Motivational control of latent inhibition in flavor preference conditioning

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ABSTRACT

In three experiments, rats given pairings of a neutral flavor with sucrose showed a preference for that flavor when subsequently allowed to choose between it and water. Preexposure to the flavor produced a latent inhibition effect (reduced the size of the preference) when the rats were hungry during the test (Experiments 1 and 2). Rats that were not hungry during the test failed to show latent inhibition (Experiments 1–3). Experiment 3 confirmed that sucrose–flavor pairings were capable of producing a preference even in nonhungry rats. It is argued that the preference shown by rats that are hungry on test depends on a flavor–nutrient association, a form of learning that is susceptible to latent inhibition in the same way as standard conditioning procedures are. The failure to obtain latent inhibition in nonhungry rats suggests that the preference obtained in these conditions depends on a different form of learning that is less susceptible to the effects of stimulus exposure.

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1. Introduction

In the conditioned flavor preference (CFP) procedure a neutral flavor serves as the conditioned stimulus (CS) and is paired with a nutrient (e.g., a sucrose solution) as the unconditioned stimulus (US). Such a US has both oral and post-oral properties, and there is reason to think that both are capable of contributing to the development of a preference for the CS flavor. Specifically, a CFP can be established using a nonnutritive but palatable US, such as saccharin (e.g., Fanselow and Birk, 1982; Holman, 1975, 1980), a phenomenon referred to as flavor–taste learning; and it can also be obtained when the nutrient US is delivered by intragastric infusion (e.g., Sclafani et al., 1993) so that its taste properties are irrelevant. This latter phenomenon is referred to as flavor–nutrient learning.

Which of these forms of learning is responsible for an observed preference appears to depend on motivational factors. In particular, although food restriction may not be necessary for acquisition, it can act to enhance the expression of a nutrient-based preference

(e.g., Fedorchak and Bolles, 1987; Yiin et al., 2005). Thus, Fedorchak and Bolles (1987) examined the effects of food deprivation on the rat's preference for flavors paired with either a sweet nonnutritive substance (saccharin) or a nutrient (sucrose), and found that the flavor that had been paired with sucrose was highly preferred when rats were tested in a food-deprived state, but that the preference decreased when testing occurred after 24 hr of ad libitum feeding. In contrast, the flavor that had been paired with saccharin was preferred regardless of the state of hunger during testing.

Motivational factors also influence the susceptibility of CFP to the effects of extinction. Harris et al. (2004) demonstrated that the preference for a flavor associated with sucrose over water was resistant to extinction in rats trained and tested while maintained on ad libitum access to food. By contrast, if the rats were food deprived during testing, their preference for the flavor showed a decrement as a result of extinction (see also Garcia-Burgos and González, 2012). If we assume that hungry rats show principally the effects of flavor–nutrient learning on test whereas sated rats show the effects of flavor–taste learning (see also Harris et al., 2000), then the results for former are what would be expected of a preference based on the formation of an orthodox flavor–nutrient association. Those for the latter are more problematic. One possibility is that their preference too is based on an association (e.g., between flavor and hedonic reactions produced by the taste of sucrose; see Harris et al., 2004) but that this association has properties that make it resistant to the effects of extinction. A different suggestion (see e.g., Campbell et al., 1988; Capaldi, 1992; Drucker et al., 1994; Fedorchak, 1997;

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Harris et al., 2004; Myers and Sclafani, 2006; Myers and Whitney, 2011; Warwick and Weingarten, 1994) is that flavor–taste learning involves a different process by which the presentation of the neutral flavor in compound with a valued taste changes the valence of the originally neutral stimulus (see Section 5). This form of learning is assumed to be insensitive to manipulation of the CS-US contingency, and thus not susceptible to extinction.

These considerations prompted an investigation of the effects of motivational state on the sensitivity of CFP to other manipulations of the CS-US contingency. In the experiments to be reported here we focused on the effects of prior nonreinforced presentations of the to-be-conditioned CS. In orthodox conditioning procedures, preexposure produces a retardation of conditioning (the latent inhibition effect; e.g., Lubow, 1989) and the effect can be expected to occur, therefore, in flavor–nutrient learning, which is taken to depend on standard associative mechanisms. It should therefore be evident in hungry animals. But will preexposure (which, after all, can be seen as a version of extinction in which the nonreinforced presentations of the CS occur prior to conditioning) also be effective in sated rats? If it is not, this outcome would both supply support for the view that the mechanisms responsible for flavor–taste learning has special properties and would also help confirm the assumption that motivational state can control which source of the CFP will govern behavior.

Such studies of latent inhibition in flavor–preference conditioning as are currently available do not directly address this question. De la Casa et al. (2009) gave rats that were both hungry and thirsty preexposure to water, almond, or citric acid prior to pairings of both almond and citric acid with sucrose. In a two-bottle, almond vs. citric acid, choice test, the preexposed flavored solutions were consumed less than the nonpreexposed flavors. Assuming that hunger selects the expression of flavor–nutrient association in the control of performance on test, these data demonstrate that this form of learning is sensitive to latent inhibition; they do not tell us, however, about flavor–taste learning, which, given our assumptions, will be evident only when the subjects are not hungry on test.

Delamater (2011, Experiment 2) has explored the effects of preexposure to the CS on CFP in rats that were thirsty but not hungry. In this case, nonreinforced presentations of one flavor (F1) occurred prior to the conditioning phase in which both F1 and a second flavor (F2) were paired with sucrose. Some rats then received a sucrose-devaluation treatment (sucrose consumption was paired with the effects of lithium chloride, LiCl); others received the sucrose and LiCl unpaired, serving as a nondevalued control group. A choice test (F1 vs. F2) revealed no significant difference in intake between F1 and F2; that is, there was no effect of preexposure in this case. A difference did emerge however when the animals were tested again after they had been exposed to presentations of sucrose. On this later test the non-devalued group preferred F2 over F1, but the devalued group preferred F1 over F2. Why an effect of preexposure should appear only on the later test is unclear. Post-training exposure to sucrose modulates experimental extinction in non-hungry rats (perhaps by weakening flavor–taste associations, Harris et al., 2004) but it is not obvious how these effects would influence expression of latent inhibition. We conclude that the results reported by De la Casa et al. (2009) for hungry animals suggest that the CS exposure produces a LI effect for a preference based on the post-ingestive effects of nutrient, but that the position is much less clear for animals that are not hungry.

The purpose of the present experiments, therefore, was to compare directly the effect of CS preexposure on flavor–taste and flavor–nutrient learning in the CFP procedure (see Table 1) using a palatable nutrient (sucrose) as the US. We attempted to arrange this by manipulating the motivational state of the subjects (rats). In all experiments the rats were thirsty to ensure that they readily drank the flavored solutions offered, but their access to food was manipulated. On the basis of the results reported by De la Casa et al. (2009) we anticipated that a latent inhibition effect would be obtained in rats that were hungry. The effect of CS preexposure on animals that are not food-deprived remains to be determined, but if flavor–taste learning is responsible for the preference obtained under these conditions, and this form of learning is less sensitive to the effects of separate presentations of the CS, then latent inhibition may be absent.

Experiment 1 included a pair of groups (one preexposed to the CS and one not) that were food-deprived throughout the experiment (i.e., during the preexposure phase, the conditioning trials, and for the preference test). These should allow replication of the latent inhibition effect observed by De la Casa et al. (2009). A second pair of groups received the same treatment during preexposure and conditioning, but was given free access to food prior to the test. Will latent inhibition be seen under these conditions when the preference shown, according to Harris et al. (2000, 2004), will be solely generated by the flavor–taste learning mechanism? Experiment 2 replicated the essential features of Experiment 1, differing only in that the subjects were allowed free access to food across preexposure and conditioning phases. Experiment 3 was conducted to confirm the chief finding of Experiment 2 (an absence of latent inhibition in rats that were not food deprived) and to demonstrate that reliable flavor–nutrient learning could be obtained under these conditions in nonpreexposed subjects.

2. Experiment 1

The design of Experiment 1 is presented in the top panel of Table 1. There were four groups, two of which were given preexposure to the flavor to be used as the CS (the PE groups) and two given no preexposure (the NPE groups). All received conditioning trials in which the flavor was paired with sucrose. All were hungry (as well as thirsty) during these stages of training. The final test consisted of a choice between the flavor and unflavored water. Prior to the test, one pair of groups was given free access to food (they remained water deprived; groups PE/Th and NPE/Th). The other rats remained both food and water deprived (groups PE/H and NPE/H). Latent inhibition would be evidenced by a reduced preference for the CS flavor in a final, flavor vs. water, choice test.

2.1. Method

The subjects were 32 experimentally naïve male Wistar rats at least 14 weeks old and with a mean body weight of 263 g at the start of the experiment. They were housed in individual home cages and kept in a colony room at the University of Granada that was lit from 8:00 a.m. to 8:00 p.m. each day. Experimental procedures took place with the rats in their home cages and during the light period of the cycle. Inverted 50-ml plastic tubes equipped with stainless steel ball-bearing-tipped spouts were used to present fluids in these cages. Consumption was estimated by weighing the tubes before and after fluid presentation to the nearest 0.1 g. The solutions used were made up with tap water and consist of 1% (v/v) almond essence (Silver Spoon, London, UK), and a 1% almond essence and 10% sucrose (w/v) compound. Initially, all animals were placed on a food and water deprivation schedule, a regime that was maintained during preexposure and conditioning. The food and water were removed from the home cage 24 hr before the start of the experiment. Then all rats were given 3 days to accommodate to the deprivation schedule, in which access to water was allowed for 30 min at 9:30 a.m. and access to water and food for 90 min at 2:00 p.m. The rats were weighed and allocated to two weight-matched groups (PE and NPE, $n = 16$ in each) prior to the preexposure phase, which was conducted over 8 days, with half

Table 1
Experimental designs.

	Group	Preexp.	Condit.	Test
Experiment 1		*Hunger*	*Hunger*	
	PE/Th	8 A−		*Th*: A vs. water
	PE/H		2 A+	*H & Th*: A vs. water
	NPE/Th	8 water		*Th*: A vs. water
	NPE/H			*H & Th*: A vs. water
Experiment 2				2 cycles
		Non-hunger	*Non-hunger*	
	PE/Th	8 A−		*Th*: A vs. water
	PE/H		2 A+	*H & Th*: A vs. water
	NPE/Th	8 water		*Th*: A vs. water
	NPE/H			*H & Th*: A vs. water
Experiment 3				2 cycles
		Non-hunger	*Non-hunger*	*Non-hunger*
	PE/PA	8 A−	2 A+	
	PE/UN		2 A/+	
	NPE/PA	8 water	2 A+	A vs. water
	NPE/UN		2 A/+	

Note: Animals were maintained under a state of thirst throughout all of the stages of each experiment in this series. PE, preexposed; NPE, non-preexposed; PA, paired presentations of flavor and sucrose; UN, unpaired presentation of flavor and sucrose; A, almond; +, sucrose; −, nonreinforcement; Th, thirsty on test; H or H & Th, hungry & thirsty on test.

the rats being given access to 5 ml of the flavored solution (the PE groups) and half (the NPE groups) access to 5 ml of water at 9.30 a.m. All were allowed daily 90-min access to food and water at 2:00 p.m.

Conditioning occurred over 2 days. On each day, the rats had 10-min access to 10 ml of almond + sucrose at 9.30 a.m. After this phase, the rats were divided into four groups: PE/Th (n = 8), PE/H (n = 8), NPE/Th (n = 8), and NPE/H (n = 8), according to motivational state on test. For those in the H groups the deprivation schedule remained as before; rats in the thirsty-only groups (groups Th) were given ad libitum access to food overnight prior to the test. The test phase consisted of a single session at 9:30 a.m. in which rats had 15-min access to two bottles, one containing 20 ml of the almond solution and the other 20 ml of water. The positions of the bottles were counterbalanced across subjects.

For all statistical analyses, a significance level of $p < .05$ was adopted. Data were analyzed using analysis of variance (ANOVA). Reliable interactions were followed, when appropriate, by simple effects analyses. Two-tailed t-tests were used to evaluate data not involving multiple comparisons. Preference ratios for the test stage were calculated as the intake of the target flavor over the total amount consumed.

2.2. Results and discussion

During preexposure the rats drank less than the full amount available, but there was no difference between the groups. The PE subjects consumed a mean of 2.2 g of almond over all trials; the NPE subjects a mean of 2.0 g of water. These scores did not differ significantly, $t < 1$. During conditioning, the rats drank less on the first than on the second trial, but again the groups did not differ. The mean amount consumed (g) of the almond + sucrose compound across the 2 conditioning days was 6.5 and 10.0 for the PE subjects, and 6.5 and 9.9 for NPE subjects. A 2 (Preexposure) × 2 (Trial) ANOVA showed there to be a significant main effect of trial, $F(1, 30) = 89.20$. No other main effect or interaction was significant ($Fs < 1$).

Fig. 1 displays the mean almond preference ratios on the test as a function of almond preexposure (PE vs. NPE) and motivational state (thirsty vs. thirsty and hungry). A 2 (Preexposure) × 2 (Motivational state) ANOVA of almond preference provided a significant main effect of preexposure, $F(1, 28) = 4.33$, and a significant Preexposure × Motivational state interaction, $F(1, 28) = 4.60$. No significant main effect of motivational state was found ($F < 1$). Exploration of the interaction showed there to be a lesser almond preference in

group NPE/Th than in group NPE/H, $t(14) = 7.76$, and a lesser almond preference in group PE/H than in group NPE/H, $t(14) = 18.13$. The absolute scores for consumption of water and almond, from which the preference ratios were derived, are presented in Table 2. They show that consumption of almond was lower in group PE/H than in the other three groups. A 2 (Preexposure) × 2 (Motivational state) ANOVA of the almond intake revealed a main effect of preexposure, $F(1, 28) = 7.09$, and a significant Preexposure × Motivational state interaction, $F(1, 28) = 6.69$. Exploration of the interaction showed there to be a higher almond intake in group PE/Th than in group PE/H, $t(14) = 3.51$, and a lesser almond intake in group PE/H than in group NPE/H, $t(14) = −4.07$. An equivalent ANOVA conducted on the water scores revealed only a main effect of motivational state, $F(1, 28) = 7.58$, reflecting lower water intake in the rats that were hungry as well as thirsty.

These results demonstrate a strong preference in nonpreexposed animals tested hungry, but a reduced preference in the equivalent preexposed group. The occurrence of a latent inhibition effect in rats that were hungry throughout, confirms the finding of
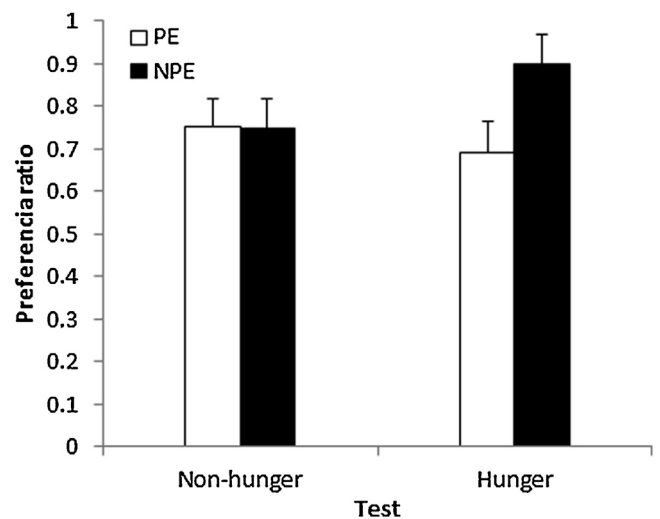

Fig. 1. Experiment 1. Mean almond preference ratios (±SEM) for the almond vs. water choice test shown separately for the preexposed (PE) and non-preexposed (NPE) groups when tested thirsty (Non-hunger) and when tested thirsty and hungry (Hunger).

Table 2
Mean almond and water consumption (g) on test for Experiments 1–3.

	Group	Almond	Water
Experiment 1			
	PE/Th	7.5 (.8)	2.3 (.5)
	PE/H	4.1 (.5)	1.8 (.3)
	NPE/Th	7.1 (.7)	2.2 (.3)
	NPE/H	7.0 (.5)	0.7 (.1)
Experiment 2			
	PE/Th	8.7 (1.1)	3.6 (1.1)
	PE/H	4.8 (.7)	1.6 (.2)
	NPE/Th	7.7 (.1)	4.3 (.8)
	NPE/H	5.6 (.8)	0.9 (.2)
Experiment 3			
	PE/PA	8.0 (.8)	3.9 (.5)
	NPE/PA	6.5 (.6)	4.2 (.5)
	PE/UN	4.5 (.7)	5.1 (.4)
	NPE/UN	4.0 (.5)	5.9 (.5)

Note: Mean almond and water consumption for the test was collapsed across the two test trials, except for Experiment 1. PE, preexposed; NPE, non-preexposed; PA, paired presentations of flavor and sucrose; UN, unpaired presentation of flavor and sucrose; Th, thirsty on test; H, hungry & thirsty on test. SEMs appear between brackets.

De la Casa et al. (2009) that latent inhibition will occur under these conditions. Although it was not as pronounced as that shown by the NPE/H group, both of the groups tested just thirsty showed a reliable preference for the CS flavor and this preference did not differ between the groups. Thus latent inhibition was not obtained in the nonhungry groups.

The critical finding of this experiment is, from one point of view, a null result (i.e., it is the absence of latent inhibition in animals that are not hungry). This raises the possibility that difference obtained between the hungry and nonhungry groups may be simply a matter of the sensitivity of the test procedure – that making the rats hungry increases the sensitivity of the test procedure allowing latent inhibition to be readily observed (or, equivalently, that satiating them for food has the reverse effect of reducing the sensitivity of the test).

Although we must acknowledge the general validity of this argument, we should point out that its application to the specifics of our experiment does not readily explain our findings. Thus, the most obvious effect of motivational state is that the preference in nonpreexposed animals is greater for hungry than for nonhungry rats; but if hunger tends to enhance the size of any preference then it might be expected that one might be seen in the hungry preexposed group – but it was this group that showed a clear latent inhibition effect. Another effect of motivational state is that it influences the total amount of fluid consumed. Nonhungry animals drink substantially more than hungry animals, and this may seem to allow the possibility that a "ceiling effect" could operate to obscure evidence of a preference in the nonhungry groups (if these subjects are especially keen to drink, they may drink plain water as readily as the almond solution). But again, this analysis does not explain the pattern of results obtained. Our "null result" is in fact the presence of a preference; that is, the striking finding is that nonhungry preexposed rats show a preference for almond as great as that shown by their nonpreexposed counterparts. In short, the "ceiling" argument works well when the critical result is the absence of a preference – but our critical result is that a preference is found even in the preexposed animals when they are not hungry on test.

This outcome is consistent with the view that the mechanism responsible for the flavor preference shown by hungry rats is different from that responsible when the rats are not hungry. It further implies that these two forms of learning differ in their sensitivity to CS preexposure, with flavor–nutrient learning showing the standard effect of preexposure to the CS (i.e., latent inhibition), whereas flavor–taste learning does not.

An alternative interpretation of the present results, that does not require us to accept the dual-mechanism account of flavor–preference learning, comes from consideration of the context-specificity of latent inhibition. It is well established that latent inhibition is attenuated when the context is changed between the preexposure and test phases (e.g., Channell and Hall, 1983). Although the physical context was not changed in this experiment, the rats that failed to display latent inhibition (the PE/Th group) experienced a change of motivational state between training and testing phases, and deprivation state may function as a contextual cue (see e.g., Davidson, 1998). A theory of latent inhibition that attributes the effect to interference between rival associations formed during conditioning and preexposure at the time of testing (see e.g., Bouton, 1993) could thus explain our result by assuming that the appropriate context is needed for the information acquired during preexposure to be retrieved. Experiment 2 addresses this issue.

3. Experiment 2

In this experiment we repeated the essential features of Experiment 1 except for the fact that the rats were not food-deprived during preexposure and conditioning. The design is presented in the central panel of Table 1. All rats were water deprived throughout the experiment; half (the PE groups) were preexposed to almond and half (the NPE groups) were not, prior to conditioning trials with the almond + sucrose compound. All the rats had ad libitum access to food during the preexposure and conditioning phases. Before the test the two main groups were divided: one pair of groups (groups PE/Th and NPE/Th) continued as before, but the other pair (groups PE/H and NPE/H) was food-deprived.

The possible accounts offered for the results of Experiment 1 make different predictions about the outcome of this procedure. If context-specificity is the critical factor, then latent inhibition can be expected in the comparison of PE/Th and NPE/Th groups, as these subjects remained in the same motivational state (just thirsty) throughout the experiment. Latent inhibition should be abolished or attenuated, however, in the other pair of groups, as these experienced a motivational change (were made hungry) at the time of the test. On the other hand, if the preference shown by nonhungry rats is a consequence of a form of learning not susceptible to the effects of CS preexposure, then latent inhibition should be absent in the PE/Th and NPE/Th groups. The prediction of the dual-mechanism account for the other pair of groups is less clear. One possibility is that flavor–nutrient learning might be possible during the conditioning trials (even though the rats are not hungry at this stage). If making the rats hungry at the time of test allows this form of learning to show itself in behavior (and there is evidence to support this suggestion: Capaldi et al., 1994; Fedorchak and Bolles, 1987; González et al., 2010; Yiin et al., 2005), then a latent inhibition effect could be obtained in the PE/H and NPE/H groups.

3.1. Method

The subjects were 32 male Lister hooded rats with a minimum age of 14 weeks and a mean body weight of 425 g at the start of the experiment. All subjects had earlier participated in a study of conditioned suppression which involved previous experience of food deprivation, but they were naïve to the stimuli and other procedures used in this experiment. The experiment was run at the University of York. Housing, general maintenance, and apparatus (including the solutions) were the same as described for Experiment 1.

All animals were maintained on a water deprivation schedule throughout the experiment. Water was removed from the home cage 24 hr before the start of the experiment. The rats were given 3 days to accommodate to a schedule in which access to water was presented for 30 min at 9:30 a.m. and 90 min at 2:00 p.m.

The rats were weighed and randomly allocated to two weight-matched groups ($n = 16$) for the preexposure phase. All animals were given the experimental session at 9:30 a.m. and allowed 90-min access to water at 2:00 p.m. The procedure for preexposure was as described for Experiment 1.

The conditioning and test phases were run in 2 cycles, providing the opportunity for repeated testing of the developing preference over the course of acquisition. In each cycle, conditioning occurred over 2 days with one trial each day at 9:30 a.m. In each trial, animals had 10-min access to 10 ml of an almond + sucrose compound. After the first conditioning cycle, the rats were divided into four groups: PE/Th ($n = 8$), PE/H ($n = 8$), NPE/Th ($n = 8$), and NPE/H ($n = 8$), according to motivational state on test (Th: thirsty; H: hungry and thirsty). Then, before the test phase of the first conditioning–testing cycle, the rats were given 3 days in which the schedule of water deprivation remained as before; but, for the rats to be tested hungry, food was made available only for the 90-min period beginning at 2:00 p.m. The test consisted of 15-min access to two bottles at 9:30 a.m., one bottle containing 20 ml of the almond solution and the other 20 ml of water. After this first test, ad libitum food was made available for all subjects prior to the conditioning trials of the second conditioning cycle. After the second conditioning trial of this cycle, rats to be tested hungry receive limited 90-min access to food. A second test was given on the morning of the following day. The positions of the bottles during tests were counterbalanced across subjects and cycle.

3.2. Results and discussion

During preexposure the rats drank almost all the fluid made available. There was no difference between the groups. Mean consumption (g) of almond for group PE over all trials was 4.5; of water for group NPE was 4.4. These scores did not differ significantly, $t < 1$.

As before, during conditioning the subjects drank almost all of the almond + sucrose compound, but with some minor fluctuation across trials. Mean consumption (g) of the compound across conditioning trials was 10.4, 9.7, 10.4, and 9.7 for group PE, and 9.7, 9.7, 10.3, and 9.8 for group NPE. A 2 (Preexposure) × 4 (Trial) ANOVA showed there to be a significant main effect of Trial, $F(3, 90) = 9.04$. No other main effect or interaction was significant; largest $F(3, 90) = 2.15$. The main effect of trial reflected the fact that intake on Trial 3 was higher than on Trials 2 and 4.

As a preliminary analysis revealed that there were no main effect or interactions involving the factor test [largest $F(1, 28) = 2.81$, $p = .11$], the data of two tests were collapsed. Fig. 2 shows the mean almond preference ratio collapsed across the two test sessions as a function of almond preexposure (PE vs. NPE) and motivational state (thirsty vs. both thirsty and hungry). The hungry animals showed a latent inhibition effect (a lesser preference for almond in the PE than in the NPE subjects). The rats that were just thirsty did not show latent inhibition; in fact preference was somewhat higher in the PE than in the NPE group. A 2 (Preexposure) × 2 (Motivational state) ANOVA of almond preference yielded a significant main effect of motivational state, $F(1, 28) = 6.28$, and a significant Preexposure × Motivational state interaction, $F(1, 28) = 4.12$. No other main effect or interaction was significant, largest $F(1, 28) = 2.8$. Exploration of the interaction showed a lesser almond preference for group NPE/Th compared with group NPE/H [$t(14) = 14$, $p < .01$]; and a lesser almond preference in group PE/H compared with group NPE/H [$t(14) = 7.73$]. The absolute levels of consumption of almond and water consumption on the test are presented in Table 2.
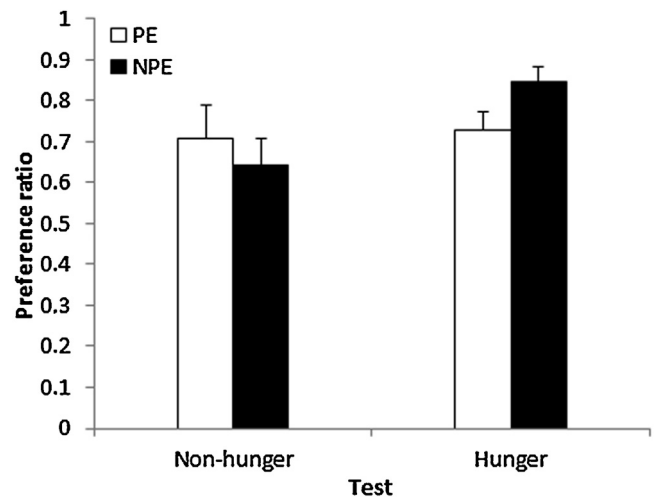

Fig. 2. Experiment 2. Mean almond preference ratios (±SEM) collapsed across the two almond vs. water choice tests shown separately for the preexposed (PE) and non-preexposed (NPE) groups when tested thirsty (Non-hunger) and when tested thirsty and hungry (Hunger).

Although groups PE/H consumed less almond than group NPE/H, an ANOVA conducted on the almond consumption scores, with preexposure condition and motivational state on test as the variables, failed to reveal a statistically reliable interaction. The analysis revealed only a main effect of motivational state, $F(1, 28) = 20.79$, showing a higher almond intake in thirsty than hungry rats. An equivalent analysis of water intake again revealed a main effect of motivational state, $F(1, 28) = 22.22$, with water intake being higher in thirsty than hungry rats.

The results of this experiment confirm the finding of Experiment 1 that latent inhibition is not observed in the conditioned flavor preference shown by animals that are not hungry on the test. The results from the analysis of the preference ratios support the proposal that latent inhibition can be obtained in rats that are trained just thirsty but made hungry for the test. This pattern of results does not accord with the suggestion that those of Experiment 1 were a consequence of the context-specificity of latent inhibition – latent inhibition was not seen in subjects that experienced no change in (motivational) context; and it was obtained in subjects that experienced such a change (in accord with some previous investigations of this issue; see e.g., Westbrook et al., 2000).

Taken together, Experiments 1 and 2 indicate that the critical factor in determining whether or not latent inhibition will be obtained is the motivational state of the animal at the time of the test. This outcome is consistent with the proposal that flavor–nutrient learning (expressed when the rats are hungry on the test) is susceptible to latent inhibition whereas flavor–taste learning (which determines preference when the animals are not hungry on the tests) is not. It is true that the subjects in this experiment that showed latent inhibition received their initial training when they were not hungry, but, as we have noted, there is evidence that food deprivation primarily affects the expression rather than the acquisition of flavor–nutrient learning. Although trained just thirsty, these animals may have acquired the flavor–nutrient association; making them hungry for the test may have allowed this association to control behavior, and thus allowed latent inhibition to be seen.

4. Experiment 3

The results presented so far support the proposal that the mechanism responsible for the flavor preference shown by hungry rats is different from that responsible when the rats are not hungry;

they also suggest that only the first of these (flavor–nutrient learning) is susceptible to latent inhibition. But before accepting this suggestion, an alternative interpretation should be considered. In both experiments, a sizeable preference for the CS flavor was evident only in the NPE/H groups. That hunger might enhance the preference for a flavor paired with nutrient is already established (e.g., Drucker et al., 1994; Fedorchak and Bolles, 1987); rather our concern is that the lesser preference shown by the thirsty-only rats truly represents an effect of conditioning – the nonassociative consequences of mere exposure to the almond flavor might be enough to produce such a preference. If this were so, the absence of a difference between preexposed and non-preexposed groups in these animals may be due not to the ineffectiveness of CS-preexposure in retarding conditioning, but to the failure to form a reliable almond–sucrose association at all.

In Experiment 3 we looked at the effect of CS preexposure in rats that were thirsty but not hungry throughout the experiment, thus allowing the possibility of replicating our failure to obtain latent inhibition in the previous experiments. We also included the control groups necessary to demonstrate that the preference obtained after flavor–sucrose pairings was as a result of conditioning. The design of the experiment is presented in the lower panel of Table 1. As in Experiments 1 and 2, half the rats were exposed to almond alone (groups PE), whereas the remainder received water (groups NPE) during the preexposure phase. In the conditioning phase, the sucrose was paired with almond for half of the rats in each of these conditions (groups PE/PA and NPE/PA); for the remaining rats (the unpaired groups, PE/UN and NPE/UN) the almond and sucrose were presented separately. If the preference shown by the nonpreexposed thirsty rats was due to the formation of a flavor–sucrose association during conditioning, then rats that have received the flavor paired with sucrose should show a higher level of preference for the flavor than animals for which the flavor was unpaired with sucrose. Additionally, if CS preexposure is not effective in rats tested thirsty, no difference between groups PE/PA and NPE/PA should be found, as in the subjects tested just thirsty in the previous experiments.

4.1. Method

The subjects were 32 experimentally naïve male Wistar rats with a minimum age of 14 weeks old and a mean body weight of 274 g at the start of the experiment. Housing, general maintenance, and apparatus (including the solutions) were the same as in Experiment 1. The experiment was run at the University of Granada.

The procedure for the preexposure phase was same as that described for Experiment 1, except for the fact that the rats were water but not food-deprived throughout the experiment. Half of the rats were given access to 5 ml of the flavored solution (the PE groups) and half (the NPE groups) access to 5 ml of water. After the preexposure phase, the rats were divided into four groups: PE/PA (n = 8), PE/UN (n = 8), NPE/PA (n = 8), and NPE/UN (n = 8), according to the flavor–sucrose relationship established during the conditioning phase. As in Experiment 2, but unlike Experiment 1, there were two conditioning-test cycles. The conditioning and test procedures for the paired groups (PE/PA and NPE/PA) were the same as those described for Experiment 2. In each cycle, conditioning occurred over 2 days with one trial each day of exposure to 10 ml of an almond + sucrose compound for 10 min. Test consisted of a single session of 15-min access to two bottles. The unpaired groups (PE/UN and NPE/UN) differed in that on the days on which the paired groups received pairings of 10 ml of almond and sucrose for 10 min, the unpaired groups received access to 10 ml of almond for 10 min in the morning session and to 10 ml of the sucrose solution for 10 min at 2.00 p.m. As rats in group PE/PA drank more almond than animals in group PE/UN on the first day of the conditioning
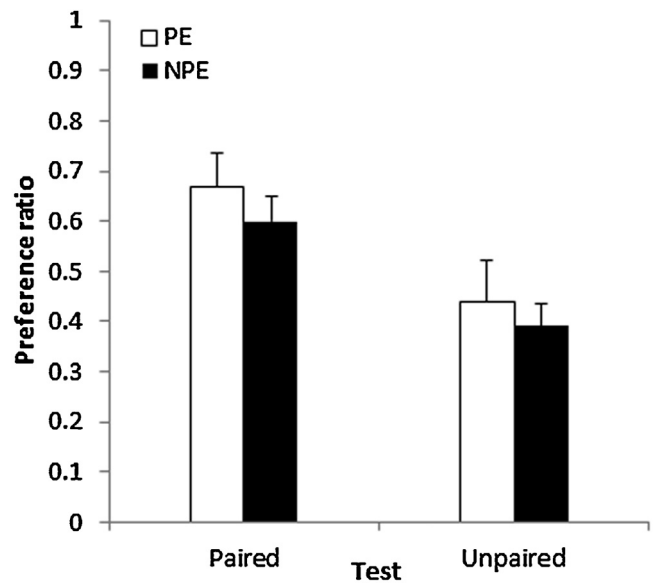

Fig. 3. Experiment 3. Mean almond preference ratios (±SEM) collapsed across the two almond vs. water choice tests shown separately for the paired groups and unpaired groups that received paired or unpaired presentations the almond and sucrose during conditioning. Ad libitum food access was maintained throughout the experiment.

phase, the unpaired groups received a further 10-min period of exposure to almond following immediately the first, on the second day of the first cycle of conditioning, in order to equalize almond intake. Details not specified here were the same as those described for Experiment 1.

4.2. Results and discussion

The rats consumed almost all of the fluid made available during preexposure, and there was no difference between the subjects given water and those given almond. Mean consumption of fluid during preexposure was 4.4 g, both for the PE and the NPE groups.

Mean consumption (g) of the almond + sucrose compound across conditioning trials was 9.3, 9.4, 9.2, and 9.4 for group PE/PA, and 8.8, 9.4, 9.32, and 9.4 for group NPE/PA. Mean consumption of almond alone across conditioning days (including the additional 10-min exposure to almond on the second trial for the UN groups) was 9.1, 9.4, 9.1, and 9.3 for group PE/UN, and 9.0, 9.4, 9.2, and 9.2 for group NPE/UN. A 2 (Preexposure) × 2 (Contingency; paired or unpaired) × 4 (Trial) ANOVA was used to test for differences on almond or almond + sucrose intake. This yielded only a significant main effect of trial, $F(3, 84) = 3.91$; no other main effect or interaction was significant ($Fs < 1$). The main effect of trial reflected the fact that intake on Trial 1 was lower than on subsequent trials. Consumption of sucrose alone for the unpaired groups showed a similar pattern. Group mean scores (g) over the four presentations were 8.8, 9.3, 9.2, and 9.3 for group PE/UN, and 8.9, 9.4, 9.1, and 9.3 for group NPE/UN. A 2 (Preexposure) × 2 (Contingency) × 4 (Trial) ANOVA showed there to be a significant main effect of trial, $F(3, 84) = 6.05$, but no other main effect or interaction was significant, largest $F(1, 28) = 1.16$. The main effect of trial again reflected a lesser fluid intake on Trial 1.

As a preliminary analysis revealed that there were no main effects or interactions involving the factor test [largest $F(1, 28) = 1.93$, $p = .17$], the data of two tests were collapsed. Fig. 3 presents group mean almond preference scores for the test, collapsed across the two test trials. It shows that a preference was present only in the paired groups (mean scores for the unpaired groups were slightly below .5). Preexposure had little effect, either

in the paired or the unpaired groups. A 2 (Preexposure) × 2 (Contingency) ANOVA of almond preference yielded only a significant main effect of contingency, $F(1, 28) = 19.46$. No other main effect or interaction was significant, largest $F(1, 28) = 1.93$. The absolute levels of consumption on which the ratios were based, are presented in Table 2. Consumption of almond tended to be higher, and consumption of water lower, in the paired than in the unpaired groups. ANOVAs of almond intake and of water intake, with preexposure condition and contingency as the variables showed only a significant main effect of contingency in each case, $F(1, 28) = 20.61$ and $F(1, 28) = 8.27$ respectively.

These test results confirm the finding of Experiments 1 and 2 that preexposure to the CS does not produce a latent inhibition effect in rats that are not hungry on test. The results of the unpaired groups demonstrate that the pairing of sucrose and almond was effective in producing a preference. It may be noted that the mean preference score for the unpaired subjects (.41) was significantly below the .5 level, $t(15) = -2.54$. This may reflect the persistence of some unconditioned aversion to almond, or it may be that the negative almond–sucrose contingency was capable of generating inhibitory learning (see Boakes et al., 2010; Harris et al., 2000). The former seems more likely given that the size of the aversion decreased across the two test trials (it was .36 on the first and .47 on the second). The most plausible interpretation, therefore, is that enhanced preference shown by the paired subjects is the consequence of an association between almond and sucrose, which overcomes the animals' slight unconditioned aversion to almond.

5. General discussion

The experiments reported here have examined the role of motivational factors in determining the effects of preexposure to the CS in flavor–preference conditioning with sucrose as the reinforcer. Latent inhibition was obtained when the subjects were food-deprived during the preference test (Experiments 1 and 2), but it was consistently absent when they were given free access to food at the time of the test (Experiments 1–3). The absence of latent inhibition in non-hungry animals was not due to a deficit in the acquisition or expression of the flavor–preference itself (Experiment 3). These effects were independent of the motivational state of the rats during training (i.e., during preexposure and conditioning). Animals trained hungry and thirsty but tested just thirsty (Experiment 1) did not show latent inhibition, whereas animals trained thirsty but tested hungry (and thirsty) did (Experiment 2). This pattern of results is consistent with the following hypotheses: that pairing a neutral flavor with sucrose can generate both flavor–taste and flavor–nutrient learning; that which of these forms of learning determines performance on the preference test depends on the animal's motivational state at the time of test; and that flavor–nutrient learning is sensitive to the effects of CS preexposure, whereas flavor–taste learning is not.

One obvious interpretation of this pattern of results is that flavor–nutrient learning depends upon a standard associative-learning process (and is thus prone to latent inhibition) whereas flavor–taste learning involves some other mechanism (the absence of latent inhibition being taken as evidence of this). But before developing this notion in any greater detail we should consider the proposal that both forms of learning are associative (e.g., Harris et al., 2004), and determine if our standard theories of latent inhibition give any grounds for supposing that CS preexposure might influence flavor–nutrient, but not flavor–taste associations. We need to consider two classes of theory; those based on an interference mechanism, and those that attribute latent inhibition to a deficit in acquisition.

According to retrieval-interference theories (e.g., Bouton, 1993, 1997; Kraemer and Spear, 1992) latent inhibition occurs when information acquired during preexposure is retrieved on test and competes for expression with the association formed in the conditioning phase. Such theories can predict the absence of latent inhibition if the context present during the test, which will include the subject's motivational state, fails to match that present during preexposure, so that the effects of CS preexposure are not retrieved. As we have already noted, this general proposal has difficulty in explaining the results of Experiment 2. What our results show is that, although the motivational state on test is critical, the match between preexposure and test states is not – there is no latent inhibition in rats that are not hungry when tested, regardless of the motivational state in which prior training was given.

We should consider, however, the version of a retrieval-interference theory developed by Killcross and Balleine (1996), which can go some way toward explaining our findings. They suggested that, during CS-alone exposure, subjects learn that the CS is unrelated to the class of reinforcer relevant to their current motivational state; as a consequence, subsequent learning will be retarded when the CS is associated with a reinforcer of relevance to that state. This account can readily explain why, in the CFP procedure, latent inhibition is found in rats that are hungry throughout and not in rats that are just thirsty. Rats that are hungry during preexposure will learn that the CS flavor is unrelated to the availability of food and this can be expected to hinder subsequent flavor–sucrose conditioning. There are no grounds for expecting latent inhibition in the rats that are just thirsty throughout, and for two reasons. First, for these animals the flavor is in fact relevant to their motivational state (it is presented along with water); and second, the preference shown on the test is between two fluids, so that learning about the relevance of a flavor to the relief of thirst will be irrelevant. This account can also explain why latent inhibition should fail to appear in rats that were hungry during preexposure but not on the test. In this case learning that the CS is unrelated to hunger-relieving nutrients would not be expected to have an influence of a preference generated not by flavor–nutrient learning but by flavor–taste learning. What remains a problem for this account is the finding that latent inhibition is obtained when the rats have been thirsty throughout training but are rendered hungry for the test. Although in this case the preference on test may be taken to depend on flavor–nutrient learning, the conditions of preexposure (in which the rats are not food-deprived) do not provide the opportunity for learning about the irrelevance of the CS to the presentation of food. The Killcross and Balleine account requires that the rats be hungry during the preexposure phase.

Acquisition-deficit theories of latent inhibition (e.g., Hall and Rodriguez, 2010; Mackintosh, 1975; Pearce and Hall, 1980) assert that preexposure to the CS produces a reduction in its conditionability or associability; the CR is reduced on test, therefore, because the basic association has been poorly acquired. On the face of things such theories are not well placed to deal with the present results. Preexposure is assumed to produce a loss of associability that is specific to the CS and thus evidence of poor acquisition should be found when the test procedure reveals the strength of a flavor–taste association as when it is controlled by a flavor–nutrient association. To accommodate this pattern of results it is necessary to assume that the associability of the CS can differ for different reinforcers. The proposal that the learning that underlies latent inhibition depends on the nature of reinforcer is not novel – it is to be found in Mackintosh's (1975) theory of attention, which proposes that associability of a given stimulus may be reinforcer-specific, and is adopted by the model proposed by Hall and Rodriguez (2010). To that extent, it is consistent with standard associative theorizing.

We turn now to consideration of proposition that flavor–taste and flavor–nutrient learning differ in their susceptibility to latent

inhibition because quite different mechanisms underlie the two forms of learning. Evidence taken to support this view comes from both physiological and behavioral analysis. From a physiological perspective, the neurochemical responses to food-associated cues are differentially modulated by the affective and the nutritive characteristics of food (e.g., Azzara et al., 2001; Yu et al., 2000). Dopamine (DA) released in the nucleus accumbens (NAc) appears to be involved in flavor preference learning based on affective significance of food, whereas preference based on associations between flavor and the outcome of consumption involves D1-like receptors in amygdala and lateral hypothalamus (Touzani et al., 2008). In addition, the expression of both types of learning depends on different neurobiological substrates, with the activation of DA receptors in NAc being critical for the expression of flavor–taste learning but not of flavor–nutrient learning (see Touzani et al., 2010).

From a behavioral perspective, evidence that motivational state differentially affects the expression of the two kinds of flavor preference, and modulates the effectiveness of extinction in rodents has already been discussed. The two forms also appear to affect different components of the feeding behavior (Myers and Hall, 1998; but see Myers and Hall, 2000) and show different sensitive to temporal training parameters (Holman, 1975; Sclafani and Ackroff, 1994; but see Delamater et al., 2006). In human studies, the emerging literature has also generated some dissociations. For instance, Mobini et al. (2007) found that the pleasantness of a flavor CS associated with sweet taste (aspartame) increased slightly regardless of whether the flavor was consumed when hungry or sated, but that when participants that had consumed the drink with added sucrose, the change in pleasantness was affected by hunger state (but see Yeomans and Mobini, 2006). That associations between a flavor and the post-ingestive effects of a nutrient (e.g., sucrose or maltodextrin) can increase subsequent flavor intake, independent of changes in liking changes, has also been demonstrated (Yeomans et al., 2008).

Theoretical interpretations of the basis of the proposed distinction have been varied and plentiful (see e.g., Campbell et al., 1988; Drucker et al., 1994; Dwyer and Quirk, 2008; Fedorchak, 1997; Harris et al., 2004; Harris and Thein, 2005; Myers and Sclafani, 2006; Myers and Whitney, 2011; Tarner et al., 2004; Warwick and Weingarten, 1994). Possible sources of the flavor–taste learning have included, for example: an association between the flavor and the hedonic reaction produced by the sweet taste (e.g., Harris et al., 2004); some nonassociative mechanism such as configural learning (e.g., Pearce, 2002); a process of evaluative conditioning (e.g., De Houwer et al., 2001; Havermans and Jansen, 2011).

Although our results do not allow choice among these possibilities they may have relevance to the interpretation offered by Drucker et al. (1994) who proposed that pairing a flavor with a nutrient will produce both expectancy learning and hedonic learning. Expectancy learning involves the acquisition of knowledge about the predictive relationship between the flavor cue and the post-ingestive consequences of the nutrient. By contrast, hedonic learning refers to a process by which the presentation of the neutral flavor in compound with a valued taste changes the valence of the originally neutral stimulus (see also Rozin and Zellner, 1985, who argued that the result of simultaneous flavor–taste pairings cannot be explained in terms of anticipated consequences, since the CS does not "predict" the US). In this context it is worth noting that current theories of latent inhibition are largely based on data from conditioning preparations involving successive events, with the premise that CS acts as signal for US during conditioning. From this point of view, if the latent inhibition seen in these preparations reflects a change in the ability of a stimulus to come to predict its consequences, then an effect on flavor–nutrient but not on flavor–taste learning is to be expected.

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