Perceptual learning in flavor preference conditioning:

Restricting generalization of acquired preferences between flavors

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Abstract

Two experiments with rats investigated perceptual learning using a conditioned preference procedure. Experiment 1 used a between-subject procedure in which rats received either intermixed preexposure (AX, BX, AX, BX…) or blocked preexposure (AX, AX…, BX, BX…) to flavor compounds before a conditioned preference was established to AX by pairing it with sucrose. During a test, rats given intermixed preexposure showed a greater preference for AX over BX than those given blocked preexposure. Experiment 2 showed that after intermixed preexposure to AX and BX, and a block of preexposure to CX, a preference established to AX was less likely to generalize to BX than to CX. These results represent the first demonstration of the impact of the schedule of preexposure on perceptual learning using a flavor preference procedure, and they parallel those previously observed using flavor aversion procedures.

Keywords:

Flavor preferences; Conditioning; Generalization; Rat

The acquisition of flavor aversions and preferences is a fundamental form of behavioral adaptation that is observed across the animal kingdom. These learning processes have been studied at multiple levels of analysis in rodents (i.e., behavioral, neural systems, molecular mechanisms; e.g., Sclafani, 1997). However, until recently much of the behavioral research in rodents has focused on flavor aversions, where their rapid development and generalization to other similar flavors have been studied in detail. For example, an aversion established to one novel flavor compound (e.g., salt+lemon; denoted AX) will generalize to another similar compound (e.g., sucrose+lemon; BX), but such generalization is reduced in rats that have received prior exposure to AX and BX (Mackintosh, Kaye & Bennett, 1991; see also, Honey & Hall, 1989). This instance of perceptual learning (see Goldstone, 1998) has not been studied in the context of flavor preference learning and it is important to do so for the following three reasons.

First, the development of flavor aversions and preferences is based on different neural systems (e.g., Myers & Sclafani, 2006) and it cannot be assumed that the same principles of perceptual learning will apply to both forms of adaptation. Second, the study of how the generalization of food preferences could be limited through a process of perceptual learning might have considerable translational significance in the context of the human obesity epidemic (Rolls et al., 1981; Temple, Giacomelli, Roemmich, & Epstein, 2008). Finally, whereas the unconditioned response to novel flavors (neophobia) matches the conditioned response (a reduction in consumption) in the case of flavor aversion procedures, this is not the case in flavor preference procedures, which result in increased consumption. The latter point is potentially important when interpreting examples of perceptual learning. Thus, rats will often show a reluctance to consume a novel flavor (i.e., show neophobia; see Domjan, 1977), a reluctance that dissipates over successive presentations of that flavor (a form of habituation; see, Honey, Pie, Lightbaum, Rey, & Hall, 1992). In demonstrations of perceptual learning using flavor aversion procedures, the behavioral effect anticipated on the basis of

a reduction in the generalization of an aversion between familiar flavors (i.e., an increase in consumption) is equivalent to that expected if flavor preexposure results in habituation of flavor neophobia. One obvious way to uncouple these two potential influences of flavor preexposure is to use a flavor preference procedure. Here, any reduction in generalization that occurs as the result of preexposure will be manifest as a reduction in consumption, which opposes the effect that would be expected on the basis of the habituation of neophobia (i.e., an increase in consumption).

One important feature of perceptual learning in flavor aversion procedures is that the way in which rats are familiarized with the two flavor compounds, rather than familiarity *per se*, is important. Thus, when the two flavor compounds are presented in an intermixed or alternating fashion (AX, BX, AX, BX…) the perceptual learning effect is more pronounced than when they are presented in blocks (AX, AX, ….BX, BX…; e.g., Symonds & Hall, 1995). This intermixed/blocked effect has been demonstrated in flavor aversion procedures in humans (Dwyer, Hodder, & Honey, 2004; Mundy, Dwyer, & Honey, 2006; see also Lavis & Mitchell, 2006), and in other preparations and species (Honey & Bateson, 1996; Honey, Bateson, & Horn, 1994). There are a variety of theoretical explanations for this scheduling effect (for reviews, see Mackintosh, 2009; Mitchell & Hall, 2014) that are equally applicable to flavor preferences as they are to flavor aversions. However, the possibility that the scheduling effect observed in flavor aversion procedures might be a product of differences in the habituation of neophobia, as opposed to differences in generalization, has not been addressed adequately. For example, showing that rats that have not been given an effective flavor aversion conditioning regime with AX do not show a scheduling effect is not the most convincing way to counter alternative interpretations (see Experiment 1c, Blair & Hall, 2003). With this fact in mind, the two experiments reported here investigated whether or not the scheduling effect is evident when perceptual learning is assessed in a flavor preference procedure. To do so, two experiments were conducted in which the schedule of preexposure to two flavor cocktails was manipulated using

a between-subjects design in Experiment 1 and a within-subjects design in Experiment 2. Following the preexposure period, one compound was paired with sucrose, and then generalization of this preference to other compounds was assessed.

Experiment 1

The design of Experiment 1 is summarized in Table 1. There were two groups of rats that both received preexposure to two flavor compounds (AX and BX; caramel+quinine and chocolate+quinine) over a set of morning and afternoon sessions. Rats in Group INT received intermixed exposure to AX and BX (AX, BX, AX, BX...), whereas those in Group BLK received a block of exposure to AX, for example, followed by a block of exposure to BX (AX, AX...BX, BX...). Subsequently, rats received pairings of AX with sucrose; and then received two tests: one in which the generalization of the preference to BX was assessed with reference to the consumption of water (Test 1), and one in which consumption of BX was directly contrasted with AX (Test 2). A scheduling effect would be evident if rats in Group INT were less likely to consume flavor compound BX than those in Group BLK.

Table 1: Design of Experiment 1

Group	Preexposure	Conditioning	Adapt	Test 1	Test 2
INT	AX, BX, AX, BX...	AX+SUC	W	BX vs. W	AX vs. BX
BLK	AX, AX...BX, BX...				

Note: Group INT received intermixed preexposure and those in Group BLK received blocked preexposure to the compound flavors AX and BX; SUC = sucrose, and W = water.

Methods

Subjects and apparatus

The subjects were 16 naïve male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the start of the procedure of 286 g (range: 231-315g). The rats were individually housed in translucent plastic cages measuring 35x22x18 cm, with wood shavings as bedding. They were maintained in a 12-h light/dark cycle (starting at 8 a.m.). All of the solutions were prepared with tap water on each day of the experiment, and were administered in inverted 50 ml centrifuge tubes with stainless steel, ball-bearing-tipped spouts in the home cage. Fluid consumption was calculated by weighing the tubes before and after the drinking sessions. The flavor compounds (AX and BX) were constructed from 2% caramel or chocolate (A and B; counterbalanced) flavor solutions (Shepcote Distributors Ltd, Yorkshire, UK) with a 0.046 g/l quinine sulphate solution. On conditioning trials, the unconditioned stimulus, 160 g/l sucrose, was added to AX.

The procedures described in this paper were approved by the Comité de Ética en Experimentación Animal (Ethics Committee in Animal Research) at the University of Granada, and are classified as low severity according to the European guidelines. Rats were monitored daily by the individual responsible for animal welfare in the research center. The rats were housed individually during the course of the experiments, because of the need to monitor the consumption of each rat. When rats had water and food restrictions, they received a supplement of ad libitum water and food every day to cover their needs.

Procedure

Rats were water deprived by restricting their fluid consumption to two 15-min drinking sessions per day, one that began at 10 A.M. and the other at 4 P.M. During the first 2 days of

deprivation, rats received access to water during these sessions. The two principal groups (INT and BLK) were matched in terms of their weights (means: 291 g and 281 g, $F < 1$) and water consumption during these 2 days (means: 10.58 ml and 10.50 ml, $F < 1$). On each of the four preexposure days, rats received two 10-ml presentations of the flavored solutions, one at 10 A.M. and the other at 4 P.M. Half of the rats in Group INT received AX in the morning sessions and BX solution in the afternoon sessions over the course of four days, while the other half received the reverse order. Half of the rats in the Group BLK received AX in both sessions on the first two days and BX on the remaining days, with the other half receiving the reverse order. During the four days of conditioning, all rats received access to 20 ml of AX together with 160 g/l sucrose in the morning session. In the afternoon session, they had ad libitum access to water for 15 min. In the afternoon of the fourth conditioning day, food was removed from all cages and, on the following day, rats received only water in the morning, and an hour of water and food ad libitum in the afternoon. The food deprivation procedure was intended to ensure that a preference for AX was exhibited. The first test took place after this adaptation day. All tests involved a choice, in which rats had ad libitum access to two bottles with different solutions. On the first test day, they received BX in one bottle and water in the other; on the next test day, they received AX in one bottle and BX in the other.

Statistical analysis

We adopted a rejection level of $p < 0.05$, and used Greenhouse-Geisser corrections when needed. Partial eta squared (η^2_p) and Cohen's d were used to measure effect sizes.

Results and Discussion

The levels of consumption during preexposure (P1-P4) and conditioning (C1-C4) are presented in Table 2. Inspection of the table shows that there was some neophobia when the rats

first encountered the flavors. This manifested itself as low levels of consumption on the initial presentations of AX and BX in Group INT, and low levels of consumption during the initial presentations of AX and then again when BX was first presented in Group BLK. An ANOVA was conducted with group (INT/BLK), trial and session (morning/afternoon) as the factors. This analysis revealed a significant effect of trial, $F(3, 42) = 63.24$, $\eta^2_p = 0.82$, which is consistent with an attenuation of neophobia across trials. There was also a significant group x session interaction, $F(1, 14) = 8.59$, $\eta^2_p = 0.38$, which is consistent with the observation that Group BLK drank less fluid in the morning of the third day, when BX was presented for the first time. Analysis of the consumption scores from the conditioning stage (C1-C4), with group and trial as factors, confirmed that there was an effect of trial, $F(3, 42) = 11.54$, $\eta^2_p = 0.45$, reflecting an increase in consumption across trials, but no effect of group and no interaction between these factors, Fs < 1.

Table 2: Mean (+SEM) consumption in ml in Experiment 1

	P1		**P2**		**P3**		**P4**		**C1**	**C2**	**C3**	**C4**	**T1**		**T2**	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	AM	AM	AM	BX	W	AX	BX
INT	3.1	2.2	7.4	6.9	8.8	8.3	9.1	8.2	7.7	11.8	10.8	11.9	1.7	2.4	2.9	0.6
	(0.5)	(0.3)	(0.9)	(0.8)	(0.3)	(0.4)	(0.1)	(0.5)	(1.2)	(0.5)	(0.9)	(0.9)	(0.4)	(0.8)	(0.4)	(0.2)
BLK	2.3	3.6	6.6	7.1	5.9	7.7	8.7	8.4f	6.9	11.1	10.3	11.8	1.8	2.0	2.5	1.2
	(0.4)	(0.8)	(1.0)	(0.8)	(0.8)	(0.6)	(0.3)	(0.5)	(1.1)	(1.3)	(1.0)	(1.0)	(0.4)	(0.5)	(0.4)	(0.2)

Note: Group INT received intermixed exposure (i.e., AX, BX..AX, BX..) and Group BLK received blocked exposure (AX, AX..BX, BX..); AM = morning session and PM = afternoon session; P = preexposure trial (1-4), C = conditioning trial (1-4), T = test trial (1 and 2); AX and BX = compound flavors, and W = water.

The levels of consumption from which the preference ratios were derived are presented on Table 2. Preference ratios during the two types of test were calculated by dividing the consumption of the relevant solution by the total consumption during the test: BX consumption divided by BX plus water (Test 1) and BX divided by BX plus AX (Test 2). Using these ratios, scores closer to 0 in Test 1 indicate little preference for BX and scores close to 0 in Test 2 indicate that rats are able to

discriminate BX from AX (i.e., the preference for AX does not generalize to BX). For Test 1 (BX versus water) the ratios were very similar (0.47 for Group INT and 0.50 for Group BLK), and a one-way ANOVA showed that there was no significant difference between the groups ($F < 1$). However, inspection of Fig. 1 shows that during the second test (involving a choice between AX and BX) the ratios were closer to 0 in Group INT than in Group BLK. That is, rats in Group INT were better able to discriminate between AX and BX than were those in Group BLK. A one-way ANOVA confirmed that there was a significant effect of group, $F(1, 15) = 4.33$, $\eta^2_p = 0.24$.

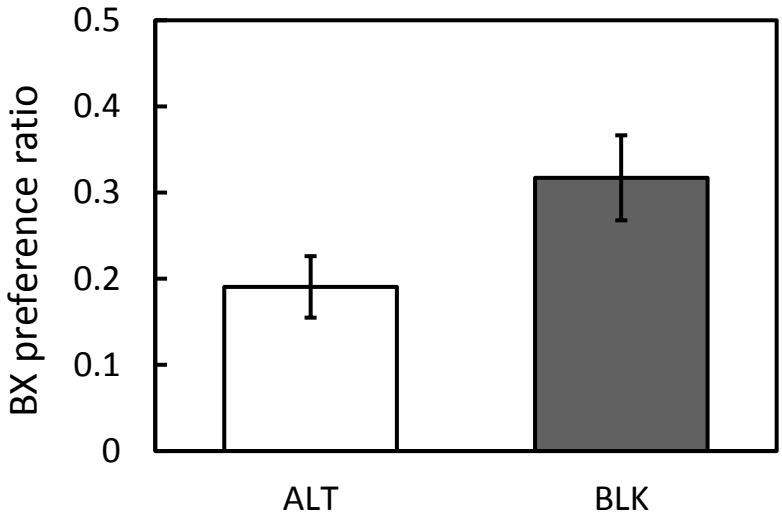

Fig. 1. Mean (±SEM) BX preference ratios from the test with AX and BX in Experiment 1. Prior to the test, Group INT received intermixed exposure (AX, BX, AX, BX...), and Group BLK received blocked exposure (AX, AX…BX, BX...); and then both groups received pairings of AX with sucrose.

The results of the second test in Experiment 1, involving a choice test between AX and BX, revealed an intermixed/blocked effect in a flavor preference procedure. The fact that there was no effect in the test that contrasted consumption of BX with water might have reflected a lack of sensitivity of the test. However, because one type of test revealed a difference and the other did not

there is a need to confirm the reliability of the effect of interest. In an effort to do so we attempted to replicate an intermixed/blocked effect in Experiment 2 using a within-subjects design.

Experiment 2

The design of Experiment 2 is shown in Table 3 and is modeled on the flavor aversion procedure employed by Blair and Hall (2003). All rats received intermixed preexposure to a pair of compounds (AX and BX), and a block of preexposure to a further compound (CX). After the preexposure stage, rats in Group COND received conditioning trials in which AX was paired with sucrose and those in Group UNP received unpaired presentations of AX and sucrose. The inclusion of these groups should allow an assessment to be made of whether or not differences during the critical tests (with BX and CX) reflected differences in generalization of a preference as opposed to some other effect of the preexposure schedule. Following the conditioning trials, all rats received a test in which AX and W were presented to assess the formation of a preference. We anticipated that rats in Group COND would show a more marked preference for AX than would Group UNP. During the critical tests, all rats received a choice between BX and CX. It was anticipated that the preference in Group COND would be less likely to generalize to BX than to CX; and, to the extent that this difference reflected a difference in the generalization of the conditioned AX preference, then it should not be evident in Group UNP.

Table 3: Design of Experiment 2

Group	Preexposure	Conditioning	Adapt	Test 1-2	Test 3-4
COND	AX, BX_CX	AX+SUC	W	AX vs. W	BX vs. CX
UNP		AX/SUC			

Note: In Group COND, AX was paired with sucrose (SUC) and in Group UNP AX and sucrose were unpaired. AX, BX and CX were compound flavors and W denotes water.

Methods

Subjects and apparatus

The subjects were 16 male Wistar rats (supplied by Janvier Labs), with a mean ad libitum weight at the beginning of the procedure of 489 g (range: 416-536g). The rats were previously used in a conditioned flavor aversion experiment but were naïve with respect to all of the flavors used in this procedure. BX and CX were solutions of 2% caramel or chocolate (counterbalanced) flavoring with 0.046 g/l quinine sulphate solution. AX was a solution of 2% vanilla flavoring (Shepcote Distributors Ltd, Yorkshire, UK) with the same concentration of quinine as BX and CX. In Group COND, 160 g/l sucrose was added to AX during the conditioning trials, whereas in Group UNP, AX and sucrose were separately presented.

Procedure

The procedure is depicted in Table 3. In the same way as in Experiment 1, on the first two days rats received access to water for 15 min at 10 A.M. and 4 P.M. Two groups of rats were then created, counterbalancing for their previous experience. The two groups had similar mean weights (means: 494 g and 484 g, $F < 1$) and consumed similar amounts of water during the water deprivation schedule (means: 12.96 ml and 12.88 ml, $F < 1$). The preexposure phase consisted of two daily presentations of 10 ml of the flavored solutions. Half of the rats in each group received AX in the morning session and BX in the afternoon session for four days, and then CX in the morning and afternoon sessions for the next two days. The other half received the reverse order, starting with CX. During the four days of conditioning, rats in Group COND received 10 ml of AX together with 160 g/l sucrose in the morning sessions, and water in the afternoon sessions. Rats in Group UNP received 10 ml of AX alone in the morning and 10 ml of the sucrose solution in the afternoon. In the afternoon of the fourth conditioning day, food was removed from all cages, and

on the following day rats received only water in the morning, and an hour of water and food ad libitum in the afternoon. The first test took place after this adaptation day. All tests consisted of a choice with ad libitum access to two bottles containing different solutions. During the first two days, they received AX in one bottle and water in the other. The efficacy of the conditioning stage was assessed by expressing the amount of AX consumed divided by the consumption of AX plus W, with scores above 0.50 indicating a preference for AX. On the next two days, rats received BX in one bottle and CX in the other. The relative amount of generalization of the AX preference to BX and CX was assessed by dividing consumption of CX by consumption of CX plus BX. With this ratio, scores above 0.50 indicate more generalization to CX than BX. All details of the procedure that have not been mentioned were the same as in Experiment 1.

Results and Discussion

The levels of consumption during preexposure (P1-P6) and conditioning (C1-C4) are shown in Table 4. Inspection of this table reveals that there was an increase in consumption across days and that as consumption increased rats came to consume more in the morning than in the afternoon sessions. ANOVA revealed significant effects of Trial, $F(5, 70) = 14.03$, $\eta^2_p = 0.50$, Session, $F(1, 14) = 50.41$, $\eta^2_p = 0.78$, and an interaction between these two factors, $F(5, 70) = 5.38$, $\eta^2_p = 0.28$. There was no effect of group or any further interactions, largest $F(1,70) = 1.97$, $p > 0.18$. During the conditioning trials, rats in Group COND consumed more than did Group UNP, consistent with the development of an acquired preference for AX in Group COND, but not Group UNP. ANOVA confirmed that there was a significant effect of Group, $F(1, 14) = 6.27$, $\eta^2_p = 0.30$, but no effect of Trial and no interaction between these factors, largest $F(3,42)=2.58$, $p > 0.1$. The preference ratios for AX in Group COND, with means (and SEMs) for Tests 1 and 2 of 0.59 (0.12) and 0.59 (0.12), were higher than the corresponding scores in Group UNP, with means of 0.37 (0.07) and 0.23 (0.06).

ANOVA confirmed that there was a significant effect of Group, $F(1, 14) = 9.10$, $\eta^2_p = 0.39$, but no effect of trial and no interaction between these factors, Fs < 1.

Table 4: Mean (+SEM) consumption in ml in Experiment 2

	P1		**P2**		**P3**		**P4**		**P5**		**P6**	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
COND	2.5	3.6	7.1	6.1	7.7	4.8	8.0	5.7	8.0	5.4	9.0	5.9
	(0.8)	(1.1)	(0.8)	(1.0)	(0.8)	(0.9)	(0.7)	(0.6)	(0.5)	(1.0)	(0.2)	(0.6)
UNP	4.3	3.7	8.9	6.1	8.6	5.5	8.9	5.9	8.4	4.7	9.1	5.8
	(1.0)	(1.0)	(0.2)	(0.9)	(0.3)	(1.1)	(0.2)	(0.9)	(0.5)	(0.9)	(0.2)	(0.6)
	C1	**C2**	**C3**	**C4**	**T1**		**T2**		**T3**		**T4**	
	AM	AM	AM	AM	AX	W	AX	W	BX	CX	BX	CX
COND	8.0	9.3	9.6	9.6	3.7	2.6	3.2	2.4	1.1	1.9	0.6	0.9
	(0.8)	(0.4)	(0.1)	(0.1)	(0.9)	(0.8)	(0.8)	(0.9)	(0.4)	(0.4)	(0.2)	(0.3)
UNP	8.3	8.2	9.2	7.9	1.6	3.3	0.6	3.6	1.9	2.2	1.8	1.4
	(0.5)	(0.4)	(0.1)	(0.6)	(0.2)	(0.8)	(0.1)	(1.4)	(0.6)	(0.8)	(0.5)	(0.3)

Note: Group COND received pairings of AX with sucrose and those in Group UNP did not; AM = morning session and PM = afternoon session; P = preexposure trial (1-6), C = conditioning trial (1-4) and T = test trial (1-4); AX, BX, CX = compound flavors, and W = water.

The critical results involving the choice between BX and CX are shown in Fig. 2, with the ratios pooled across tests 1 and 2. The ratios were calculated by dividing consumption of CX (preexposed in a block of trials) by consumption of CX + BX (preexposed intermixed with AX).[1] Using this ratio, a score above 0.50 indicates more consumption of CX than BX, and suggests that there was greater generalization between AX and CX than between AX and BX. Inspection of Fig. 2 shows that the scores for Group COND were above 0.50. but this was not the case in Group UNP. ANOVA confirmed that the ratios differed between the two groups, $F(1, 13) = 6.30$, $\eta^2_p = 0.33$. Neither the effect of trial nor the interaction between group and test trial was significant (Fs<1). A further analysis of the pooled ratio scores for tests 1 and 2 showed that while those for Group COND differed from 0.50, $t(7)=2.65$, $d=0.94$, those for Group UNP did not, $t(6)=-0.84$.

[1] The results from one rat (from Group UNP) eliminated because one of the test bottles was faulty and leaked into the cage during the test.

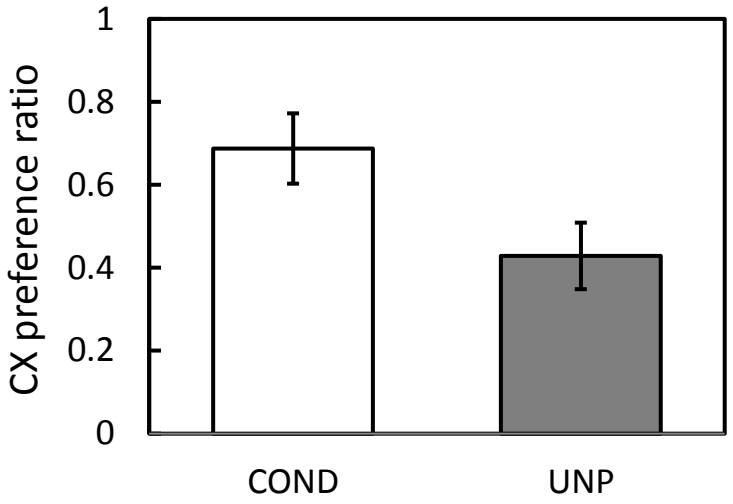

Fig. 2. Mean (±SEM) CX ratios from the tests with BX and CX in Experiment 2. Prior to the test, Groups COND and UNP had received intermixed preexposure to AX and BX and a block of preexposure to CX; and then Group COND received pairings of AX with sucrose and Group UNP were given unpaired presentations of AX and sucrose.

The results of Experiment 2 replicated those of Experiment 1: There was less generalization of a preference from AX to a test stimulus (BX) that had been presented intermixed with AX than to a test stimulus (CX) that had been presented in a separate block of trials. The fact that this effect was evident in Group COND but not Group UNP, confirms that the differences in consumption between BX and CX were a product of differences in the generalization of a preference, as opposed to some other product of the different schedules of preexposure (cf. Blair & Hall, 2003).

General Discussion

Perceptual learning effects are well established in flavor aversion procedures in rats (e.g., Blair & Hall, 2003; Honey & Hall, 1989; Mackintosh et al., 1991; Symonds & Hall, 1995). However, the development of flavor preferences and their generalization to other similar flavors in rats is an issue that has not received a great deal of investigation. Here, preferences established by

pairing one flavor compound (AX; e.g., caramel plus quinine) with sucrose generalized to other flavor compounds (BX; chocolate plus quinine) that shared a common element (X; quinine); and such generalization was modified by prior experience with the compounds. Rats that had received AX and BX intermixed within a day showed less generalization between them than rats for whom AX and BX had been presented in blocks (Experiment 1). This effect was replicated in Experiment 2 using a within-subjects procedure: after intermixed preexposure to AX and BX, and a block of preexposure to CX, the preference established to AX was more likely to generalize to CX than BX. These results mirror those seen in flavor aversion learning (e.g., Blair & Hall, 2003; Symonds & Hall, 1995).

There are a variety of accounts for instances of perceptual learning in flavor aversion procedures, and these accounts apply equally readily to demonstrations of perceptual learning seen here using the flavor preference procedures (for reviews, see Mitchell & Hall, 2014; Montuori & Honey, 2015). The essence of these accounts is that, in one way or another, intermixed exposure to AX and BX results in the unique elements of the two compounds (i.e., A and B) coming to dominate processing of the two compounds. In this way, any property acquired by AX will be less likely to generalize to BX because A and B are being processed rather than X. The results of Experiments 1 and 2 do not allow one to select between different variants of this type of account, but they do demonstrate that the critical (scheduling) effects can be observed when the assessment of perceptual learning uncouples the potential effects of preexposure on the habituation of neophobia and generalization: In a flavor preference procedure, habituation of neophobia will increase consumption while a reduction in generalization will reduce consumption; whereas in a flavor aversion procedure the operation of both processes will affect an increase in consumption.

On a more general note, the mechanisms underlying the development and generalization of flavor preferences have both ongoing theoretical import and relevance to our understanding of the control of food choice and consumption. Certainly, some flavors will come to be preferred because they have been paired with nutritive consequences, and others will also be preferred to the extent that they are similar. However, Experiments 1 and 2 show that the generalization of acquired flavor preferences is not a fixed property of the physical characteristics of flavors but is instead affected by the nature of encounters with the flavors before they have gained any motivational significance or value. Thus, the development of a palate can be shaped in advance of the learning processes that result in the formation of preferences. This observation carries with it the prospect of developing guidance on how to encourage healthy diets through either limiting or encouraging the generalization of preferences (and aversions). This type of research is in its infancy in humans (for a review, see Raynor & Epstein, 2001; see also, Bouhlal, Issanchou, Chabanet, & Nicklaus, 2014; de Wild, de Graaf, & Jager, 2013, 2015; Methven, Langreney, & Prescott, 2012), but including consideration of how prior experience with flavors affects their later processing might provide one useful means of shaping appropriate behavior.

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