other hand, Retrieval theories predict that a new learning takes place during the extinction, interfering with the conditioning learning retrieval. In this case, conditioning and extinction establish competing memories which are modulated by the context, which plays the role of occasion setter (see Bouton, 1993, 2004). In the present study, no test was included to measure the conditioning level of the contexts, which would have allowed us to distinguish between the Acquisition theories and Retrieval theories. However, it is suggested that the association between the context and the US is not enough to explain the phenomenon (Bouton and Peck, 1989) and it has been shown in conditioned suppression that the context-US association was not necessary for the context influence in CS performance (see Bouton and King, 1983, 1986). In addition, Acquisition theories can only explain ABA but not AAB or ABC because in the last paradigms the renewal test is performed in a context which has not been paired with the US, so the excitatory strength between the conditioning context and the US cannot be affect to the renewal effect in ABC and AAB (Harris et al., 2000; Rosas et al., 2006). According to this argument, the present results are best explained by Retrieval theories.

In Experiment 2, the renewal effect results are congruent with some studies which support the prediction of Retrieval theories that the magnitude of the renewal should be equivalent among the three paradigms (e.g., Bernal-Gamboa et al., 2012; Todd et al., 2012; Todd, 2013). However, several studies provided differences among them, showing a higher renewal effect in ABA paradigm than AAB (e.g., Bouton et al., 2011; Rosas et al., 2007; Thomas et al., 2003), ABC (e.g., Balooch et al., 2012; Bustamante et al., 2016; Harris et al., 2000) or both of them (e.g., Bernal-Gamboa et al., 2014). It has been proposed that in ABA renewal there are three associative mechanisms involved (the excitatory strength of the conditioning context, the inhibitory strength of the extinction context and the control of the CS-US association by the conditioning context during the extinction), improving the renewal effect in this paradigm, whereas in ABC and AAB renewal only the last two associative mechanisms are involved (see Rosas et al., 2006). The effect of them over the renewal paradigms could justify the differences in the renewal magnitude observed in several studies mentioned before. Also, they could explain that extinction in multiple contexts affects ABC renewal but not ABA renewal as it was observed in Balooch et al. (2012), Bernal-Gamboa et al. (2017) and Bustamante et al. (2016). Thus, although the associative strength among the stimuli (the excitatory strength of the conditioning context, the inhibitory strength of the extinction context mechanisms) is not enough to explain renewal, this proposal could be explaining the differences in the renewal magnitude among the three paradigms. However, there is a lack of evidence in the literature which shows that only these mechanisms are involved in the magnitude of the renewal effect and the present study cannot clarify this claim because there are several parameters which are not taken into account such as the inclusion of multiple extinction contexts or an explicit comparison among different levels of extinction. Therefore, it would be interesting to explicitly compare the three renewal paradigms using several conditioning procedures, measuring the conditioning level reached by the contexts.

As for the study of neural mechanisms, it has been shown in vertebrate species that the hippocampus is involved in renewal (e.g., Ji and Maren, 2005, 2007; Maren and Hobin, 2007) in contrast with some studies in which there is no effect of hippocampal damage upon renewal (e.g., Todd et al., 2017; Wilson et al., 1995). Also, it is observed that the hippocampus is involved in other learning phenomena specific of the context as latent inhibition or LI (e.g., Lubow and Weiner, 2010; Solomon and Moore, 1975; Puga et al., 2007; Weiner, 1990). However, the study of learning phenomena in invertebrates has increased considerably in the last decade (see Loy et al., 2021 for a review), and therefore, the evidence reported about context specificity in learning phenomena (e.g., McComb et al., 2002, renewal in *Lymnea stagnalis*; Loy et al., 2020, renewal in *Cornu aspersum*; Pedreira et al., 1995; Pedreira et al., 1996; Pereyra et al., 2000, context specificity of habituation in crabs; Reyes-Jiménez et al., 2020, 2021, effect of the context specificity of habituation in earth worms; Lau et al., 2013; Rankin, 2000, effect of the context specificity of habituation in *C. elegans*; see Dissegna et al., 2021, for a review about the effect of the context in habituation; Jacob et al., 2021, context specificity of LI in *Drosophila melanogaster*, Muñiz-Moreno and Loy, 2022, context specificity of LI in *Cornu aspersum*) and now, the present results of the three renewal paradigms in *Cornu aspersum*. These studies do not call into question the involvement of brain areas in psychological processes (such as perception, attention, memory or motivation) which underling the association in vertebrates but, although the hippocampus plays a relevant role in context processing for these species, the demonstration of renewal and context specificity of latent inhibition, plus other contextual effects, in invertebrates provides that a differently structured nervous system, which lacks of hippocampal-like structure, is equally suited to process the context as a discrete cue that can acquired predictive value and/or as an "occasion setter" of the CS-US association.

CRediT authorship contribution statement

Authors declare that their participation in the experimental work and the development of the manuscript was equal.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

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