Universidad de Oviedo

Departamento de Psicología

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TESIS DOCTORAL

Programa de Doctorado en Educación y Psicología

Línea Lenguaje, Aprendizaje y Memoria

CONTEXT SPECIFICITY OF ASSOCIATIVE LEARNING IN THE SNAIL
CORNU ASPERSUM

Judit Muñiz Moreno

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Autora: **Judit Muñiz Moreno**
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RESUMEN DEL CONTENIDO DE TESIS DOCTORAL

1.- Título de la Tesis	
Español/Otro Idioma: "Especificidad contextual del aprendizaje asociativo en el caracol *Cornu aspersum*".	Inglés: "Context specificity of associative learning in the snail *Cornu aspersum*".

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RESUMEN (en español)

El presente trabajo es una investigación experimental de dos efectos contextuales del aprendizaje (inhibición latente o IL y renewal) en el caracol *Cornu aspersum* mediante procedimientos de Condicionamiento Clásico. La exposición repetida a un estímulo condicionado o EC (olor) sin consecuencia alguna antes de usar ese EC en un condicionamiento de bajada de tentáculo, produce un debilitamiento de dicho condicionamiento que desaparece si la preexposición y el condicionamiento se realizan en contextos diferentes (especificidad contextual de la IL). También la extinción de la respuesta condicionada (RC) de bajada de tentáculo realizada en un contexto diferente al del condicionamiento, experimenta una recuperación cuando el caracol es situado nuevamente en el contexto inicial del condicionamiento (renewal). Los resultados pueden interpretarse como pruebas de especificidad contextual de la IL y del renewal, constituyendo la primera demostración experimental de dichos fenómenos en moluscos terrestres. Este trabajo es una contribución al creciente interés por la investigación de procesos cognitivos relativamente complejos en invertebrados y tiene implicaciones generales para comprender la evolución de la cognición y su relación con el sistema nervioso.

Universidad de Oviedo

RESUMEN (en Inglés)

The present work is an experimental research of two learning contextual effects (latent inhibition or LI and renewal) in the snail *Cornu aspersum*, using Classical Conditioning procedures. The repeated exposure of the conditioned stimulus or CS (odour) without any consequence before using that CS in tentacle lowering conditioning, produces a weakening of that conditioning and it disappears if the preexposure and conditioning phases are performed in different contexts (context specificity of LI). Also, when the extinction of the conditioned response of tentacle lowering (CR) is carried out in a different context to the conditioning one, this CR is recovered if the snail is placed again in the conditioning context (renewal). The results can be interpreted as evidence of the contextual specificity of LI and renewal, showing the first experimental demonstration of these phenomena in terrestrial molluscs. This work is a contribution to the increasing interest in the study of relatively complex cognitive processes in invertebrates. Moreover, it provides general implications to understand the evolution of cognition and its relationship to the nervous system.

SR. PRESIDENTE DE LA COMISIÓN ACADÉMICA DEL PROGRAMA DE DOCTORADO EN EDUCACIÓN Y PSICOLOGÍA

The results of Chapter 2: Context specificity of latent inhibition in the snail *Cornu aspersum* were published in the journal *Animal Cognition*:

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The results of Chapter 3: First evidence of ABA renewal in the snail *Cornu aspersum* were published under the title "Renewal of conditioned tentacle lowering by circadian contextual cues in snails *Cornu aspersum*" in the journal *Behavioural Processes*:

- Loy, I., Fernández-Victorero, S., & Muñiz-Moreno, J. (2020). Renewal of conditioned tentacle lowering by circadian contextual cues in snails *Cornu aspersum. Behavioural processes*, *178*, 104144. https://doi.org/10.1016/j.beproc.2020.104144

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A mi familia, mi director de tesis, mis compañeros/as de laboratorio y a todas aquellas personas de las que he tenido el placer de aprender a lo largo de mi vida.

"Sin sensibilidad ningún objeto nos sería dado y, sin entendimiento,

ninguno sería pensado. Los pensamientos sin contenido son vacíos;

las intuiciones sin conceptos son ciegas".

Immanuel Kant - Crítica de la razón pura

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Resumen

El presente trabajo es una investigación experimental de dos efectos contextuales del aprendizaje (inhibición latente o IL y renewal) en el caracol *Cornu aspersum* mediante procedimientos de Condicionamiento Clásico. La exposición repetida a un estímulo condicionado o EC (olor) sin consecuencia alguna antes de usar ese EC en un condicionamiento de bajada de tentáculo, produce un debilitamiento de dicho condicionamiento que desaparece si la preexposición y el condicionamiento se realizan en contextos diferentes (especificidad contextual de la IL). También la extinción de la respuesta condicionada (RC) de bajada de tentáculo realizada en un contexto diferente al del condicionamiento, experimenta una recuperación cuando el caracol es situado nuevamente en el contexto inicial del condicionamiento (renewal). Los resultados pueden interpretarse como pruebas de especificidad contextual de la IL y del renewal, constituyendo la primera demostración experimental de dichos fenómenos en moluscos terrestres. Este trabajo es una contribución al creciente interés por la investigación de procesos cognitivos relativamente complejos en invertebrados y tiene implicaciones generales para comprender la evolución de la cognición y su relación con el sistema nervioso.

Abstract

The present work is an experimental research of two learning contextual effects (latent inhibition or LI and renewal) in the snail *Cornu aspersum*, using Classical Conditioning procedures. The repeated exposure of the conditioned stimulus or CS (odour) without any consequence before using that CS in tentacle lowering conditioning, produces a weakening of that conditioning and it disappears if the preexposure and conditioning phases are performed in different contexts (context specificity of LI). Also, when the extinction of the conditioned response of tentacle lowering (CR) is carried out in a different context to the conditioning one, this CR is recovered if the snail is placed again in the conditioning context (renewal). The results can be interpreted as evidence of the contextual specificity of LI and renewal, showing the first experimental demonstration of these phenomena in terrestrial molluscs. This work is a contribution to the increasing interest in the study of relatively complex cognitive processes in invertebrates. Moreover, it provides general implications to understand the evolution of cognition and its relationship to the nervous system.

Chapter 1: Introduction

1. Theoretical framework

Since its emergence in the framework of the Darwinian revolution, the investigation in animal learning was established in the dynamic and fruitful research field of Experimental Psychology as an index of different types of intelligence. Its importance is not limited exclusively to the interesting phenomena discovered and the relevant theories developed, but also, it has always played an important role in understanding the origin and nature of human cognition (Loy et al., 2021).

Traditionally, learning was only studied in a few vertebrate species, mainly rodents. However, in recent years, the interest of learning in simpler animals such as invertebrates has been increased (Mizunami et al., 2018), providing some theoretical limitations in the current learning theories (Abramson and Wells, 2018), and giving rise to a new way of interpreting the relationship between psychological processes and the neural mechanisms involved in them (Hawkins and Byrne, 2015; see Loy et al., 2021).

Associative learning has been observed in all invertebrate species except for chordates, maxillipods, myriapods, and rotifers (Ginsburg and Jablonka, 2019; Perry et al., 2013; see Loy et al., 2021 for a review) and the evidence of associative learning found is increased when the nervous system of the invertebrate species is more complex. For example, in nonbilaterian or basal species (Holland, 2011) the evidence is limited and not replicated (cnidaria), whereas in the bilaterian invertebrate *phyla* (platyhelminthes, molluscs, annelida, arthropoda or nematoda) several learning phenomena has been observed such as conditioned inhibition, extinction, latent inhibition, blocking, or

overshadowing (see Álvarez et al., 2017 for a review). Next figures show a phylogenetic

map of the animals in which learning has been observed (Loy et al., 2021).

Figure 1

Phylogenetic Map of all phyla in Animalia from Loy et al. (2021, p.236)
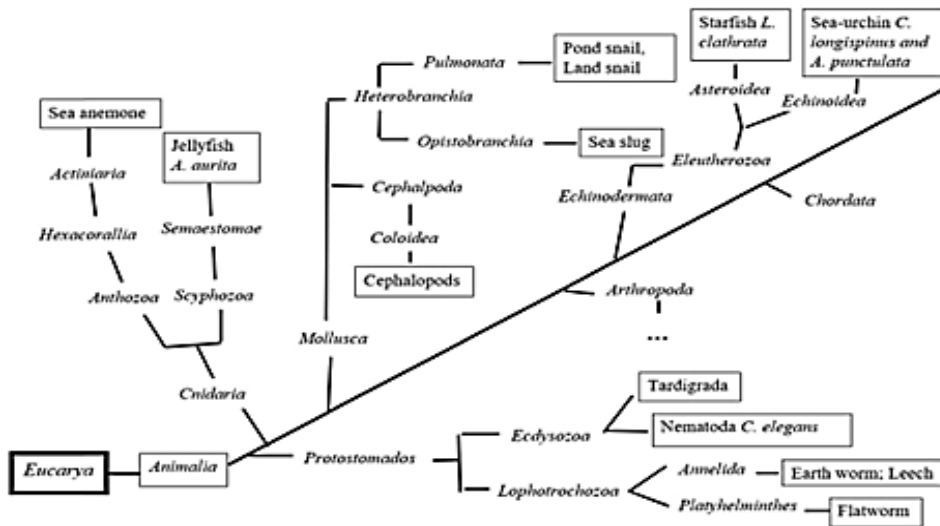
Figure 2

Phylogenetic Map of Arthropoda from Loy et al. (2021, p.237)
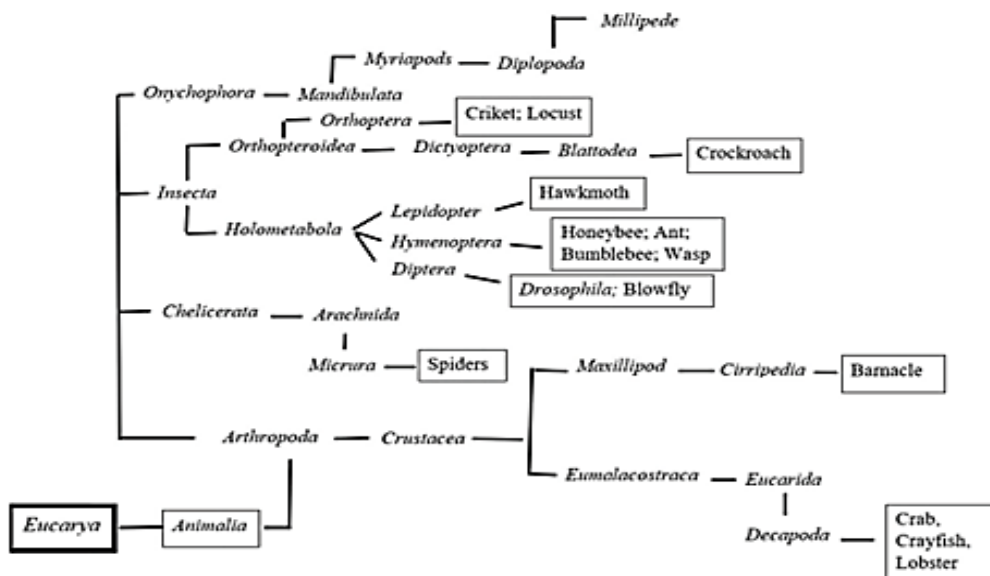
In the advanced in learning research, it has been observed that the context had an effect on the associations between stimuli, showing more complex learning phenomena (Loy, 1995). This context effect opened a new debate in which only the interpretation of this one in terms of contingencies is not enough, giving rise to the Interference theories which suggest that the recovery of acquired association is modulated by the context (see Bouton, 2004).

The effect of context on learning phenomena has been studied mainly in vertebrate animals, for example: context specificity of habituation (e.g., Siegel, 1977; see Dissegna et al., 2021 for a review), negative transfer (e.g., Swartzentruber and Bouton, 1986), renewal (e.g., Bernal-Gamboa et al., 2012; Bouton and Bolles, 1979a; Mesich et al., 2021) or overshadowing (Kwok and Boakes, 2017). Nevertheless, as the interest in the relationship between context and learning has increased, the interest in context specificity of learning in invertebrates has also increased, showing several phenomena.

For example, in arthropods it has been shown spatial navigation (e.g., Cheng, 2005, 2006; Colborn et al., 1999; Collet et al., 2006), perception of contextual size illusions (Howard et al., 2017), context specificity of latent inhibition (Jacob et al., 2021) and context specificity of habituation (Hermitte et al., 1999; Pedreira et al., 1995, 1996; Pereyra et al., 2000; Tomsic et al., 1998). In molluscs, it has been observed spontaneous recovery, reinstatement (Álvarez et al., 2014) and renewal (McComb et al., 2002). In platyhelminthes, cue competition effects have been provided (Prados et al., 2013). Finally, context specificity of habituation has also been observed in annelids (Reyes-Jiménez et al., 2020, 2021) and nematode (Lau et al., 2013; Rankin, 2000; see Dissegna et al., 2021 for a review about the context effect in habituation).

The present work is framed in this line of research, and it is focused on the study of context effect in latent inhibition (LI) and the renewal phenomena in the garden snail

Cornu aspersum, using an appetitive Pavlovian Conditioning of Tentacle Lowering procedure.

Classical Conditioning procedures have been demonstrated to be useful for the study of the cognitive processes (such as working memory, short- and long-term memory, attention, perception, etc.) involved in learning from humans and other more complex animals (vertebrate species) to simpler animals (invertebrate species) and other organisms (plants and protists) (see Loy et al., 2021 for a review). Moreover, the appetitive Pavlovian Conditioning of Tentacle Lowering procedure is a robust preparation which has revealed a wide range of associative phenomena such as simple conditioning (Ungless, 1998, 2001); latent inhibition (LI), overshadowing, second order conditioning and sensory preconditioning (Loy et al., 2006); conditioned inhibition (Acebes et al., 2009); blocking (Acebes et al., 2012; Prados et al., 2013); spontaneous recovery and reinstatement (Álvarez et al., 2014).

A difficulty added in the investigation of contextual effects in invertebrates is to establish the stimuli dimensions which can play the role as context. According to the literature, external cues, internal states, recent events or the time can be contexts (Bouton, 2000). However, the stimuli must be salient enough to be perceived, but not so intense that they compete with the stimulus used as the CS. Furthermore, contextual effects involve discrimination learning, a skill which could be beyond the capacity of these organisms. Unpublished studies in our laboratory failed to find any contextual influence when such cues consisted of textured floor surfaces or vibrations of the experimental set (Acebes, 2002). It is well established that odours can be used by snails as signals for food; therefore, odours were used as context. Nevertheless, the use of odours for this purpose has the problem that it can mix with the odour of the CSs, (typically employed in tentacle lowering conditioning with snails) producing a configural learning. As an alternative, the

photoperiod (defined by the hour of the day and the illumination) was employed and it was related with the locomotive activity in the *Cornu aspersum* (Attia, 2004; Bailey, 1981). Then, only the use of the illumination simplifies the procedure.

2. Latent Inhibition experiments

In appetitive Pavlovian Conditioning, a CS becomes associated with the taste and/or the nutritive properties of an unconditioned stimulus (US), usually food. It is possible to modulate the strength of this association by manipulating the variables effective in standard conditioning paradigms. One of the most relevant variables is the experience with the CS prior to conditioning. When the CS is repeatedly exposed to a neutral stimulus subsequent conditioning is retarded when that stimulus is used as a CS (Lubow and Weiner, 2010). This phenomenon, named Latent Inhibition (LI), has been explained by two basic approaches: one is based on failure in the CS-US acquisition (Acquisition theories) and the other on the CS-US association retrieval (Interference theories). In addition, LI shows contextual specificity (Hall and Honey, 1989) and this effect is predicted by both theoretical accounts.

LI has been broadly study in vertebrate species, including humans (e.g., Ginton et al., 1975; Lubow and Moore, 1959; Silver, 1973; Zalstein-Orda and Lubow, 1995), rodents (e.g., Hall and Pearce, 1979; Kiernan and Westbrook, 1993; Lubow et al., 1968; Reiss and Wagner, 1972), fishes (e.g., Ferrari and Chivers, 2006; Mitchell et al., 2011; Shishimi, 1985) or amphibians (Daneri and Muzio, 2015; Ferrari and Chivers, 2009, 2011; Gonzalo et al., 2013). Moreover, a considerable amount of literature has been published on context specificity of LI in vertebrates (e.g., Archer et al., 1986; Hall and Channell, 1985; Hall and Honey, 1989; Lovibond et al., 1984; Miller et al., 2015; Miguez et al., 2018; Molero-Chamizo, 2018; Westbrook et al., 2000).

According to Lubow and Weiner (2010), the involvement of the hippocampus is necessary for LI to occur. Also, these authors suggest that the simple nervous system of invertebrates does not allow them to distinguish the context from the rest of stimuli, so in organisms which lack of complex neuronal structures should not be observed complex learning phenomena neither context specificity. Nevertheless, considered each species that exist, the "invertebrate's nervous system" is a wide range of structures so diverse structurally and functionally that it is grossly simplifying to qualify it as "simple". Thus, contrary to the assertion of these authors, the studies which show LI in invertebrates increased in the last years (e.g., Acquistapace et al., 2003 in crustaceans; Abramson et al., 2005; Abramson and Bitterman, 1986; Bennett et al., 2021; Bitterman et al., 1983; Chandra et al., 2000, 2001, 2010; Cook et al., 2019; Fernández et al., 2012; Jacob et al., 2021; Petersen, 2017, in insects; Escobar et al., 2014; Loy et al., 2006 in gastropods). In addition, context specificity of LI has been recently provided by Jacob et al. (2021) in *Drosophila melanogaster*. In this study, it was shown that flies preexposed to the CS in a different context than conditioning and the test context reached equivalent levels of CR as flies which were preexposed to a different stimulus than the CS (Jacob et al., 2021).

Taking into account the literature of contextual effect and LI in invertebrates, the aim of this work is to study the context specificity of LI in the snail *Cornu aspersum*, using the Pavlovian Conditioning of Tentacle lowering procedure. According to the stimulus employed as context, the work reported here was made in two different experiments. In the first one, the circadian experiment, the context used was the photoperiod (defined by the hour of the day and illumination). In the second one, the light experiment, only the illumination was used as context. It was expected to observe the same results of the circadian experiment, providing a simpler procedure, because the element "hour of the day" is abolished and the experiment is carried out in fewer hours.

3. Extinction and Renewal effect experiments

After pairing a CS with an US, animals can learn to produce a CR in the presence of the CS alone (Pavlovian Conditioning). Then, when the CS is presented in the absence of that US, a decrease of the CR was produced and this phenomenon is named extinction (Pavlov, 1927/1970). Extinction exhibits context specificity (e.g., Bouton, 1993, 2004; Bouton and Bolles, 1979a), so certain manipulations can cause the recovery of the CR that seemed to be lost (Álvarez et al., 2014). 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 (e.g., Rescorla and Wagner, 1972; Mackintosh, 1975; Pearce and Hall, 1980). On the other hand, the Interference theories predict that a new learning takes place during the extinction, interfering with the conditioning learning retrieval (see Bouton, 1993, 2004).

Extinction and the recovery of the extinguished response are a basic process in some fields of applied psychology such as therapies or education, so an increment of research in extinction processes allow us to develop better techniques for behavioural therapy (Bouton, 1988; Mystkowski and Mineka, 2007). Several treatments in therapies are limited to the context, and the recovery of the response is sensible to the period of time which elapses between the extinction training and the test (spontaneous recovery, e.g., Pavlov, 1927/1970), the reexposure of the unconditioned stimulus (US) after the extinction (reinstatement, e.g., Bouton and Bolles, 1979b) and the context change (renewal, e.g., Bouton, 2004). According to the experimental phase in which the context change is carried out, there are three paradigms of renewal: when extinction is tested in a different context than conditioning (ABA, e.g., Chaudhri et al., 2008; Anderson and Petrovich, 2015; Khoo et al., 2020; Mesich et al., 2022), when the context change is made during renewal test (AAB e.g., Bouton and Ricker, 1994) and when conditioning,

extinction and renewal were made in three different contexts (ABC, e.g., Khoo et al., 2020).

Renewal effect has been broadly studied in vertebrates such as humans (e.g., Balooch et al., 2012; Bustamante et al., 2016; Effting and Kindt, 2007; Effting et al., 2013; Krypotos et al., 2014; Lipp et al., 2021; Nelson et al., 2011; Neuman and Kitlertsirivatana, 2010; Ritchey et al., 2021; Üngör and Lachnit, 2008; Vervliet et al., 2010; see Vervliet et al., 2013 for a review in fear conditioning), rats (e.g., Anderson and Petrovich, 2015; Bernal-Gamboa et al., 2012; Bernal-Gamboa et al., 2014; Bernal-Gamboa et al., 2022; Bouton, 1993, 2000; Bouton and King, 1983,1986; Bouton and Peck, 1989; Bouton and Rickert, 1994; Bouton et al., 2011; Chaudhri et al., 2008; Harris et al., 2000; Knapska and Maren, 2009; Khoo et al., 2020; Nieto et al., 2020; Polack et al., 2013; Rosas et al., 2007; Tamai and Nakajima, 2000; Thomas et al., 2003; Todd, 2013; Todd et al., 2012; Wilson et al., 1995), mice (e.g., Nowak et al., 2013; Lattal et al., 2003; Waddell et al., 2004), rabbits (e.g., Weidemann and Kehoe, 2004), dogs (e.g., Chia, 2020), pigeons (e.g., Donoso et al., 2021; Packheiser et al., 2021; Packheiser et al., 2019; Rescorla, 2008), amphibians (e.g., Mesich et al., 2021) or zebrafish (e.g., Kuroda et al., 2017a, 2017b; Kuroda et al., 2020; Kuroda et al., 2021). However, there are only one study of renewal in invertebrates (McComb et al., 2002). In McComb et al.'s (2002) study ABA renewal was observed in the freshwater snail *Lymnaea stagnalis*, using an Operant Conditioning procedure and food or no food odorant as context. Snails were trained in two different contexts: the standard context (no food odorant) or a carrot context (food odorant), followed by the extinction sessions in which half of the subjects received the treatment in the same context as training whereas, the other half received the treatment in a different context. This study showed that extinction did not occur if the extinction training context was different than training context (McComb et al., 2002).

The aim of Chapter 3 was to study renewal in the snail *Cornu aspersum*, using an appetitive Pavlovian Conditioning of Tentacle Lowering procedure and two experiments were carried out for this purpose. Snails experienced an odorous CS paired with the US (conditioning), followed by the exposition to the CS without any consequence (extinction). Then, they were exposed to the CS in the same context as conditioning (renewal test). In Experiment 1, odours were used as context. However, as it stated above, the use of odours as context could mix with the odorant CS and the results obtained can be explained by configural learning. So, in Experiment 2 the photoperiod, defined by the hour of the day and the illumination, was employed as context.

In these experiments ABA renewal was studied. Nevertheless, there are two renewal paradigms more: AAB and ABC renewal and, according to our review, there is no evidence of both paradigms in invertebrates.

Therefore, in Chapter 4, several experiments were conducted to address the renewal phenomenon. Experiment 1a was designed to replicate ABA renewal, 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. The last experiment (Experiment 2) was carried out to compare the magnitude of the recovery in the three renewal paradigms.

According to Interference theories (Bouton, 1993, 2004), the magnitude of the three renewal paradigms would be equal (see Bernal-Gamboa et al., 2012) and some studies are congruent with this claim. For example, Tood (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 Tood 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 there were no differences between both paradigms. Another example is the work of Bernal-Gamboa et al. (2012), in which a Pavlovian Conditioning procedure of Taste Aversion Learning (CTA) 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 which provide differences among the three paradigms, and 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 CTA procedure in rats, in which the increase in the number of extinction trials removed 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 last one. Finally, Üngör and Lachnit (2008) compared the three renewal paradigms in humans with a predictive learning experiment and the renewal effect was found to be equivalent in ABA and ABC, whereas AAB renewal was not observed.

Other studies provide differences in the magnitude of renewal between ABA and ABC paradigms. Effting and Kindt (2007), using a differential fear conditioning in humans, observed a higher recovery of the extinguished response in ABA than in ABC. In another study of fear conditioning in humans (Neumann et al., 2010), a higher renewal effect was showed 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 was attenuated when extinction was carried out in multiple contexts. In a similar direction, Bustamante et al.'s (2016) work 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.

According to Rosas et al. (2006), the differences in the renewal magnitude among the three paradigms can be explained by three mechanisms: in the first one (the excitatory strength of the conditioning context), the conditioning context acquires excitatory strength which can contribute to responding when the renewal test is conducted in that context; in the second one (the inhibitory strength of the extinction context), the extinction context acquires an inhibitory strength, decreasing the response in this one, but not in other contexts during the renewal test; 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, and for this reason, the retrieval of this association is poor in a different context from the conditioning one. 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 (see Rosas et al. 2006). However, considering the existing literature on the topic, there is no conclusive evidence confirming this

explanation, nor the claim of the Interference theories. Therefore, the debate about this issue is still open.

4. Implications

The investigation of learning phenomena in invertebrates suggests that the involvement of brain areas such as hippocampus is not a necessary condition for learning to occur. These results reinforce the searching for physiological correlates of learning on neuromodulators which could be present in both vertebrate and in invertebrate animals (e.g., Van Damme et al., 2021), focusing the relationship between psychological processes and the biochemical mechanism of the nervous system involved, in which psychology is not surpassed by physiology. Also, it could be given raise a new vision of the consciousness evolution.

5. Objectives

The aim of the present work was to study the context effect of associative learning in the invertebrate species *Cornu aspersum*. Specifically, evidence of LI and renewal were reported in order to better understand the psychological processes involved in them. Moreover, learning theories which predict these phenomena were also debated.

The experiments in Chapter 2 were conducted to provide a replica of LI, showing in the study of Loy et al. (2006), and assess whether this phenomenon is specific of the context. It was expected that subjects which received the CS preexposure in the same context as the conditioning one showed a LI effect whereas, subjects which received the CS preexposure in a different context than conditioning one, showed an abolishment of the LI effect.

The next experiments from Chapter 3 were carried out to show the basic paradigm of renewal (ABA) in this species of snails. In both experiments it was expected to observe that subjects which had received a context change during the extinction provided a recovery of the extinguished response, in contrast with subjects which had received all the experimental treatment in the same context.

The investigation reported in Chapter 4 offers all the renewal paradigms and compare the magnitude of the renewal effect throughout them. The hypothesis in ABA, AAB and ABC experiments was that subjects which had received a context change provided a recovery of the CR. In addition, there were not differences in the magnitude of the renewal effect among the three paradigms, congruent with the Interference theories' claim.

Finally, in Chapter 5 the implications of the present results for modern learning theories, the general conception of invertebrate psychology and the study of the evolutionary development were debated.

Chapter 2: Context specificity of Latent Inhibition in the snail *Cornu aspersum*

The present study was conducted to assess the context specificity of latent inhibition (LI) in the snail *Cornu aspersum*, using an appetitive Pavlovian Conditioning of Tentacle Lowering procedure. Snails experienced an odorous conditioned stimulus (CS) without any consequence before being conditioned with food. The CS preexposure can occur in the same or in a different context than the conditioning and the test. The study was performed in two experiments in which the photoperiod (defined by level of illumination and time of day) was used as context (circadian experiment) or only the illumination was employed as context (light experiment). It was expected that subjects which were preexposed to the CS1 in the same context as conditioning would show a delay in the conditioning acquisition, congruent with LI. In addition, subjects preexposed to the CS1 in a different context than conditioning were expected to show the acquisition of the CS-US association, congruent with context specificity of LI.

1. Method

1.1. 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.

52 adult snails were employed, with a mean shell diameter of 25.94 mm (range 20–32 mm) for the circadian experiment, whereas 53 adult snails with a mean shell

diameter of 29.06 mm (range 22–33 mm) were used for the light experiment. 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 22 ℃ 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. At the end of the 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 to avoid their recapture.

1.2. Apparatus and stimuli

The experimental set was a plastic perforated 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 and the experimental room was maintained at 22 ℃. The context stimuli were two types of lights to reproduce the light/dark context in both experiments. A white light (LED 5.5 W) was used as the light context, whereas a red light (LED 3 W) was used as the dark context, given that prior research established the snail's spectral sensitivity range in 390–580 nm (Barker, 2006), which is lower than the red light range (620–750 nm), so the red light cannot be perceived by snails. By contrast, the red light is perceived by humans and the use of this light allows us to observe the response of the subject properly. Also, two solutions, one obtained from mango and another one from coconut (oil brand La Casa de Los Aromas, 2 ml/L of distilled water) were used as the CSs, and carrot was used as the US. The pieces of carrot had a mean diameter of 27 mm (range 22–29 mm) and were 1 mm thick.

1.3. Procedure

In this experiment, tentacle lowering was measured as the conditioned response or 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).

Snails were randomly divided into four groups based on the context in which subjects received the preexposure and the kind of stimulus presented during the preexposure. Subjects from same context-preexposure group were preexposed to the odour used during conditioning (CS1) in the same context as the conditioning and the tests. On the contrary, subjects from different context-preexposure group were preexposed to the CS1, but in a different context than the conditioning and the tests. From same context-no preexposure group, subjects were preexposed to a different odour from that used during conditioning (CS2) in the same context as the conditioning and the tests. Finally, subjects from different context-no preexposure group were preexposed to the CS2 in the different context. The role of the odours was not counterbalanced, so the odour of mango was used as CS1 and the odour of coconut was used as CS2.

In addition, this study was carried in two experiments: the circadian experiment, in which the photoperiod was used as context and the light experiment, in which only illumination was used as context. In both one, the context was counterbalanced so, for half of the subjects in each group, the conditioning and the tests were made in the light context and for the other half, they were made in the dark context. The circadian experiment was started at 8:00 a.m. and 8:00 p.m. and finished at 13:00 p.m. and 01:00 a.m., respectively, and the light experiment started at 8:00 a.m. and finished at 13:00 p.m.

At the beginning of each trial, snails were sprayed with fresh water to induce their 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.

i. Pre-Test

In this phase, the tentacle lowering response was measured for each subject individually. Based on the group to which they belonged, snails were exposed to CS1 or CS2 for 2 min. 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.

ii. Preexposure

During the preexposure phase, the odour (CS1 or CS2) was presented for 2 min. The odour was placed in the same way as pre-test and 6 trials were made during the day with an intertrial interval (ITI) of 58 min.

iii. Conditioning and Test

In the conditioning phase, all the groups were exposed to CS1 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 in the previous phases. 3 trials were performed during the day with an ITI of 58 min (see Figure 1).

Figure 1

Conditioning Phase.
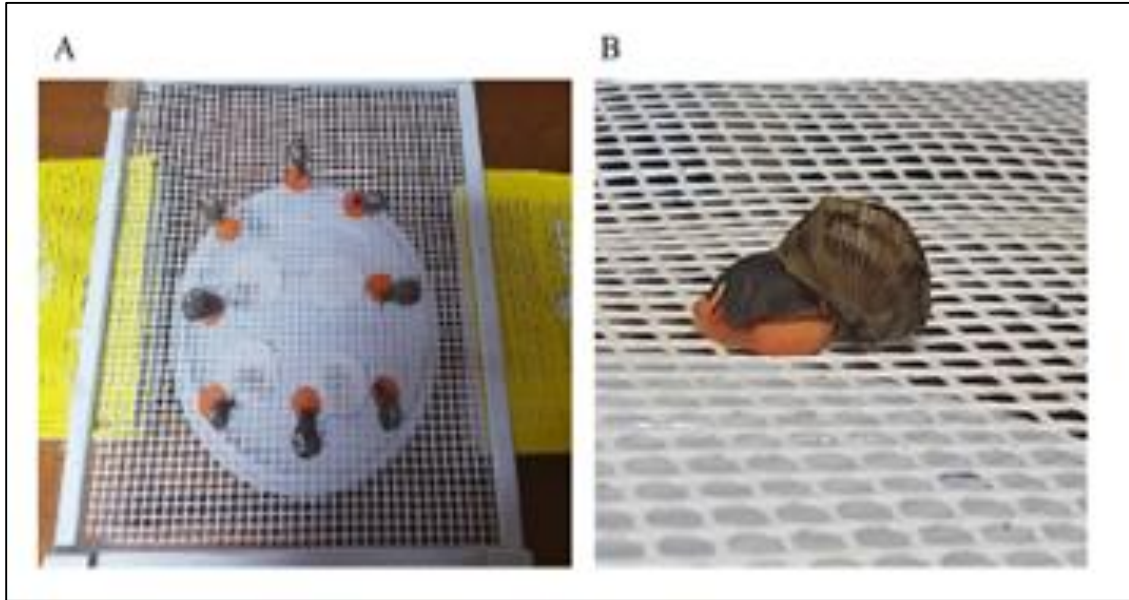
Note. Panel A shows the experimental setting and how conditioning was performed in groups. Panel B shows a snail eating during conditioning.

On a different day than the conditioning phase, the test was carried out in the same way as the pre-test, using the same context as conditioning. The conditioning-test cycle was made 3 times, so conditioning was repeated 9 times and the test 3 times. The experimental design is summarized in Table 1.

Table 1

Experimental design for both experiments.

Groups	Pre-Test (Day 1)	Preexposure (Day 2)	Conditioning (Days 3-5-7)	Test (Days 4-6-8)
Same context preexposure	(Sa) CS_1	(Sa) CS_1		
Different context preexposure	(Di) CS_1	(Di) CS_1		
			(Sa) CS_1+US	(Sa) CS_1
Same context no preexposure	(Sa) CS_2	(Sa) CS_2		
Different context no preexposure	(Di) CS_2	(Di) CS_2		

Note. CS1 was a mango solution, CS2 was a coconut solution, US was a piece of carrot. The abbreviation "Sa" indicates "same context" used throughout all the experimental treatment and the abbreviation "Di" indicates the different context (the contextual cue was the photoperiod in the circadian experiment and light was the contextual cue in the light experiment). Also, the light and the dark contexts were counterbalanced, so for half of the subjects Sa was the dark context and Di was the light context and for the other half Sa was the light context and Di was the dark context. The symbol "+" indicates that stimuli were presented simultaneously.

1.4. Statistical Analysis

The number of times that subjects lowered the left tentacle during the pre-tests and tests was measured. One-way analysis of variance was used in the pre-test analysis. Also, the repeated-measures ANOVAs were carried out to observe if there were any differences in the counterbalanced training context and to analyse the main results shown in Figure 2. Finally, the differences among the groups observed in test 2 were compared using the Univariate ANOVA and the Bonferroni pairwise comparisons. These analyses

were taken into account for each experiment. In addition, the level of significance used was $\alpha = 0.05$ and the effect sizes for ANOVAs were reported as partial Eta-square ($\eta 2p$). Data management and analysis was performed using SPSS v21 (SPSS Inc., Chicago, IL, USA).

2. Results

Figure 2 shows the tentacle lowering mean for each group in the three conditioning tests. Panel A presents the results of the circadian experiment, whereas Panel B provides the results of the light experiment. As can be seen from Panel A, all groups showed an equivalent level of conditioning throughout the three tests except for the group same context-preexposure. This group presented a lower conditioning level than the rest of the groups in the first two tests, this difference being higher in test 2. Nevertheless, CR for the same context-preexposure group increased during test 3, showing an equivalent level of conditioning to the other groups. This description was corroborated by the statistical analyses. The same effect was observed in Panel B, but during test 1 the CR of the same context-no preexpsoure group was higher than the CR for the rest of the groups. However, this difference was not significant as the statistical analyses show.

Figure 2

Experimental Results.
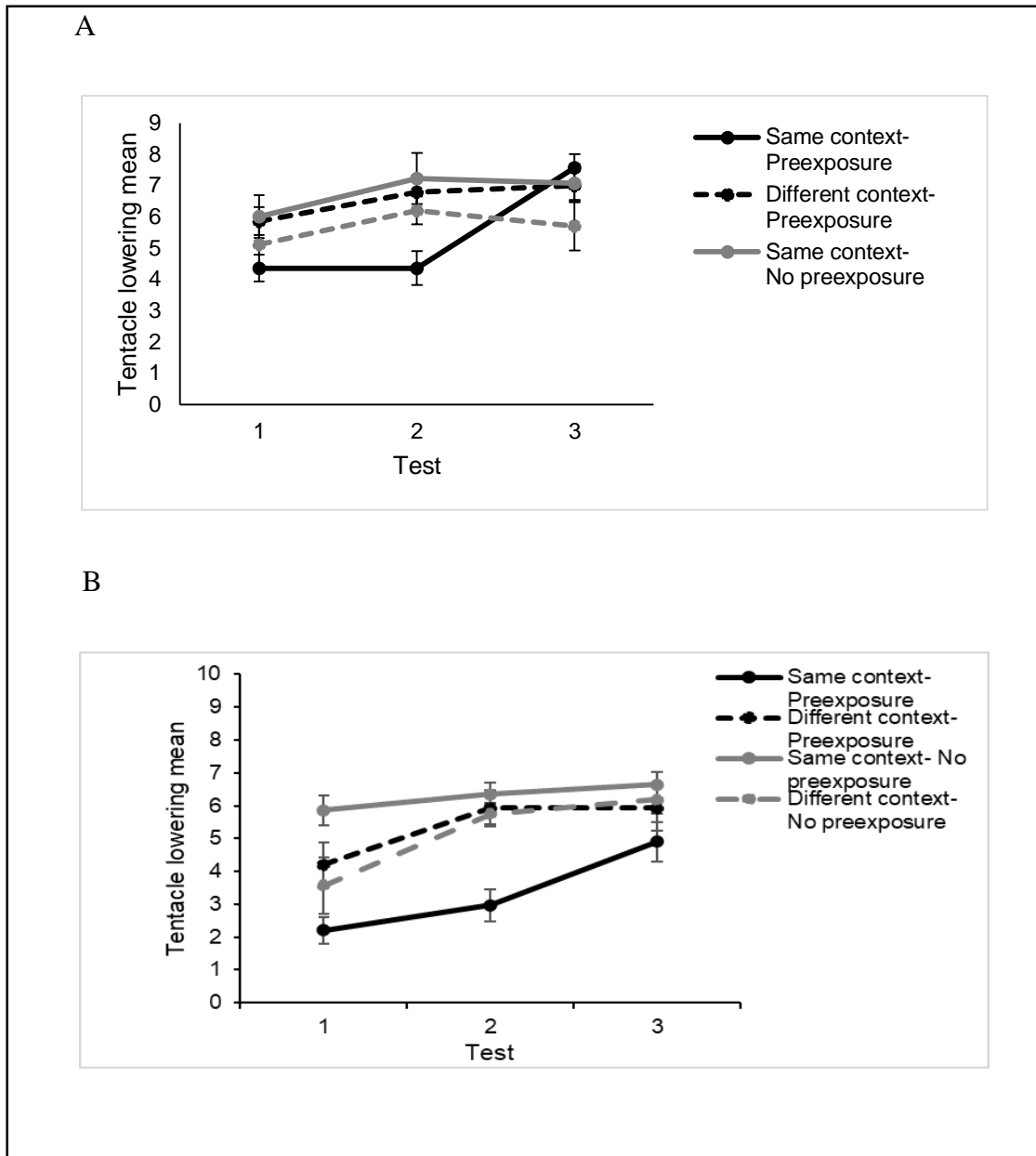
Note. This figure represents the mean number of tentacle-lowering responses (CR) made by the different groups: same context-preexposure, different context-preexposure, same context-no preexposure and different context-no preexposure* among the three experimental tests for the circadian experiment (panel A) and the light experiment (panel B). Vertical bars represent SEMs.

The first set of analyses examined the effect of context counterbalancing to see if there were any significant differences in the CR between-subjects which received the conditioning and the tests in the light context and the subjects which received the conditioning and the tests in the dark context. A repeated-measures ANOVA was carried out with the pre-test and the tests as the within-subjects factor, and the preexposure context (if the preexposure was made in the same context as conditioning or in the different context), the stimulus preexposure (the CS1 preexposure or CS2 preexposure) and the training context (if the conditioning and the tests were performed in the light or in the dark context) as the between-subjects factors.

In the circadian experiment, the effect of the training context was significant [ANOVA: $F_{1,\ 44} = 6.786$, $P = 0.012$, $\eta 2p = 0.134$], but there were no significant interactions between the training context and the other factors, neither with the stimulus preexposure [ANOVA: $F_{1,44} = 0.710$, $P = 0.404$, $\eta 2p = 0.016$] nor with the preexposure context [ANOVA: $F_{1,\ 44} = 1.721$, $P = 0.196$, $\eta 2p = 0.038$]. Also, the second-degree interaction was not significant [ANOVA: $F_{1,44} = 0.676$, $P = 0.415$, $\eta 2p = 0.015$]. These results reflect higher means in one context than in the other but, since they are counterbalanced, the effect was offset and it did not affect the validity of the results. Thus, the data were collapsed.

In the light experiment, the analyses did not show a significant effect of the training context [ANOVA: $F_{1,\ 45} = 0.336$, $P = 0.565$, $\eta 2p = 0.007$]. Also, there were no significant differences in the interaction of the training context with the stimulus preexposure [ANOVA: $F_{1,\ 45} = 0.926$, $P = 0.341$, $\eta 2p = 0.020$], the interaction with the preexposure context [ANOVA: $F_{1,\ 45} = 0.098$, $P = 0.755$, $\eta 2p = 0.002$] and in the second-degree interaction [ANOVA: $F_{1,\ 45} = 0.015$, $P = 0.902$, $\eta 2p = 0.000$]. As in the circadian experiment, these data were collapsed.

The second set of analyses was made to find out whether there was a preference for one of the odours during the pre-test for each experiment. One-factor ANOVA was made with the pre-test as dependent variable and the four groups as independent variable. In both one, there were no significant differences in the preference for one odour: the circadian experiment [ANOVA: $F_{3, 48} = 1.004$, $P = 0.399$, η2p $= 0.059$] and the light experiment [ANOVA: $F_{3, 49} = 1.439$, $P = 0.243$, η2p $= 0.081$].

Then, several analyses were performed to examine the data represented in Figure 2. For each experiment, a repeated-measures ANOVA was carried out with the tests as the within-subjects factor, whereas the preexposure context and the stimulus preexposure were the between-subjects factors.

In the circadian experiment, the analysis indicated a significant effect of the tests [ANOVA: $F_{2, 96} = 10.743$, $P < 0.001$, η2p $= 0.183$], but not of the stimulus preexposure [ANOVA: $F_{1, 48} = 0.247$, $P = 0.621$, η2p $= 0.005$] or of the preexposure context [ANOVA: $F_{1, 48} = 0.001$, $P = 0.979$, η2p $= 0.000$]. Moreover, it showed a significant effect of the interactions between the tests and the stimulus preexposure [ANOVA: $F_{2, 96} = 5.057$, $P = 0.009$, η2p $= 0.095$], the tests and the preexposure context [ANOVA: $F_{2, 96} = 3.619$, $P = 0.032$, η2p $= 0.070$], and the preexposure context with the stimulus preexposure [ANOVA: $F_{1, 48} = 5.928$, $P = 0.019$, η2p $= 0.110$]. Nevertheless, the second-degree interaction was not significant [ANOVA: $F_{2, 96} = 2.091$, $P = 0.129$, η2p $= 0.042$].

For the light experiment, the statistical analyses presented a significant effect of the tests [ANOVA: $F_{2, 98} = 20.667$, $P < 0.001$, η2p $= 0.297$] and the stimulus preexposure [ANOVA: $F_{1, 49} = 9.771$, $P = 0.003$, η2p $= 0.166$], but not a significant effect of the preexposure context [ANOVA: $F_{1, 49} = 0.748$, $P = 0.391$, η2p $= 0.015$]. In addition, the analyses of the interactions showed a significant effect between the preexposure context and the stimulus preexposure [ANOVA: $F_{1, 49} = 16.508$, $P < 0.001$, η2p $= 0.252$] and the

preexposure context with the tests [ANOVA: $F_{2,98} = 3.119$, $P = 0.049$, $\eta 2p = 0.060$], but not for the interaction between the preexposure and the tests [ANOVA: $F_{2,98} = 0.850$, $P = 0.410$, $\eta 2p = 0.017$] or for the second-degree interaction [ANOVA: $F_{2,98} = 2.393$, $P = 0.108$, $\eta 2p = 0.047$].

The results in both experiments suggested that subjects showed different CR levels depending on the stimulus preexposed (CS1 or CS2) and the context of the preexposure phase (light or dark context). According to Figure 2, in both panels (A and B), the main differences among the groups were observed in test 2. So, an analysis of the effect of the test was carried out with the Bonferroni pairwise comparisons to corroborate this issue.

Both experiments showed that there were significant differences between test 1 and test 2 (circadian experiment: test1 MDS 5.34 ± 0.28, test2 MDS 6.13 ± 0.34, $P = 0.026$; light experiment test1 MDS 3.96 ± 0.35, test2 MDS 5.26 ± 0.28, $P < 0.001$) and test 1 and test 3 (circadian experiment test1 MDS 5.34 ± 0.28, test3 MDS 6.92 ± 0.28, $P < 0.001$; light experiment test1 MDS 3.96 ± 0.35, test3 MDS 5.83 ± 0.28, $P < 0.001$). Nevertheless, there were no significant differences between test 2 and test 3 (circadian experiment test2 MDS 6.13 ± 0.34, test3 MDS 6.92 ± 0.28, $P = 0.117$; light experiment test2 MDS 5.26 ± 0.28, test3 MDS 5.83 ± 0.28, $P = 0.055$).

These results supported the idea that the main differences among the groups take place in test 2. The results shown in test 2 were analysed with a Univariate ANOVA for each one. The context preexposure and the stimulus preexposure were the between-subjects factors.

The analysis of test 2 in the circadian experiment did not show a significant effect of the preexposure context [ANOVA: $F_{1,48} = 1.234$, $P = 0.272$, $\eta 2p = 0.025$] or the

stimulus preexposure [ANOVA: $F_{1, 48} = 3.183$, $P = 0.081$, η2p $= 0.062$]. However, it showed significant differences in the interaction between them [ANOVA: $F_{1, 48} = 7.314$, $P = 0.009$, η2p $= 0.132$].

In the light experiment, a significant effect of the preexposure context was revealed [ANOVA: $F_{1, 49} = 7.304$, $P = 0.009$, η2p $= 0.130$] as well as in the stimulus preexposure [ANOVA: $F_{1, 49 =} 13.457$, $P < 0.001$, η2p $= 0.215$]. Furthermore, as in the circadian experiment, the effect of the interaction between them was significant [ANOVA: $F_{1, 49} = 16.571$, $P < 0.001$, η2p $= 0.253$].

In test 2, both one showed a significant effect of the interaction between the preexposure context and the stimulus preexposure. This interaction was analysed with the Bonferroni pairwise comparisons. It showed significant differences between same context-preexposure group and same context-no preexposure group (circadian experiment: MDS 4.36 ± 0.55, MDS 7.21 ± 0.82 respectively, $P = 0.002$; light experiment: MDS 2.96 ± 0.47, MDS 6.36 ± 0.34 respectively, $P < 0.001$) in which the tentacle-lowering mean of same context-preexposure group was lower than the tentacle-lowering mean of same context-no preexposure group. These results indicated that there were not equivalent CR in the same context-preexposure groups with respect to those that received another CS and it is congruent with the LI effect.

In addition, there were significant differences in the tentacle-lowering mean between same context-preexposure group and different context-preexposure group (circadian experiment: MDS 4.36 ± 0.55, 6.79 ± 0.54 respectively, $P = 0.007$; light experiment: MDS 2.96 ± 0.47, MDS 5.93 ± 0.56, respectively $P < 0.001$), so the results suggest that there was an effect of the context involved in the LI performance, which is congruent with context specificity of LI.

However, the analyses did not show significant differences (circadian experiment $P = 0.536$; light experiment $P = 0.779$) between the tentacle-lowering mean of the different context-preexposure group and the mean of the different context-no preexposure group (circadian experiment: MDS 6.79 ± 0.54, MDS 6.2 ± 0.44; light experiment: MDS 5.93 ± 0.56, MDS 5.75 ± 0.33, respectively). These results indicate that there were equivalent conditioning levels in the different context-preexposure groups with respect to those that received another CS.

Also, there were no significant differences (circadian experiment $P = 0.286$; light experiment $P = 0.343$) between the same context-no preexposure and different context-no preexposure (circadian experiment: MDS 7.21 ± 0.82, MDS 6.2 ± 0.44; light experiment MDS 6.36 ± 0.34, MDS 5.75 ± 0.33, respectively). These results indicate that there were equivalent conditioning levels in both control groups.

According to Figure 2 and the statistical analyses for both experiments, during test 1 and test 2 subjects which were preexposed to the CS1 in the same context as the conditioning and the tests presented a lower CR, in contrast with subjects which were preexposed to the CS2 or were preexposed to CS1 but in a different context. These differences among the groups were significant in test 2. Finally, the differences disappeared in test 3 as all the groups showed an equivalent CR. The results of these experiments support the idea that subjects from the group same context-preexposure exhibited a conditioning acquisition delay, which can be interpreted as LI. Also, subjects from the group different context-preexposure showed an attenuation of LI phenomenon produced by a context change (the context specificity of LI). This effect takes place regardless of the experiment, therefore, both context cues (the photoperiod or the light) were equally effective.

Chapter 3: First evidence of ABA renewal in the snail *Cornu aspersum*

1. Experiment 1

The Conditioning of Tentacle Lowering procedure in snails provides them the opportunity to eat (US) in the presence of an odour (CS). This treatment increases the number of tentacle lowerings in the presence of the odour (Loy et al., 2006). After conditioning, it is possible to expose the snails to the CS odour without any consequences (extinction trials) in the presence of an additional odour. This additional odour is designed to play the role of differentiating the extinction context from the conditioning context. If odours can provide contextual cues, then no reinforced presentations of a CS in the presence of a new odour could produce a reduction in conditioned response (CR), but this reduction will be specific to that context (Bonardi et al., 1990) and, as a result, an increase in the CR will occur when the CS odour is presented and the contextual odour is no longer present.

1.1. Method

1.1.1. Subjects and housing

Subjects were 40 adult snails with a mean shell diameter of 28 mm (range 24−38 mm) which were taken from the wild. Snails were individually housed in plastic cages ($50 \times 50 \times 100$ mm) with air holes. They were given access to a small amount of water and ad libitum food. The boxes were placed in a room at a constant temperature of 22°C. Snails were deprived of food for 10 days prior to the start of the experiment. After the experiment, snails were given food ad libitum and placed back into the wild, in a different place from their collection.

1.1.2. Apparatus and stimuli

The experimental setting used was a plastic perforated surface (390 mm x 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 22 °C and illuminated with a red light (LED 3 W). The stimuli used were two solutions, one of mango and other of coconut (oil brand La Casa de Los Aromas, 2 mL/L) which served as either the conditioned stimulus (CSs) or the context (C); carrots served as the unconditioned stimulus (US).

1.1.3. Procedure

In this experiment, tentacle lowering was measured as CR by two observers. This measure consisted in counting on 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). During test sessions the observers were unaware about the group each subject belonged.

Snails were randomly assigned to two groups: "same context" and "different context". The context was determined by the presence or absence of a novel odour during the extinction phase. In the "same context" group, conditioning and extinction were performed with the same odour (CS) whereas, in the group of "different context" extinction was carried out with two odours simultaneously, the conditioned stimulus and a new odour as context (CS + C). Furthermore, the role of the odours as CS or C was counterbalanced, so for half of the subjects the CS was mango and the C was coco and for the other half the CS was coco and the C was mango. At the beginning of each trial, snails were placed on their sides and sprayed with fresh water to induce activity.

Conditioning training and extinction was made in groups of 10 subjects. Experimental design is summarized in Table 1.

Table 1

Experimental design renewal with odours.

Group	Pre-Test (Day 1)	Training (Day 2)	Conditioning Test (Day 3)	Extinction (Day 4)	Extinction Test (Day 5)	Renewal (Day 6)
"Different Context"	CS	6 CS + US	CS	6 CS+C	CS+C	CS
"Same Context"	CS	6 CS + US	CS	6 CS	CS	CS

Note. The CS and the C employed were a solution of mango or coconut counterbalanced and the US employed was a piece of carrot. The symbol "+" indicates that stimuli were presented simultaneously.

i. Pre-Test

On the first day, tentacle lowering was measured for each subject. Snails were exposed to the CS for 2 min. 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.

ii. Training

On the second day, the CS was paired with access to food (US) for 2 min. A piece of carrot was placed in front of the snail whereas the odour was placed below the perforated surface in a dish containing four cotton pads, each containing 2 mL of essence. This trial was made in groups of 10 snails and it was repeated six times during the day with an inter-trial interval (ITI) of 58 min.

iii. Conditioning Test

The day after the training, tentacle lowering was measured, with the same procedure used in the pre-test.

iv. Extinction

The following day snails were exposed to the CS for 2 min in each extinction trial, but they did not have access to the US. Snails of the group "same context" were exposed to the same odour as during conditioning whereas, snails of the group "different context" were exposed to the odour which was employed as CS and a new odour which was taken as C simultaneously. In "same context" group four cotton pads with 2 mL of essence per pad as previously, whereas in "different context" group there were eight cotton pads, four for CS and four for C, with again 2 mL of essence per pad, and their positions were intermixed. Each extinction trial was carried out with in squads of 10 snails, as during training, and there were six trials on the single extinction day, with an ITI of 58 min.

v. Extinction Test

The day after the extinction, tentacle lowering was measured. The "same context" group was exposed to CS and "different context" group was exposed to CS and C simultaneously in the same way as the previous extinction day and the procedure was the same as the pre-test and conditioning test.

vi. Renewal Test

The renewal test was conducted on the final day. This test consisted in measuring tentacle lowering in the presence of the CS only. The procedure was the same as for the previous tests.

1.1.4. Statistical analyses

The number of times that the subjects lowered the left tentacle were measured. An analysis of variance and t-Student tests were used for statistical analyses and the mean score of the two observers was used in the statistical analysis. These analyses were run using SPSS v21 (SPSS Inc., Chicago, IL, U.S.A.). An inter-judge reliability analysis was done and the Kappa rate showed a moderate agreement between the researchers: pre-test (Kappa: k = 0.633), conditioning test (Kappa: k = 0.515), extinction test (Kappa: k = 0.669), renewal test (Kappa: k = 0.458) (K value: <0.20 = lower, 0.21−0.40 = weak, 0.41−0.60 = moderate, 0.61−0.80 = well, 0.80–1.00 = high) (see Cerda and Villarroel, 2008).

1.2. Results of Experiment 1

The data were collapsed because the counterbalance was not significant: no effect of odour allocation ($F_{1,36}$ = 2.963, P = 0.95) and no interaction between odour and treatment ($F_{1,36}$ = 0.679, P = 0.416).

Panel A of Figure 1 shows the tentacle lowering mean of the two groups for the pre-test and conditioning test. Both groups showed similar tentacle lowering in pre-test ("same context" group: 2.25 ± 0.44 "different context" group: 2.37 ± 0.43) whereas, in conditioning test subjects in "different context" group (6.3 ± 0.51) showed a slightly higher tentacle lowering than subjects in "same context" group (5.25 ± 0.26) but this difference was not significant.

Figure 1

Experimental results renewal with odours.
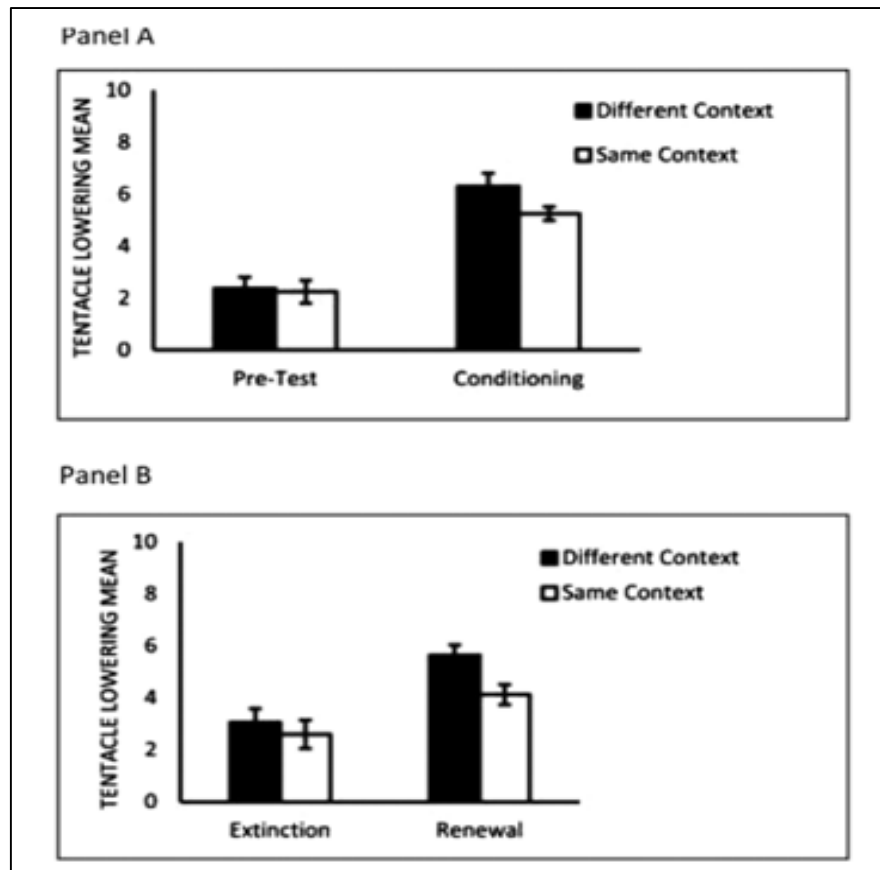
Note. Mean number of tentacle-lowering responses (CR) made by "different context and same context" groups during experiment 1. Pre-test and conditioning test were shown in Panel A whereas, extinction and renewal test were shown in Panel B. Vertical bars represent SEMs.

An ANOVA was carried out with the experimental phase (pre-test and conditioning test) and the group ("different context" group and "same context" group) as the variables. The main effect of the experimental phase was highly significant (ANOVA: $F_{1, 38} = 84.118$, $P < 0.001$, η2p $= 0.689$) showing a similar increase in CR after conditioning in both groups. However, the statistical analysis did not show differences for the effect of the group (ANOVA: $F_{1, 38} = 1.621$, $P = 0.211$), and neither for the interaction between the experimental phase and the group (ANOVA: $F_{1, 38} = 1.501$, $P = 0.228$).

Panel B of Figure 1 shows a similar mean number of tentacle lowerings in the groups during extinction test. There were no differences between subjects which received the extinction trials in the same context as the conditioning ("same context" group: 2.6 ± 0.37) and subjects which made the extinction in a different context ("different context" group: 3.05 ± 0.5). This reduction in CR was significant comparing to level of CR reached after conditioning. An ANOVA with the experimental phase (conditioning test and extinction test) and the group ("different context" and "same context") as the variables showed a significant effect of the experimental phase (ANOVA: $F_{1, 38} = 52.429$, $P < 0.001$, $\eta 2p = 0.580$), but no effect of groups (ANOVA: $F_{1, 38} = 2.878$, $P = 0.098$) and no interaction (ANOVA: $F_{1, 38} = 0.542$, $P = 0.466$). Therefore, after extinction, the exposure to the CS (odour) alone ("same context" group) or in compound with another odour ("different context" group) produced a similar reduction in CR.

The critical results of the experiment were shown in renewal test (panel B of Figure 1). Subjects receiving the extinction in compound with an additional odour ("different context" group: 5.65 ± 0.54) showed a higher level of CR than subjects receiving the extinction just with the CS ("same context" group: 4.12 ± 0.39) and this difference was confirmed by statistical analysis (t Student: $t_{38} = 2.277$, $P = 0.029$, d = 0.719).

These results showed a recovery of the extinguished response when the CS is tested in the original conditioning context, which is equivalent to renewal effect. However, several learning phenomena could be involved too. The experimental design is similar to conditioned inhibition and second order conditioning designs (Pavlov, 1927/1970) but both paradigms affect the added stimulus, and in this experiment the odour which plays the role as context and the acquired learning of context stimulus was not tested. In addition, it is worth noting that the use of an odour as a contextual cue could have influenced the perception of the CS and the presentation of a new odour along with the

CS in the extinction phase can be perceived as a different odour, so in that case the result would be the consequence of simple discrimination between the CS and other odour. Furthermore, the order of CS + C and CS presentation was not counterbalanced, so that half of the subject would have received CS + US, CS + C, CS treatment and the other half (CS + C) +US, CS, CS + C treatment, but the counterbalance of the odour as CS and the other odour as context is also suitable to equate the experience with the odours in both groups and ensure that there is no preference for one of them. For these limitations the results cannot be interpreted as an instance of renewal effect. Consequently, Experiment 2 was carried out to further study ABA renewal using other context cues in such a way that the results cannot be interpreted as configural learning.

2. Experiment 2

To continue the study of ABA renewal, in Experiment 2 the same procedure as Experiment 1 was employed but in this case circadian cues, which were defined by the hour of the day and changes in the light cycle, were used as context stimulus because it is relevant in the locomotive activity of *Cornu aspersum* (Bailey, 1981; Attia, 2004) and it is not expected that circadian cues influence the perception of an odour CS. In this experiment it was expected that the results´ pattern were the same as previous one whatever it would show ABA renewal evidence in this kind of subject.

2.1. Method

2.1.1. Subjects and housing

Subjects were 20 adult snails with a mean shell diameter of 30.23 (range 26−35 mm) which were taken from the wild. The house boxes were placed in a room with a

reversed 12 light/dark cycle and the dark period starting at 06:00 h. All other housing details were identical to those in Experiment 1.

2.1.2. Apparatus and stimuli

The experimental setting was identical to the first one used in Experiment 1, but in this case two types of lights were used to reproduce the light/dark cycle (photoperiods): a red light (LED 3 W) in dark cycle and a white light (LED 5.5 W) in light cycle. The stimuli used were a solution of mango (oil from La Casa de Los Aromas, 2 mL/L) as the conditioned stimulus (CS) and carrot as the unconditioned stimulus (US).

2.1.3. Procedure

Snails were randomly assigned to two groups: "same context" and "different context". The context was determined by the hour of the day and the illumination (photoperiod). In the "same context" group conditioning and extinction were performed in the same light period whereas in the "different context" group extinction was performed in a different light period than conditioning. Furthermore, the time of day in which the treatment was performed was counterbalanced so, for half of the subjects in each group, conditioning was performed in light cycle and for the other half conditioning was performed in dark cycle. The treatment was started at either 08:00 h. or 20:00 h. and it was made in the same way as Experiment 1. However, the observation was made only by one observer who was unaware of which condition each snail was in and conditioning training and extinction was made in groups of 5 subjects per group instead of 10 subjects per group. Unlike the previous experiment, two extinction sessions (two days of extinction and two tests of the extinction) were made because in the first one, extinction was not significant. The experimental design is summarized in Table 2.

Table 2

Experimental design renewal with circadian cues.

Group	Pre-Test (Day 1)	Training (Day 2)	Conditioning Test (Day 3)	Extinction (Days 4-6)	Extinction Test (Day 5-7)	Renewal (Day 8)
"Different Context"(B)	(A) CS	6 (A) CS + US	(A) CS	6 (B) CS	(B) CS	(A) CS
"Same Context"(A)	(A) CS	6 (A) CS + US	(A) CS	6 (A) CS	(A) CS	(A) CS

*Note. The CS employed was a solution of mango, The A and B (context) employed were the circadian cues, which were determined by the hour of the day and the lighting, and US employed was a piece of carrot. The symbol "+" indicates that stimuli were presented simultaneously.

2.1.4. Statistical analyses

The statistical analyses were the same as in Experiment 1. Furthermore, throughout the experiment a subject from "same context" group died and it was removed of the data.

2.2. Results of Experiment 2

The data were collapsed because the counterbalance was not significant: no effect of the photoperiod ($F_{1, 15} = 0.692$, $P = 0.419$) or the interaction between the photoperiod and the treatment ($F_{1, 15} = 1.755$, $P = 0.205$).

Panel A of Figure 2 shows the group means for number of tentacle lowerings in the pre-test ("same context" group: 3.89 ± 0.56 "different context" group: 4.1 ± 0.53) and conditioning test ("same context" group: 8.66 ± 0.97 "different context" group: 8.7 ± 0.47). Both groups showed similar tentacle lowering in the pre-test and in conditioning test and no group differences were detected.

Figure 2

Experimental results renewal with circadian cues.
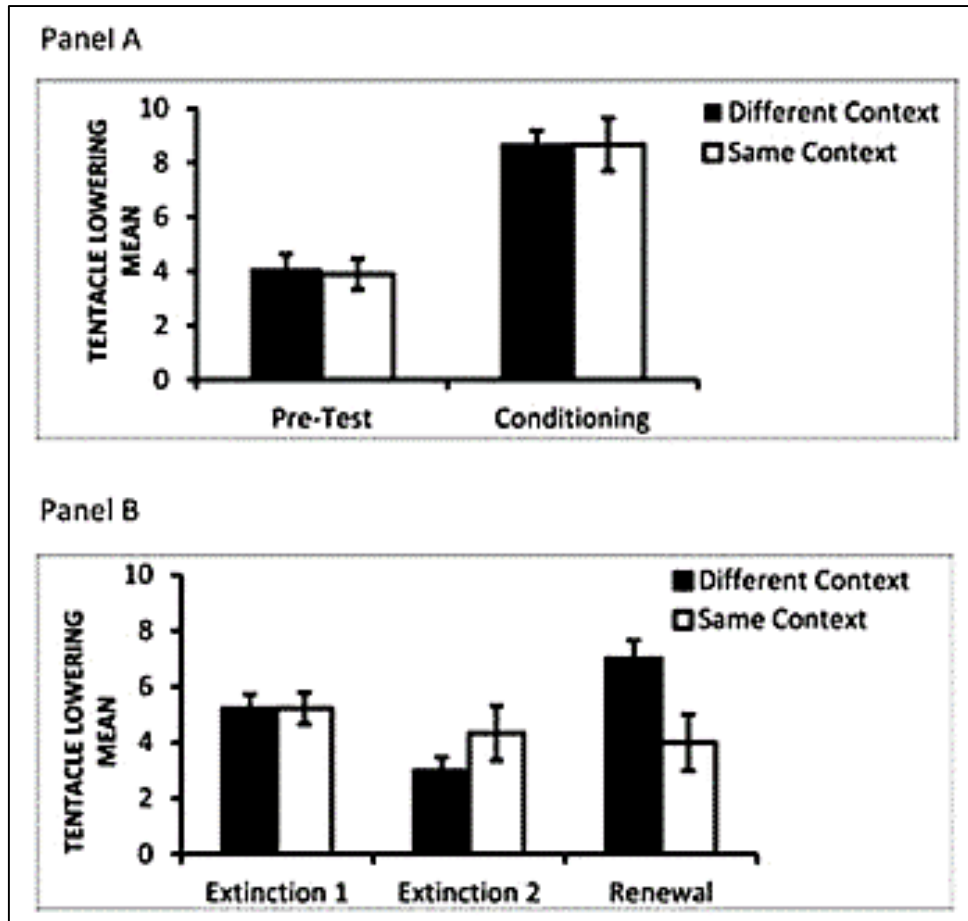
Note. Mean number of tentacle-lowering responses (CR) made by "different context and same context" groups during experiment 2. Pre-test and conditioning test were shown in Panel A and extinction and renewal test were shown in Panel B. Vertical bars represent SEMs.

An ANOVA with the experimental phase (pre-test and conditioning test) and the group ("different context" group and "same context" group) as the variables showed differences for the effect of the experimental phase (ANOVA: $F_{1, 17} = 82.388$, $P < 0.001$, η2p = 0.829) so, snails increased the level of CR after conditioning. Nevertheless, the statistical analysis did not show differences for the effect of the group (ANOVA: $F_{1, 17} = 0.026$, $P = 0.874$) neither the interaction (ANOVA: $F_{1, 17} = 0.030$, $P = 0.865$).

Panel B of Figure 2 shows tentacle lowering mean of the groups for extinction test 1 ("same context" group: 5.22 ± 1.01 "different context" group: 5.20 ± 0.66) and extinction test 2 ("same context" group: 4.33 ± 0.7 "different context" group: 3 ± 0.8). Both groups showed a decrease of their tentacle lowering mean throughout the two extinction tests. It can be observed a slight difference between groups in the second test, but an analysis of variance with the extinction trials and the group as the variables revealed a significant effect of the extinction trials (ANOVA: $F_{1, 17} = 7.497$, $P = 0.014$, $\eta 2p = 0.306$), but no effect of the group (ANOVA: $F_{1, 17} = 0.487$, $P = 0.495$) and no effect of the interaction (ANOVA: $F_{1, 17} = 1.351$, $P = 0.261$). Therefore, both extinction treatments were equally effective to reduce the level of CR acquired during conditioning, at least testing the conditioning in the different extinction contexts.

Finally, the most important result of this experiment is observed in the renewal test. As it can be seen in Panel B of Figure 2, subjects for which extinction was made in a different light period than conditioning ("different context" group: 7 ± 0.86) showed a higher tentacle lowering than subjects for which conditioning and extinction were made in the same light period ("same context" group: 4 ± 0.82). A Student t-test confirmed that the group difference was statistically significant ($t_{17} = 2.521$, $P = 0.022$, $d = 1.162$).

As in Experiment 1, the results of Experiment 2 showed a recovery of the CR when CS is tested in the conditioning context, which is congruent with the renewal effect. Moreover, the contextual cue has a different sensory modality than the CS thus, it is difficult to explain these results as a configural learning.

Chapter 4: Three types of renewal and the magnitude comparison

Taking into account the evidence of ABA renewal reported in Chapter 3, in this set of experiments the three renewal paradigms were studied and compared among them. In Experiment 1a ABA renewal was replicated. In Experiment 1b and 1c, AAB and ABC renewal were studied, respectively. Then, Experiment 2 was conducted to show a comparison of the three paradigms. The illumination was used as context.

1. Method

1.1. 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 x 50 x 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.

1.2. Apparatus and stimuli

The experimental set was a perforated plastic surface (390 X 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: a white light (LED 5.5 W) was used as the light context, a red light (LED 3W) was used as the dark context in all the experiments and a dim light (LED 7W) in Experiments 3 and 4 was included as the third 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 white and dim light range, so although the red light cannot be perceived by snails, they can perceive the white 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 light contexts were 60x118 mm and for the bulb of the dim context 50x100 mm. The distance between the bulbs and the experimental set was 700 mm.

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.

1.3. 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).

In Experiments 1a, 1b and 1c, snails were randomly assigned to two groups according to the contextual change during extinction. In the Experiments 1a and 1b, subjects from "AAA group" received the extinction and the conditioning phases in the same context, whereas subjects from "ABA and AAB groups, respectively," received the extinction phase in a different context from the renewal test one. In these experiments, two illuminations were used as contexts: the 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. For Experiment 1c, subjects from "ABB group" received only the extinction and the renewal test in the same context, whereas subjects from "ABC group" received the three experimental phases in three different contexts. Besides the above contexts, a third one was included: the dim context. Moreover, two replicas with two groups for each one (experimental and control groups) were conducted: BCA-ACC and CAB-CAA, specifically, as a counterbalance of the role of the context and, therefore, to know if snails can discriminate between a brilliant light and a dim light, which would allow us to confirm that the renewal obtained is an ABC paradigm. 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. The three contexts employed in the Experiment 1c were used here, but in this case the contexts were not counterbalanced, because in the previous experiments it was observed that snails discriminate among them. Thus, all the subjects received the conditioning in the light context (A), the extinction in the dark context (B) and the renewal test in the dim context (C).

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 Experiment was started at 8:00 a.m.

i.   Pre-Test

In this phase, tentacle lowering was measured for each subject individually. Snails were exposed to the odour (CS) for 2 minutes. This odour was placed below the perforated surface in a dish containing four cotton pads and each one was impregnated with 2ml of the solution.

ii.   Conditioning

Subjects were exposed to CS paired with access to food (US) for 2 minutes. 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 made in groups. Conditioning sessions were

conducted in 6 trials with an ITI of 58 minutes was performed until optimal levels of CR was reached.

iii.   Conditioning Test

For the conditioning test, tentacle lowering was measured with the same procedure used in the pre-test. The context for each group was the same as the conditioning phase context.

iv.   Extinction

Snails were exposed to the CS for 2 minutes 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. Extinction sessions were conducted in 6 trials with an ITI of 58 minutes until an optimal decrease of the CR was reached.

v.   Extinction Test

Tentacle lowering was measured in the same way as previous tests, considering the different contexts used for each group during the extinction.

vi.   Renewal Test

The renewal test was conducted using the same procedure as previous tests, but the context employed for all the subjects was different from the one employed in the extinction phase and the extinction test, except for the controls. The experimental design is summarized in Table 1.

Table 1

Design for each experiment.

Exp.	Groups	Pre-Test	Conditioning	Conditioning Test	Extinction	Extinction Test	Renewal Test
	ABA				(B)CS	(B)CS	
1a		(A)CS	(A)CS+US	(A)CS			(A)CS
	AAA				(A)CS	(A)CS	
	AAB						(B)CS
1b		(A)CS	(A)CS+US	(A)CS	(A)CS	(A)CS	(A)CS
	AAA						
	ABC						(C)CS
		(A)CS	(A)CS+US	(A)CS	(B)CS	(B)CS	
	AAB						(B)CS
1c	BCA	(B)CS	(B)CS+US	(B)CS			(A)CS
					(C)CS	(C)CS	
	ACC	(A)CS	(A)CS+US	(A)CS			(C)CS
	CAB						(B)CS
		(C)CS	(C)CS+US	(C)CS	(A)CS	(A)CS	
	CAA						(A)CS
	ABA				(B)CS	(B)CS	(A)CS
2	AAB				(A)CS	(A)CS	(B)CS
	ABC	(A)CS	(A)CS+US	(A)CS	(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 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 1 c and 2, A was the light context, B was the dark context and C was the dim context. The symbol "+" indicates that stimuli were paired.

1.4. Statistical analysis

The number of times which the subjects lowered the left tentacle was measured. A repeated-measures analysis of variance (ANOVA) and the analysis of the interaction with the Bonferroni corrected pairwise comparisons were carried out. In addition, the Bayesian t Student-test for independent samples and the Bayesian ANOVA were included to analyse the renewal effect. The level of significance used was $\alpha = 0.05$ and the effect sizes for ANOVAs were reported as partial Eta-square (η^2_p). These analyses were run using SPSS v21 (SPSS Inc., Chicago, IL, U.S.A.).

2. Results of Experiment 1a (ABA renewal)

Figure 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 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.

Figure 2

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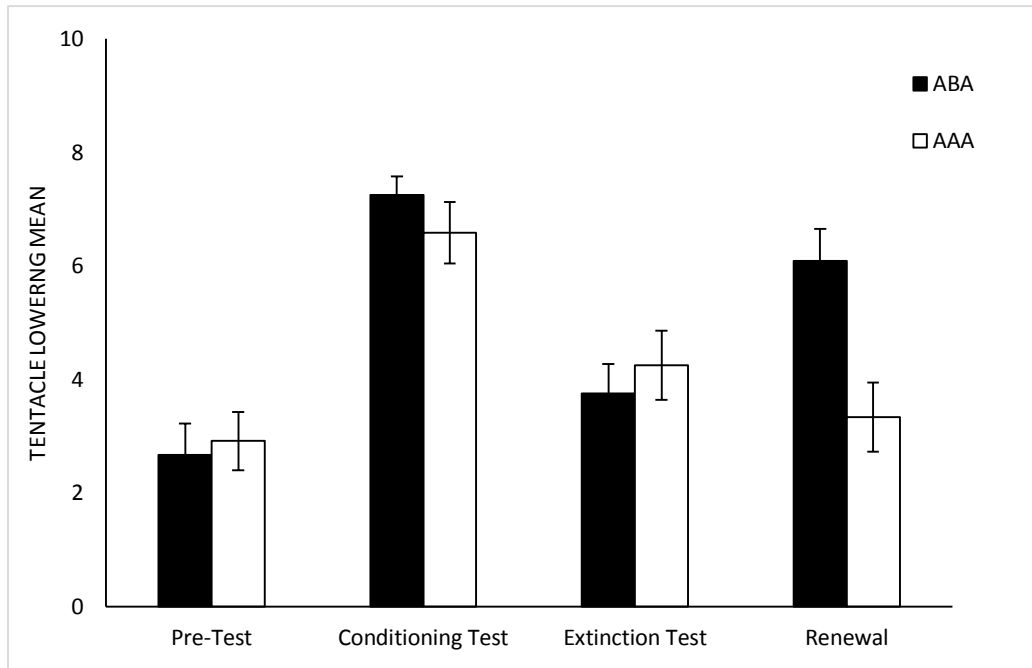
Note. Tentacle lowering mean is shown for ABA group, represented by the dark bars, and AAA group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.

Firstly, the analyses of the context counterbalancing were conducted, in which half of the subjects received the conditioning in the light context and the other half in the dark context. The effect of the context was significant [ANOVA: $F_{1,20}= 7.034$, $P = 0.015$, $\eta^2_p = 0.260$], but not the effect of the group (the "different context group" and the "same context group") [ANOVA: $F_{1,20}= 2.664$, $P = 0.118$, $\eta^2_p = 0.188$]. In addition, there were not significant interactions between the context and the groups [ANOVA: $F_{1,20}= 0.260$, $P = 0.616$, $\eta^2_p = 0.013$] and the context with the tests [ANOVA: $F_{3,60}= 0.474$, $P = 0.701$, $\eta^2_p = 0.023$]. The second-degree interaction was not significant either [ANOVA: $F_{3,60}= 0.523$, $P = 0.668$, $\eta^2_p = 0.26$]. In all the experimental phases, the snail's activity was higher when the context was dark in contrast with the light context [the 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 difference reflects higher means in one context than in another but since they are counterbalanced, the effect was offset. Thus, the data were collapsed.

The data showed in Figure 2 were analysed with the repeated-measures ANOVA, with the tests as the within-subjects factor and the groups (the "same context" and the "different context" groups) as the between-subjects factors. It showed a significant effect of the test [ANOVA: $F_{3, 66}$= 24.325, P< 0.001, η^2_p = 0.525], but not a significant effect of the groups [ANOVA: $F_{1, 22}$= 2.147, P= 0.157, η^2_p = 0.089], so in both groups an equivalent level of conditioning and extinction were observed.

The interaction between the groups and the tests was significant [ANOVA: $F_{3, 66}$= 4.416, P=0.007, η^2_p = 0.167] so, Bonferroni corrected pairwise comparisons were carried out to analyse this interaction. It revealed significant differences between groups only in the renewal test (the "same context group" 3.33 ±0.60, the "different context group" 6.08 ±0.57, P=0.003). Moreover, the Bayesian t Student-test for independent samples was conducted to show differences between both groups in the renewal test and support the Bonferroni analyses. The H_1, in which it is suggested that there were significant differences between both groups during the renewal test, showed a BF_{10} =12.043 whereas, the H_0, in which it is suggested that there were not significant differences between both groups during the renewal test, showed a BF_{01}=0.083. This is congruent with the P value of the Bonferroni corrected pairwise comparisons. Thus, 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 Chapter 3, which results were published (Loy et al., 2020) with the same invertebrate species. In addition, it is shown that the illumination is an effective context as the photoperiod, 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 the snail *Cornu aspersum* only ABA renewal was observed. For this reason, in the next experiments (Experiment 1b and Experiment 1c) AAB and ABC paradigms were studied, respectively.

3. Results of Experiment 1b (AAB renewal)

Figure 3 presents the tentacle lowering mean in both groups throughout all the experimental tests. 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 context 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.

Figure 3

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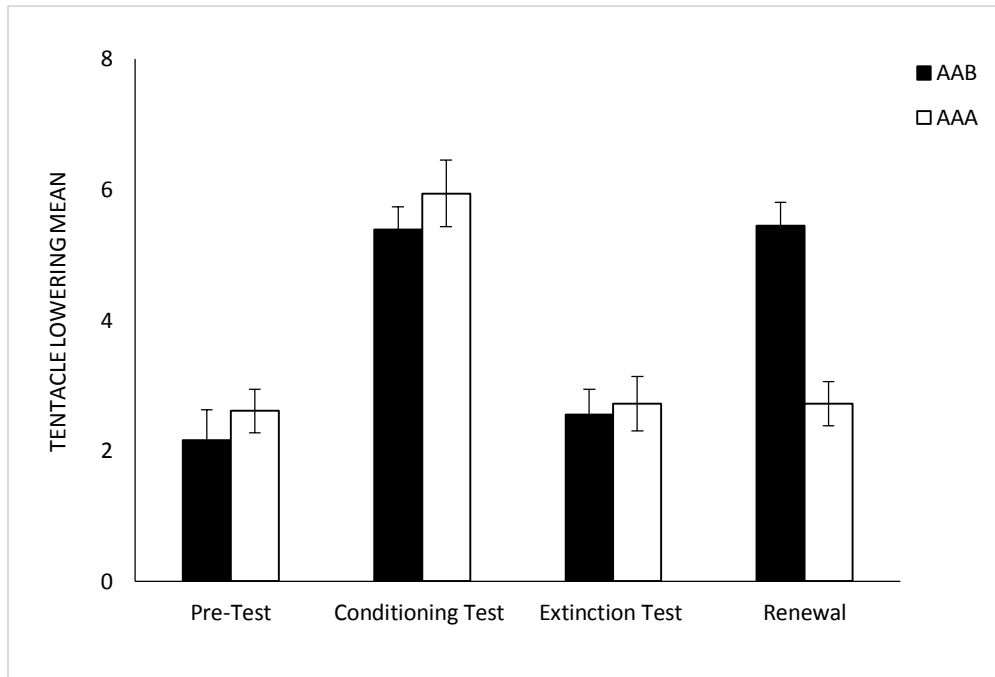
 *Note. Tentacle lowering mean is shown for AAB group, represented by the dark bars, and AAA group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.

As in the previous study, the analysis of the context counterbalancing was carried out. There was not significant effect of the context [ANOVA: $F_{1, 32}= 4.045$, $P = 0.053$, $\eta^2_p = 0.112$] and effect of the group [ANOVA: $F_{1, 32}= 1.404$, $P = 0.245$, $\eta^2_p = 0.042$]. The interaction of the context with the tests was significant [ANOVA: $F_{3, 96}= 3.516$, $P = 0.018$, $\eta^2_p = 0.099$], but not the interaction between the context and the groups [ANOVA: $F_{1, 32}= 2.283$, $P = 0.141$, $\eta^2_p = 0.067$] and the second-degree interaction [ANOVA: $F_{3, 96}= 1.019$, $P = 0.388$, $\eta^2_p = 0.031$]. 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 Figure 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: $F_{3, 102} = 29.826$, $P < 0.001$, $\eta^2_p = 0.467$], but not a significant effect of the groups [ANOVA: $F_{1, 34} = 1.644$, $P = 0.208$, $\eta^2_p = 0.046$] so, in both groups an equivalent level of conditioning and extinction were observed.

The interaction of the groups with the tests was significant [ANOVA: $F_{3, 102} = 7.978$, $P < 0.001$, $\eta^2_p = 0.190$]. The Bonferroni corrected pairwise comparisons was made to analyse this interaction and it showed significant differences between groups only in the renewal test (the "same context group" 2.72 ± 0.34, the "different context group" 5.44 ± 0.36, $P < 0.001$), showing that the AAB group differs from the other one during renewal test. Furthermore, the Bayesian t Student-test for independent samples was conducted. The H_1, in which it is suggested that there were significant differences between both groups during the renewal test, showed a $BF_{10} = 3.316.386$ whereas, the H_0, in which it is suggested that there were no significant differences between both groups during the renewal test, showed a $BF_{01} = 3.015e\text{-}4$, supporting the fact that there are significant differences between AAB and AAA groups during the renewal test. This is congruent with the P value of the Bonferroni corrected pairwise comparisons.

Results of Experiment 1b (depicted in Figure 3) and the statistical analyses showed that subjects which had received the renewal test in a different context from the other experimental phases one, presented a recovery of the extinguished response in comparison with subjects which had received all the experimental phases in the same context, 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.*

4. Results of Experiment 1c (ABC renewal)

In Figure 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.

Figure 4

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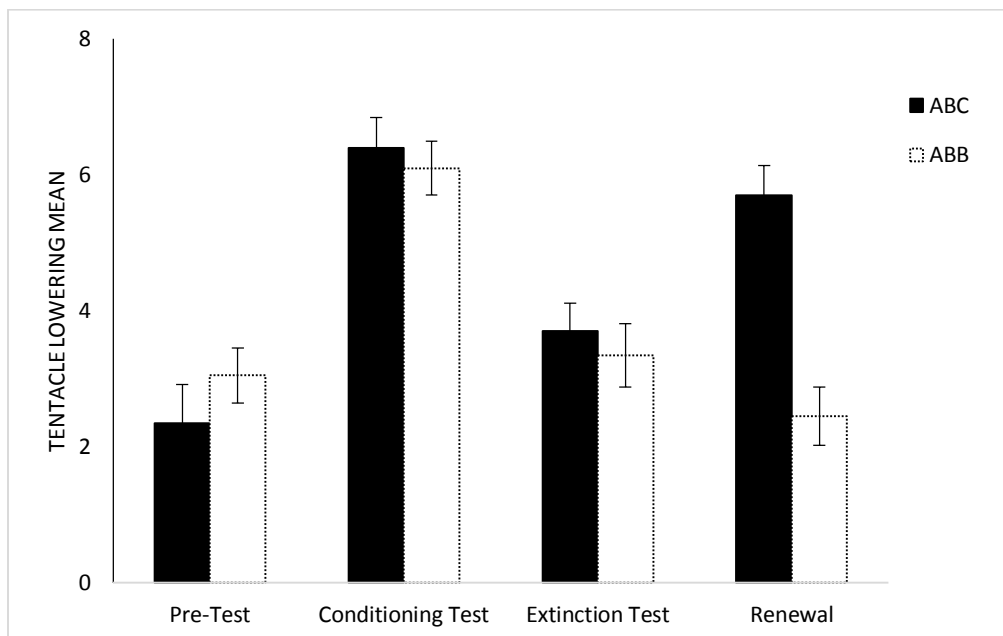
 Note. Tentacle lowering mean is shown for AAB group, represented by the dark bars, and AAA group, represented by the white bars, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.

Firstly, the analysis of the replicas ABC, BCA and CAB renewal was carried out. The effect of the replicas was not significant [ANOVA: $F_{1, 38}$=4.107, P=0.050, η^2_p =

0.164] and neither was that of the interaction of the replicas with the tests [ANOVA: $F_{3, 114}$=1.822, P=0.147, η^2_p = 0.084]. Therefore, the data were collapsed.

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: $F_{3, 114}$= 28.142, P< 0.001, η^2_p =0.425], but not a significant effect of the groups [ANOVA: $F_{1, 38}$= 4.107, P=0.050, η^2_p = 0.098]. As in the previous experiments, both groups showed an equivalent level of conditioning and extinction. There was, however, a significant effect of the interaction of the groups with the tests [ANOVA: $F_{3, 114}$=8.865, P<0.001, η^2_p = 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 (the "same context group" 2.45 ±0.42, the "different context group" 5.7 ±0.43, P<0.001). In addition, the Bayesian t Student-test for independent samples was conducted. The H_1, in which it is suggested that there were significant differences between both groups during the renewal test, showed a BF_{10} =3.151.427 whereas, the H_0, in which it is suggested that there were not significant differences between both groups during the renewal test, showed a BF_{01}=3.173e-4. Thus, there are significant differences between ABC and ABB groups during the renewal test and this is congruent with the P value of the Bonferroni corrected pairwise comparisons.

The data in Figure 4 indicate that subjects which received the renewal test in a third different context showed a recovery of the tentacle lowering response in contrast with subjects which received this test in the same context from the extinction one. Then, even though neither the effect of the groups nor their interaction with the tests were significant, the t Student test confirmed the differences between groups shown in Figure 4. 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.

5. Results of Experiment 2 (the renewal magnitude)

In Figure 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.

Figure 5

Results of Experiment 2 (Renewal magnitude).
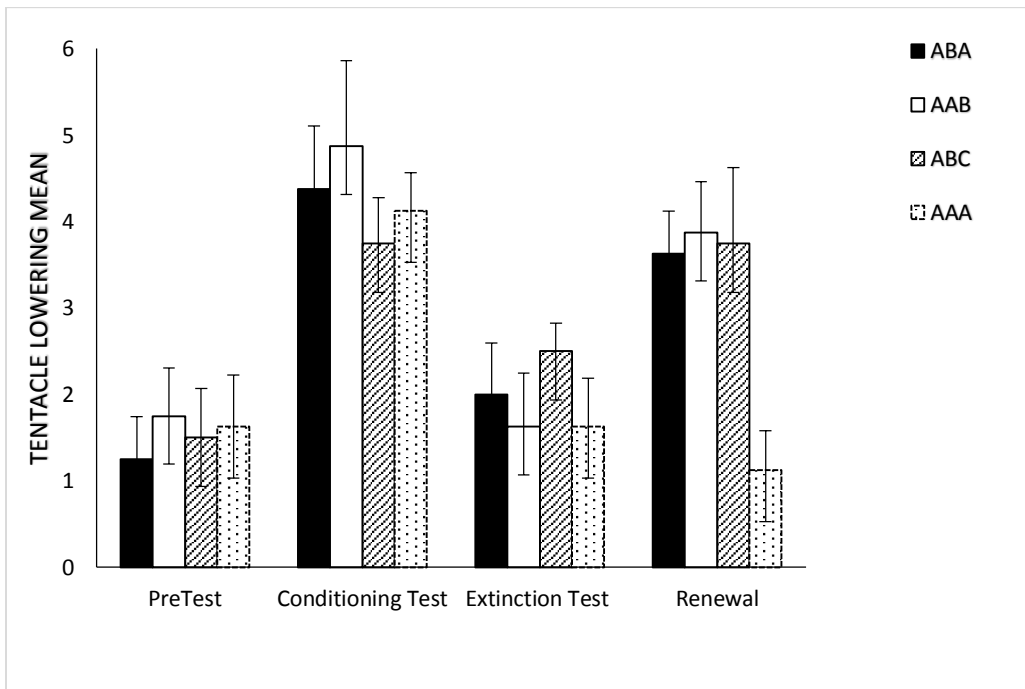
Note. Tentacle lowering mean is shown for ABA group, represented by the dark bars; AAB group, represented by the white bars; ABC group, represented by the striped bars; and AAA group, represented by

the bars with points, during the pre-test, the conditioning test, the extinction test and the renewal. Vertical bars represent SEMs.

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, η^2_p = 0.379], but not a significant effect of the groups [ANOVA: $F_{1, 59}$= 1.082, P=0.364, η^2_p = 0.052]. Taking into account these statistical analyses, the four groups showed an equivalent level of conditioning and extinction.

The interaction of the groups with the tests was significant [ANOVA: $F_{9, 177}$= 2.826, P=0.004, η^2_p = 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). A Bayesian ANOVA was conducted to show differences among groups in the renewal test. The H_1, in which it is suggested that there were significant differences among the groups during the renewal test, showed a BF_{10} =48.026 whereas, the H_0, in which it is suggested that there were not significant differences among the groups during the renewal test, showed a BF_{01}=0.021. The Post Hoc Tests were presented in Table 2.

Table 2

Post Hoc Comparisons-Groups.

Groups		$BF_{10,U}$	$BF_{01,U}$
ABA	AAB	0.440	2.271
	ABC	0.341	2.932
	AAA	32.244	0.031
AAB	ABC	0.372	2.691
	AAA	11.820	0.085
ABC	AAA	10.965	0.091

Note: $BF_{10,U}$ = the probability that there were significant differences; $BF_{01,U}$ = the probability that there were not significant differences.

As we can see in Table 2, the $BF_{10,U}$ value was higher in the comparison of the AAA group with each renewal group. However, the $BF_{01,U}$ value was lower in the comparison among the three renewal groups. Thus, all the renewal groups differ from the AAA group during renewal test. However, the renewal groups do not differ among them.

The data shown in Figure 5 and the statistics corroborated that subjects 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.

Chapter 5: Results Discussion

1. Results Summary

The present work offers a study about the effect of the context in learning phenomena for the terrestrial snail *Cornu aspersum*. Specifically, it is focused on the study of context specificity of LI and the renewal phenomenon, using an appetitive Pavlovian Conditioning of Tentacle Lowering procedure.

1.1. Context specificity of Latent Inhibition

In Chapter 2, two experiments were conducted to show context specificity of LI: the circadian experiment, in which the photoperiod (determined by the hour of the day and the illumination) was used as context; and the light experiment, in which only the light was used as context. The second one (the light experiment) was performed to reproduce the results observed in the circadian experiment and simplify the procedure. Subjects which were preexposed to the CS1 in the same context as the conditioning and the tests showed the lowest CR mean during the tests 1 and 2. Nevertheless, in test 3, these subjects reached an equivalent conditioning level as the rest of the groups. These results showed a delay of the conditioning acquisition which can be considered an instance of LI phenomenon. The second major finding was that subjects which were preexposed to the CS1 in a different context than the conditioning and the tests showed an equivalent level of CR throughout the three tests as subjects which were preexposed to the CS2. In addition, during the first two tests, these subjects presented a higher CR level than subjects which were preexposed to the CS1 in the same context as the conditioning and the tests. These results support the idea that a context change during the preexposure of the CS1 affects LI.

The present study is, therefore, the first attested evidence about context specificity of LI in terrestrial molluscs and can be added to the only study we are aware of that found contextual specificity of LI in an invertebrate species (Jacob et al., 2021). The results obtained in both experiments (the circadian and the light experiments) show that the use of the photoperiod or the light as context produces an equivalent context specificity. Nevertheless, the use of the light as context offers a simpler experimental procedure.

One limitation of the present study and the investigation based on Classical Conditioning procedures is that they are susceptible to be confused with the effects of habituation and sensitization, which call into question the LI evidence in invertebrates (Lubow and Weiner, 2010). Even though no test has been performed to rule out these alternative explanations for these experiments, a similar procedure (Loy et al., 2006, Experiment 1) showed an absence of habituation effects after 6 unreinforced exposures to CS by the unpaired group (Figure 1A, p. 307). Therefore, it is difficult to explain the results of the present analysis by a phenomenon other than LI.

1.2. Renewal

In Chapter 3, the experiments of ABA renewal were addressed. In Experiment 1, subjects which had received the CS paired with other odour during the extinction showed a higher tentacle lowering response, in contrast with subjects which had received conditioning and extinction without additional odour. In Experiment 2, an odour was again used as a punctuate stimulus (CS), but context stimuli were provided by circadian cues. Subjects which, during extinction, had received the CS in a different photoperiod (time of day and illumination) to the conditioning one showed a higher CR during renewal test in contrast with subjects which had received the CS in the same context throughout all experimental phases. The results of Experiment 1 can be explained as a consequence of a discrimination between conditioning with one odour and extinction with another

different odour, so that the presentations of the CS along with the other odour could form a configural compound stimulus (Pearce, 1994; Starosta et al., 2016) and the extinction would not have happened at all. However, the results in Experiment 2, in which the contextual stimulus was defined by time of day and lighting, are more difficult to be explained by configural account.

Several studies have reported evidence of reinstatement, spontaneous recovery and renewal in vertebrates (e.g., Bouton and Bolles, 1979a, 1979b; Brooks and Bouton, 1993; Kuroda et al., 2017a, 2017b; Rescorla, 2007). Also, reinstatement and spontaneous recovery have been observed in some species of invertebrates (e.g., Bitterman et al., 1983; Plath et al., 2012 in honey bees; Engel and Wu, 1996 in fly fruit; Nathaniel et al., 2009 in crayfish; Hepp et al., 2010; Merlo and Romano, 2008 in crabs; Álvarez et al., 2014 in molluscs), but only one study reports renewal in invertebrates and it has been conducted with an Operant Conditioning procedure and odorants as contextual cues (McComb et al., 2002 in *Lymnaea stagnalis*). Nevertheless, the results of Experiment 2 provide the only demonstration of renewal in the species *Cornu aspersum* with a Classical Conditioning procedure. Furthermore, these results show an example of extinction context specificity in which the context was an external cue (the photoperiod) which affects the internal state of the snails (a circadian cue) to modify their locomotor activity and it is congruent with the recent studies in which an interoceptive stimulus have a role as context and modulate the behaviour (see Scheper and Bouton, 2017, 2019).

Finally, Chapter 4 showed an experimental evaluation of the three types of renewal. In Experiment 1a, ABA renewal has been replicated, using only the illumination instead of the photoperiod as context. Then, in Experiments 1b and 1c, AAB and ABC renewal have been provided, respectively. Also, the illumination has been employed as context. Despite of the renewal paradigm, snails which had received the renewal test in a

different context to the extinction one showed a recovery of the extinguished response. Then, in Experiment 2 the renewal magnitude has been compared among the three paradigms, showing that the renewal magnitude was equal among them.

2. Theoretical Explanation

The context specificity in LI and in the renewal phenomena, can be explain by two theoretical approaches.

On the one hand, the Acquisition theories are based on the failure in the CS-US acquisition. Taking into account this claim, the context specificity of LI is explained in such a way that, during the preexposure, the CS is paired with the context, reducing the associative strength of the CS to establish other associations and it produces a failure in the acquisition of the CS-US association. However, if the context preexposure is different to the conditioning one, the failure in the acquisition of the CS-US association does not happen (e.g., Lubow et al., 1976, 1981; Mackintosh, 1975; McLaren et al., 1989; Pearce and Hall, 1980; Wagner, 1978, 1981; see Serra and De la Casa, 1989 for a review). In the case of the renewal these theories explain that, during the training, the conditioning context acquired an excitatory strength whereas, during the extinction, the extinction context acquired an inhibitory strength. Thus, when the renewal test is conducted in a different context to extinction one, the extinguished response is recovered (e.g., Rescorla and Wagner, 1972; Mackintosh, 1975; Pearce and Hall, 1980; Wagner, 1978, 1981).

On the other hand, the Interference theories are based on the CS-US association retrieval. In this sense, the context specificity of LI is explained by an interference of the CS preexposure in the CS-US association and this interference is modulated by the context so, the interference does not occur when CS preexposure happens in a different context (e.g., Bouton, 1993; Miller et al., 1986; Escobar and Miller, 2010; Schmajuk et

al., 1996; Weiner, 1990). In order to explain renewal phenomenon, they predict that a new learning takes place during the extinction and this new learning interferes with the previous one. Also, the interference is modulated by the context and, when the renewal test is performed in a different context from extinction, the interference of the new learning does not occur, showing the recovery of the CR (Bouton, 2004).

Both theoretical approaches can predict the context specificity in these phenomena and, in the experiments of the present work, there were not tests which would have allowed us to evaluate which of these models predict the results much better, such as a test to measure the conditioning level of the contexts and, in the case of LI, no tests in a third context (a neutral context) were also included. However, according to the literature, several studies suggest that the associative strength is not enough to explain the context specificity. For example, in conditioned suppression it has been shown the context-US association was not necessary for the context influence in CS performance (Bouton and King, 1983, 1986). Moreover, in the renewal, the Acquisition theories predict 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). Thus, it can be concluded that context specificity in LI and renewal are best explained by Interference theories.

The last experiment of renewal showed that the magnitude of the renewal effect is equal among the three paradigms and this result is congruent with some studies which support the prediction of Interference theories that the magnitude of the renewal should be equivalent among the three paradigms (e.g., Bernal-Gamboa et al., 2012; Tood et al., 2012; Tood, 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; Rescorla, 2008; Thomas et al., 2003; Üngör and Lachnit, 2008), ABC (e.g., Balooch et al., 2012; Bustamante et al., 2016; Effting and Kindt, 2007; Harris et al., 2000; Neumann et al., 2010) or both of them (e.g., Bernal-Gamboa et al., 2014). It has been proposed that in ABA renewal, three mechanisms are 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 inhibitory strength of the extinction context and the conditioning context control of the CS-US association during the extinction are involved (see Rosas et al., 2006). The effect of these mechanisms 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). However, there is a lack of evidence in the literature confirming 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 considered such as the inclusion of multiple extinction contexts or a replica with an increment in the extinction trials.

Thus, it would be interesting to explicitly compare the three renewal paradigms using several conditioning procedures, measuring the conditioning level reached by the contexts.

3. The involvement of neural mechanisms

Prior studies have noted the importance of neural mechanisms involvement in learning processes, using humans and other vertebrate species, such as rodents (e.g., Ji and Maren, 2005, 2007; Maren and Hobin, 2007; Solomon and Moore, 1975; Puga et al., 2007; Weiner, 1990). Specifically, it has been stablished that the hippocampus is implicated in the formation of contextual memory representations (Holland and Bouton, 1999), the inhibition of the response and the contextual information retrieval (Schmajuk, 1986) in LI (e.g., Lubow and Weiner, 2010; Solomon and Moore, 1975; Puga et al., 2007; Weiner, 1990) and renewal phenomena (Ji and Maren, 2005, 2007; Maren and Hobin, 2007). Furthermore, it has been shown that other brain areas are involved in both phenomena. For example, the ventral cochlear nucleus, the perirhinal cortex, the accumbens nucleus, the entorhinal cortex (Puga et al., 2007; Weiner, 2003) the mesolimbic system (e.g., Weiner, 1990) or the parabrachial nucleus (e.g., Gasalla et al., 2016) are related with LI and, in renewal, the prefrontal cortex, the amygdala (Bruchey et al., 2007) or the retrosplenial cortex (Tood et al., 2017) are implicated.

According to Lubow and Weiner (2010), complex learning phenomena should be provided by species with hippocampal structures or homologous proto-hippocampal formations such as birds or fishes, but not by species with a "simple nervous system". Taking this into account, they suggest that it would be unthinkable to observe the effect of context on learning in invertebrates.

Nevertheless, several experimental works in vertebrates showed renewal (e.g., Wilson et al., 1995; Campese and Delamater, 2013) and an enhancement of LI (e.g., Purves et al., 1995; Reilly et al., 1993) when the hippocampus was damage.

In addition, invertebrate species present a wide range of nervous systems based on a set of ganglia that make up several structures (e.g., Matsuo et al., 2011; Ghysen, 2003) which can perform several functions. As an example, in species *Helix'*s nervous system, there are approximately 20.000 in 11 ganglia only in the procerebrum involved in olfaction as it is shown in Figure 1 (Balaban, 2002).

Figure 1

Scheme of location of identified neurons from Balaban (2002, p.599).
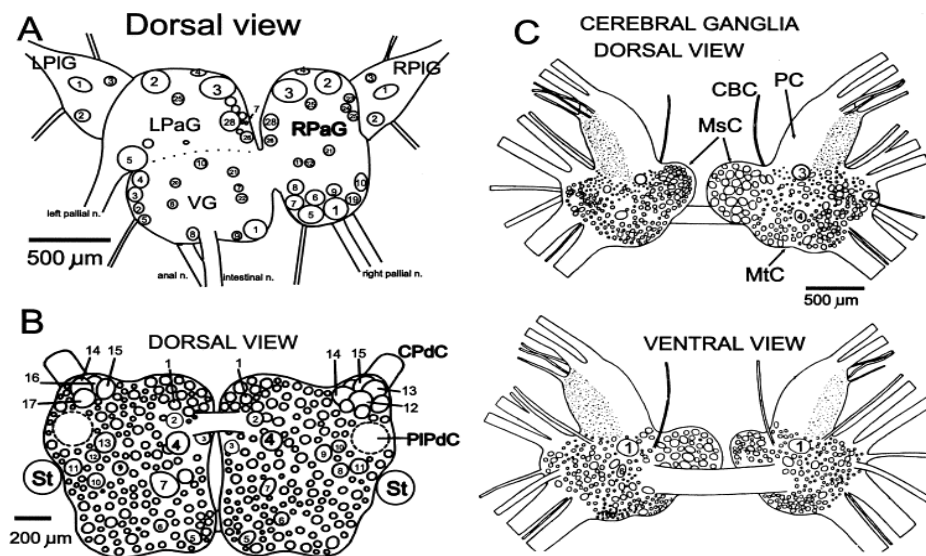
Note. Pleuro-parieto-visceral ganglia complex (A, dorsal view), pedal ganglia (B, dorsal view), cerebral ganglia (C, dorsal and ventral views). L(R) PdG, left (right) pedal ganglia; L(R) PlG, left (right) pleural ganglia; L(R) PaG, left (right) parietal ganglia; CPlC, cerebro-pedal connective; PlPdC, pleuro-pedal connective; PC, procerebrum, MsC, mesocerebrum, MtC, metacerebrum, CBC, cerebro-buccal connective; VG, visceral ganglion; St, statocyst. Identified neurons are labeled by ganglion name and number in the ganglion (see Balban, 2002, p.599).

Thus, it would not be strange that they can present learning phenomena in which the context plays an essential role. In fact, this is confirmed by the reported literature, which shows that the evidence for context specificity in learning phenomena has increased in several species of invertebrates (e.g., McComb et al., 2002, renewal in

Lymnea stagnalis; Hermitte et al., 1999; Pedreira et al., 1995; Pedreira et al., 1996; Pereyra et al., 2000; Pereyra et al., 1999; Tomsic et al., 1998, 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*). Together with the evidence about context specificity of LI and the broadly research about the renewal phenomenon reported in this work, the investigation in animals which lack of complex nervous structures suggests that the involvement of brain areas such as the hippocampus is not a necessary condition for these learning phenomena to occur, reinforcing the lines of research focused on the physiological correlates of learning on neuromodulators and supporting a two-way scheme (cognition-brain, brain-cognition).

Neural and biochemical mechanisms underlying learning and memory have been studied using invertebrate models and, according to several authors, many of the relevant memory acquisition/retrieval mechanisms in invertebrates are organised in similar basic principles as the mechanisms observed in vertebrates (e.g., Hawkins and Byrne, 2015; Rahmani and Chew, 2021; Van Damme et al., 2021).

For example, Pedreira and Romano (2013), describes the molecular features involved in memory reconsolidation, using a context signal memory model in crabs. It was observed that the cAMP and the MAPK kinase pathways participate in memory formation. Moreover, the context specificity of memory is regulated by the nuclear factor kappa B (NF-kB) transcription factor pathway and the epigenetic mechanism of histone acetylation (see Pedreira and Romano, 2013 for a review). In octopuses´ learning and memory several neurotransmitters are involved such as the glutamate, dopamine, the

acetylcholine, the catecholamine or the octopamine, an excitatory neuromodulator presents in molluscs (Stern- Mentch et al., 2022). Also, cAMP/PKA proteins, the dopamine, the serotonin and the octopamine, among other peptides, underlying associative olfactory learning in *Drosophila melanogaster* (e.g., Albin et al., 2015; Davis, 2005; Yamagata et al., 2015; Krashes et al., 2009; Sabandal et al., 2020) and in *Apis mellifera* (e.g., McQuillan et al., 2014; Rein et al., 2013; see Van Damme et al., 2021 for a review). For the snail *Helix lucorum,* it was observed that the serotonergic cell Pd4 is implicated in the acquisition of aversive withdrawal conditioning (Balaban et al., 2001). Moreover, the decline of the serotonergic system produces an extinction of the memory context (Balaban et al., 2016). In the same species, the serotonin and glutamate involvement in the reactivation of associative habit with an aversive procedure was studied, showing that the serotonin is related with mechanisms underlying extraction of the memory trace of the aversive habit whereas, the glutamate is related with the memory trace storage processes (Solntseva and Nikitin, 2008). The study of Rahmani and Chew (2021) offers a review of the implication of several neuromodulators in *C. elegans* learning, showing that the glutamate regulates learning through NMDA receptors and the serotonin regulates the aversive learning. Moreover, the dopamine supresses the mechanosensory habituation (Rahmani and Chew, 2021).

Thus, the investigation of complex learning phenomena in invertebrates does not call into question the involvement of brain areas in the psychological processes which underlie learning, but it suggests that the idea of the brain produce cognition is not enough for explaining learning. Different types of nervous systems can produce similar cognitive achievements and, at the same time, in a bidirectional relation, the cognitive processes can affect to the neural activity. Therefore, there are not simple relation between brain structures and cognitive skills and, as an alternative, the focus can be put on common

biochemical processes between vertebrate and invertebrate species. Thus, it will no longer be so strange that invertebrate organisms, which have equivalent neurochemical elements to vertebrate animals, could exhibit similar psychological processes.

4. Future investigation

The present work shows relevant results about context specificity in LI and renewal. However, some limitations of the experimental design in both learning phenomena do not allow us to rule out one of the theoretical approaches which explain the context effect in LI and renewal (Acquisition and Interference theories). Thus, for this purpose, the first step will be to replicate the experiments provided in this work, including tests to measure the conditioning level of the contexts and, for LI, tests in a neutral context.

Then, the next experiments will be conducted to further study the renewal phenomenon, showing the difference in the effect of the context between habits or goal-directed actions (Steinfeld and Bouton, 2020, 2021). Moreover, taking into account the increased interest in the contextual effect of learning phenomena in invertebrates, the context specificity will be study in other learning with snails, such as spatial navigation, habituation, conditioned inhibition or blocking, among others.

Finally, it could be interesting to include a neural tests to elucidate the neuromodulators involved in these learning phenomena in invertebrates and compared them with the neuromodulators involved in vertebrate species, showing differences and similarities between both animal models. This point of view could be improved the theoretical accounts which explain the evolution of consciousness such as Minimal Cognition.

Chapter 6: Conclusions

In this work the context specificity of LI and the renewal phenomena have been studied in the terrestrial snail *Cornu aspersum*, using an appetitive Pavlovian Conditioning of the Tentacle Lowering procedure.

It was observed that snails which were preexposed to the CS, showed a delay in the acquisition of the CS-US association, which is congruent with the LI effect. These experiments replicate the results provided by Loy et al. (2006) in the same species. However, snails which were preexposed to the CS in a different context to the conditioning one did not show a delay in the acquisition of the CS-US association, congruent with the context specificity of LI. These results are joined with the study of context specificity of LI in *Drosophila melanogaster* (Jacob et al., 2021).

In the renewal experiments, snails which were placed again in the conditioning context after receiving the extinction of the CS in a different one, showed a recovery of the extinguished response, and it is congruent with the renewal effect. Moreover, the three renewal paradigms (ABA, AAB and ABC) were provided and compared, showing an equal magnitude of the renewal effect among them.

One difficulty of the investigation of the contextual effects in invertebrates ´ learning is to choose and adequate stimuli which play the role as context, because they have to be salient enough to be perceived, but not so intense to compete with the CS. In these experiments, the photoperiod and the illumination were suitable for playing the role as contexts and their use reduces the possibility that the results could be explain by configural learning as happen in Experiment 1 of Chapter 3 (ABA renewal with odours as context).

Both learning phenomena are predicted by two theoretical approaches: based on the associative strength of the stimuli (Acquisition theories) or based on the interference of a new learning modulated by the context (Interference theories). Although the literature reported that the associative strength of the stimuli is not necessary condition to observe these phenomena (Bouton and King, 1983, 1986), the results of the present work cannot rule out one of both theoretical approaches.

The results provided in Experiment 2 of Chapter 4 (the magnitude of the renewal effect among the three paradigms), are best explained by the Interference Theories, because no differences among them were found. However, several studies showed differences among the three renewal paradigms, providing a higher renewal effect in ABA paradigm. These differences could be explained by the interaction of several mechanisms (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; see Rosas et al., 2006). Nevertheless, there is few evidence about the involvement of these mechanisms and the present experiment did not take into account several parameters which allow as to clarify this claim.

Finally, the presence of learning phenomena, generally attributed to the activity of brain structures which snails lack, requires, from an evolutionary point of view, that the study of the physiological bases of cognitive activity focus on the molecular level rather than in the structural one, to take advantage of the results that come from the investigation in invertebrates.

Capítulo 6: Conclusiones

En este trabajo se han estudiado los fenómenos de la especificidad contextual de IL y de renewal en el caracol terrestre *Cornu aspersum*, utilizando un procedimiento de Condicionamiento Pavloviano apetitivo de Bajada del Tentáculo.

Se observó que los caracoles que fueron preexpuestos al EC, mostraron un retraso en la adquisición de la asociación EC-EI, lo cual es congruente con el efecto de la IL. Estos experimentos replican los resultados del estudio de Loy et al. (2006) en la misma especie. Sin embargo, los caracoles que fueron preexpuestos al EC en un contexto diferente al del condicionamiento no mostraron un retraso en la adquisición de la asociación EC-EI, lo cual es congruente con la especificidad contextual de la IL. Estos resultados se unen al estudio de la especificidad contextual de la IL en *Drosophila melanogaster* (Jacob et al., 2021).

En los experimentos de renewal, los caracoles que fueron colocados nuevamente en el contexto de condicionamiento, después de recibir la extinción del EC en otro contexto distinto, mostraron una recuperación de la respuesta extinguida. Estos resultados son congruentes con el fenómeno de renewal. Además, se observaron y compararon los tres paradigmas de renewal (ABA, AAB y ABC), mostrando un efecto equivalente entre ellos.

Una dificultad en la investigación de los efectos contextuales en el aprendizaje de los invertebrados es elegir estímulos adecuados que desempeñen el papel del contexto, ya que deben destacar lo suficiente como para ser percibidos, pero no deben ser tan intensos como para competir con el EC. En estos experimentos, el fotoperiodo y la iluminación fueron apropiados para ser utilizados como contextos y su uso reduce la

posibilidad de que los resultados puedan explicarse por aprendizaje configural, como sucedió en el Experimento 1 del Capítulo 3 (ABA renewal con olores como contexto).

Ambos fenómenos de aprendizaje pueden ser explicados por dos enfoques teóricos: aquellos que se basan en la fuerza asociativa de los estímulos (teorías de la Adquisición) o aquellos basados en la interferencia de un nuevo aprendizaje modulado por el contexto (teorías de la Interferencia). Si bien, de acuerdo con la literatura, la fuerza asociativa de los estímulos no es condición necesaria para observar estos fenómenos (Bouton and King, 1983, 1986), los resultados del presente trabajo no pueden descartar ninguno de los dos enfoques.

Las Teorías de Interferencia explican mejor los resultados obtenidos en el Experimento 2 del Capítulo 4 (la magnitud del efecto de renewal entre los tres paradigmas), ya que no se encontraron diferencias entre los tres paradigmas tal y como predicen estas teorías. Sin embargo, varias investigaciones mostraron diferencias entre los tres paradigmas de renewal, proporcionando un mayor efecto en el paradigma ABA. Estas diferencias podrían explicarse por la interacción de varios mecanismos (la fuerza excitatoria del contexto de condicionamiento, la fuerza inhibitoria del contexto de extinción y el control de la asociación EC-EI por el contexto de condicionamiento durante la extinción; ver Rosas et al., 2006). Sin embargo, hay pocas evidencias sobre la participación de estos mecanismos y en el presente experimento no se tuvieron en cuenta varios parámetros que permitirían aclarar esta afirmación.

Finalmente, la presencia de fenómenos de aprendizaje, generalmente atribuidos a la actividad de estructuras cerebrales de las que carecen los caracoles, nos exige, sobre todo desde un punto de vista evolutivo, que el estudio de las bases fisiológicas de la actividad cognitiva se centre en el nivel molecular, más que en el estructural, y así relacionarlo con los resultados que provienen de la investigación en invertebrados.

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