



ELSEVIER

Contents lists available at ScienceDirect

Appetite

journal homepage: www.elsevier.com/locate/appet

Research report

Analysis of blocking of flavor-preference conditioning based on nutrients and palatable tastes in rats [☆]

Felisa González ^{a,*}, David Garcia-Burgos ^{1,a}, Geoffrey Hall ^{b,c,d}

^a Department of Experimental Psychology, University of Granada, Campus Cartuja s/n, 18071 Granada, Spain

^b Department of Psychology, University of York, York YO10 5DD, UK

^c School of Psychology, University of New South Wales, Sydney, NSW 2052, Australia

^d School of Psychology, Plymouth University, Plymouth, UK



ARTICLE INFO

Article history:

Received 28 November 2013

Received in revised form 28 April 2014

Accepted 6 May 2014

Available online 15 May 2014

Keywords:

Blocking

Flavor preference

Flavor–nutrient learning

Flavor–taste learning

Sweet taste

Rat

ABSTRACT

In Experiment 1 rats were given training in which a mixture of two flavors was paired with sucrose. This established a substantial preference for each of the flavors; however, when rats were given prior experience with just one of the flavors paired with sucrose, training with the compound produced only a weak preference for the other – an example of the blocking effect, well known in other associative learning paradigms. Both the palatable taste of sucrose and its nutrient properties contribute to its ability to reinforce preference acquisition. The role of these two forms of learning was examined in two further experiments in which the reinforcer used was fructose (which is considered to support preference learning because it is palatable but not through its nutrient properties) or maltodextrin (thought to support preference learning by way of its nutrient properties). In neither case was blocking observed. At the theoretical level, this outcome constitutes a challenge to the attempt to explain flavor-preference learning in terms of the standard principles of associative learning theory. Its implication at the level of application is that the potential of the blocking procedure as a technique for preventing the development of unwanted flavor preferences may be limited.

© 2014 Elsevier Ltd. All rights reserved.

Introduction

Epidemiological and experimental evidence indicates that high levels of consumption of sugar-sweetened foods in both children and adults are associated with weight gain and obesity (see Malik, Schulze, & Hu, 2006, for a review), suggesting that such foods are crucial contributors to the development of dietary-induced obesity in modern society. Consumption of diets rich in sweet-tasting foods and beverages seems to be promoted not only by innate preferences, but also by experience with sweet foods from the very beginning of life (Ventura & Mennella, 2011). In fact, through a lifetime of eating experiences, learning seems to play a major role in the development and regulation of food choice and intake (see Gibson & Brunstrom, 2007; Jansen, 2010). In our food-saturated societies there are numerous daily opportunities for learning to occur involving sweet-tasting beverages and foods. Discrete signals like visual cues,

tastes, odors, and flavors (e.g., Boakes, 2005; Dickinson & Brown, 2007; Stevenson, Boakes, & Wilson, 2000), and environmental contextual cues (as suggested by studies using rats as subjects – see Dwyer & Quirk, 2008; González, Garcia-Burgos, & Hall, 2012; Todd, Winterbauer, & Bouton, 2012) may all become associated with sweet tastes and nutrients.

It has been reported that such food-related cues promote eating behavior in rats independently of physiological hunger (e.g., Reppucci & Petrovich, 2012), confirming that food consumption is not always controlled only by primary drives or needs. In humans this seems to be the case as well. Initially neutral cues may become food related through Pavlovian conditioning, eliciting anticipatory craving and approach tendencies (e.g., Jansen, 1998; Van Gucht, Vansteenwegen, Van den Bergh, & Beckers, 2008). Such cues can produce an intense state of food cue reactivity in some individuals, (Van den Akker, Jansen, Frentz, & Havermans, 2013, suggest that impulsive people are especially susceptible) who find themselves almost incapable of controlling “hedonic” eating and overeating (Jansen, 2010). Cue/context-eating associations appear to be automatic, and many individuals lack the capacity to be aware of, ignore, or resist eating in response to such cues (Cohen & Babey, 2012). It seems likely that the properties acquired by food-related cues are capable of stimulating habitual overeating in some people, thus contributing to the possible development of obesity in these vulnerable individuals.

[☆] Acknowledgments: This research was supported by grants #PSI2009-10627 (MICINN, Spain) and #PSI2012-33552 (MINECO, Spain). The authors thank D. M. Dwyer for helpful discussion on the results presented in this paper.

* Corresponding author.

E-mail address: fgreyes@ugr.es (F. González).

¹ Present address: Department of Psychology, Clinical Psychology, and Psychotherapy, University of Fribourg, 2 Rue de Faucigny CH-1700, Fribourg, Switzerland.

Procedures that might reduce the effectiveness of, or limit learning about, food-related cues are therefore of relevance when it comes to devising strategies for the control of appetite and eating behavior generally. Research using animals as subjects has generated experimental results and theoretical models relevant to this issue. The cue exposure or extinction procedure – repeated presentation of the critical cues in the absence of the food reinforcer – is perhaps the most obvious strategy for eliminating a preference that has already been formed, and this procedure has been extensively studied in appetitive behavior, both in animals and humans (e.g., Bouton, 2011; Jansen, 2010; Todd et al., 2012; Van Gucht, Baeyens, Vansteenwegen, Hermans, & Beckers, 2010; Van Gucht, Baeyens, Hermans, & Beckers, 2013; Yeomans, 2010; Yeomans, Leitch, Gould, & Mobini, 2008; see also Baeyens, Crombez, Van den Bergh, & Eelen, 1988; Capaldi, 1996). Unfortunately, conditioned flavor preferences seem to be highly resistant to extinction under some conditions (Albertella & Boakes, 2006; Capaldi, Myers, Campbell, & Sheffer, 1983; Drucker, Ackroff, & Sclafani, 1994; Fedorchak, 1997; Sclafani, 1991; for a parallel ineffectiveness of extinction in reducing subjective craving in humans see, e.g., Papachristou, Nederkoorn, Beunen, & Jansen, 2013; Van Gucht, Vansteenwegen, Beckers, & Van den Bergh, 2008); this is especially true for those based on the hedonic properties of food (e.g., Harris, Shand, Carroll, & Westbrook, 2004; but see Delamater, 2007). In addition, extinguished responses can recover with the mere passage of time and may reappear when the trained cue is presented in a context different from that used for extinction (e.g., Bouton, 2011). Although there are some treatments aimed at reducing the recovery of extinguished response (see e.g., Urcelay, 2012), these can be time consuming and difficult to put into practice in real contexts.

An alternative is to attempt to prevent learning from occurring in the first place. Consumption of a food must, of course, be accompanied by various cues, but this does not mean that these cues will necessarily acquire new properties by way of association. For instance, exposing a cue without reinforcement prior to a conditioning procedure will retard the development of a conditioned response, the well-known phenomenon of latent inhibition (Lubow, 1989). Exposure to the distinctive flavoring used in a sweet drink, prior to experience of the drink itself, might limit the development of a preference for that flavor. There may be practical problems, of course, in exposing a food cue (e.g., a novel flavor) without the reinforcing properties of food (e.g., sweet taste, nutrient properties), as, quite often, these will have an intrinsic relation, difficult to separate outside the laboratory. Furthermore, although latent inhibition of flavor-preference conditioning has been successfully demonstrated in some procedures (e.g., De la Casa, Márquez, & Lubow, 2009), it is not always obtained. Garcia-Burgos, González, and Hall (2013) found the effect to be dependent on the motivational state of subjects. They suggested (but see also Delamater, 2011) that although latent inhibition can limit the acquisition of a preference based on an association between the flavor and the nutrient properties of a food, a preference based on the hedonic properties of the food (e.g., on the association of the flavor with a sweet taste) is less susceptible to latent inhibition.

The blocking paradigm offers another possible way of limiting learning about food-related cues. In blocking (Kamin, 1969), pretraining with one cue (A+) reduces conditioning to a second cue (B) when both are subsequently reinforced as a compound (AB+). This effect has been interpreted (e.g., Rescorla & Wagner, 1972) in terms of the predictive properties of the cues – pretraining with A allows it to predict the reinforcer; learning about the added cue B is blocked because it does not predict anything new.

The effect has been investigated for flavor-preference learning in experiments using hungry rats as the subjects and a nutritive substance as the reinforcer. Early studies using cues drawn from different modalities (i.e., tastes and odors) produced mixed results.

Holder (1991) reported results consistent with the proposal that establishing a preference for an odor (or taste) will block learning about the other cue when a compound of taste and odor is presented with sucrose. Capaldi and Hunter (1994), on the other hand, in a study with a similar design, found no blocking of learning about an odor presented in compound with a taste, after pretraining of the taste (see Dwyer, Haselgrove, & Jones, 2011, for an extensive discussion of the possible source of the discrepancy). Blocking has been reliably obtained, however, in subsequent studies using two cues from the same modality as the blocking and blocked cues. Examples are provided by Balleine, Espinet, and González (2005), who used different Kool Aid flavors; and by Dwyer et al. (2011) who used two odors (Experiments 1A, 1C), two tastes (Experiment 1B), or different Kool Aid flavors (Experiments 2A–2C). In the experiments to be reported here the cues were provided by solutions of almond and vanilla essences, both of which may be regarded primarily as odors (although both may also possess taste properties). Blocking is to be expected with these stimuli.

The use of a nutrient as the reinforcer in the experiments that successfully showed blocking makes it likely that the preferences obtained would be based, at least in part, on the formation of a flavor–nutrient association. Such learning, in which one event predicts the occurrence of a consequence, might be expected to be susceptible to processes that depend on the predictive value of the cues, and thus to blocking. It has been argued, however, that preference learning based on the taste of the reinforcer has different properties (e.g., Drucker et al., 1994; Yeomans, 2010). Flavor–nutrient learning is regarded as predictive or expectancy learning, based on the adaptive value of anticipating nutrient intake, whereas flavor–taste learning, it is suggested, involves a process that changes the hedonic value of an initially neutral flavor so that it becomes preferred, independently of its value as a nutrient signal (Drucker et al., 1994). To the extent that blocking depends on the (lack of) predictiveness of the cue, it may be questioned whether the phenomenon would be observed for a preference produced by flavor–taste learning. The observation, noted earlier, that flavor–taste learning appears to be insensitive to latent inhibition (another phenomenon readily found in predictive learning) reinforces this doubt.

Accordingly, the purpose of the experiments reported here was to analyze the effectiveness of blocking for flavor–taste and flavor–nutrient learning separately. Will flavor–taste and flavor–nutrient learning be equally prone to blocking? (And thus, does blocking have potential as a tool for reducing the acquisition of preferences based on both flavor–nutrient and flavor–taste learning?). Experiment 1 was designed to replicate the blocking effect obtained in earlier work, using sucrose as the reinforcer. With this reinforcer a preference could be the product of both flavor–nutrient and flavor–taste learning. To separate these, we went on, in Experiments 2 and 3, to look for blocking using different reinforcers, another sugar (fructose) and a non-sweet polysaccharide (maltodextrin).

Although sucrose, fructose, and maltodextrin are all nutrients and provide approximately the same amount of calories (about 4 kcal/g), they differ in their glycemic index (GI), the amount of glucose they provide in the blood after consumption, as well as in their tastes. Sucrose and maltodextrin have relatively high GIs (respectively ≈ 67 and ≈ 100 , that for pure glucose being 100; Livesey & Tagami, 2009). Fructose, on the contrary, is a poor energetic sugar, with limited absorption in the intestine; its metabolism occurs mainly in the liver and the final liberation of glucose is $\approx 50\%$: consequently its GI is low, ≈ 20 – 25 , and so is its satiating power (Anderson, 1997; Jenkins et al., 1981; Tappy & Lê, 2010). The three carbohydrates also differ in their sensory properties. Sucrose and fructose share the same sweet taste – they can be considered as naturally occurring sweeteners; and although they have qualitatively different tastes (Ramirez, 1994b) there is good generalization between them in rodents (Nissenbaum & Sclafani, 1987). Maltodextrin, which is rare or absent in nature, has

its own distinctive and palatable taste (Ramirez, 1994a, 1994b), but appears not to taste sweet to rats, as generalization between it and sucrose is weak (Nissenbaum & Sclafani, 1987).

On these grounds it has been argued that the reinforcing power of fructose derives solely or principally from its taste, whereas that of maltodextrin depends solely or principally on its nutritive properties (Elizalde & Sclafani, 1988; Sclafani & Ackroff, 1994; see also Dwyer, 2009, and Dwyer & Quirk, 2008, for the use of this strategy to separately study flavor–taste and flavor–nutrient learning). Accordingly, if flavor–nutrient learning is susceptible blocking and flavor–taste learning is not, we may expect to find the phenomenon with maltodextrin but not with fructose.

Experiment 1

The aim of this experiment was to replicate blocking of a flavor preference conditioning using sucrose as the reinforcer. The design and general procedures were the same as those used in a previous successful demonstration of blocking (Balleine et al., 2005, Experiment 1), although the flavors, sucrose concentration, and some details of training and testing conditions were different. One group of rats (paired) received initial training in which a solution of flavor A was paired with sucrose; a second group (unpaired) received separate presentations of A and sucrose at this stage. A choice test (A vs. water) was given to confirm the occurrence of conditioning in the paired group. Both groups then received pairings of a compound of two flavors (AB) with sucrose, followed by a choice test of B vs. water. Blocking would be revealed by a lesser preference in the paired than the unpaired group. The rats were water deprived throughout the experiment to ensure that they consumed the fluids offered; they were also given only restricted access to food to ensure the full effectiveness of the nutritive properties of the sucrose.

Method

Subjects and apparatus

The subjects were 16 experimentally naive male Wistar rats with a mean body weight of 300 g (range 275–310 g) at the start of the experiment. They were housed in individual home cages and kept in a colony room 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 daily with tap water and consisting of 1% (vol/vol) almond or vanilla essence (Silver Spoon, London, UK), and a 10% (wt/vol) sucrose (AB Azucarera Iberia S.L., Madrid, Spain) solution. The animals were maintained on the food and water deprivation schedule to be described later, throughout the experiment.

Procedure

Food and water were removed from the home cages 24 h before the start of the experiment. Then all rats were given 3 days to accommodate to a 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 (PA, paired; UP, unpaired; $n = 8$ each). During training the morning water drinking session was replaced by the experimental treatment; food and water continued to be given in the afternoon, immediately after the second training session for the UP group, which started at 2:00 p.m., had finished. The experimental sessions were all 30-min long.

Conditioning of flavor A occurred over 8 days. Rats in group PA had access to 6 ml (6 ml allows consumption of 5 ml, given that a small amount of fluid remains inaccessible in the drinking tube) of a mixture of flavor A (almond or vanilla, counterbalanced) and sucrose at 9:30 a.m. On these days rats in group UP were given 6 ml of flavor A during the morning session and 6 ml of sucrose during an afternoon session at 2:00 p.m. On the next day (day 9) the rats were given a test in which they had access to two bottles, one containing 20 ml of flavor A and the other 20 ml of water. The left/right positions of the bottles were counterbalanced across subjects. Following this phase, all rats were given two conditioning days in which they were offered 6 ml of a solution in which the compound AB was paired with sucrose. The next day a test for conditioning of flavor B was conducted under the same conditions as for the previous test for flavor A. All the experimental procedures were approved by the University of Granada Ethics Committee, and were in accordance with the European Union Directive of 22 September 2010 (2010/63/EU).

Results and discussion

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

The mean consumption across the eight sessions of flavor-A conditioning in group PA was 4.2 g. Rats in group UN consumed on average 3.2 g of the unreinforced flavor A solution and 4.3 g of the sucrose solution. During 2 days of conditioning with the compound AB, the mean consumption was 4.5 g, both for the PA and the UP group. Figure 1 shows group mean flavor preference ratios for the test sessions. The first test confirmed that training with A successfully established a preference for A in group PA, and that group UP showed no preference; the mean scores differed reliably, $t(14) = 4.08$. The results of the test of B given after compound conditioning are presented on the right of Fig. 1 (Table 1 shows the absolute levels of consumption on which these preference scores were based). Both groups had a preference for B over water (both had scores significantly greater than .50, smallest $t(7) = 7.82$), but the preference for flavor B was less in group PA (.61) than in group UP (.81), $t(14) = 2.32$, indicating that prior conditioning with A had blocked learning about B. We conclude that the previously reported result

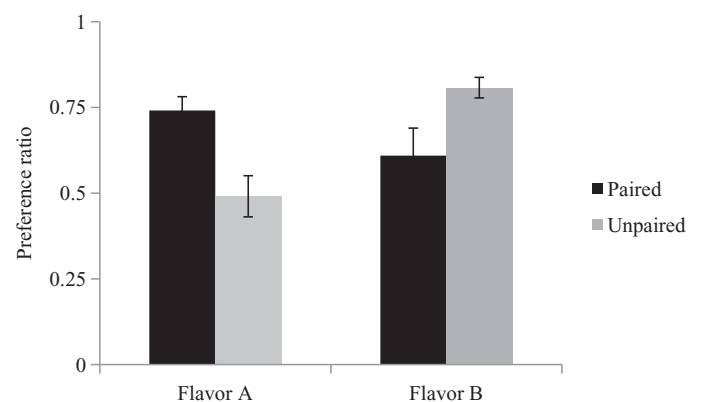


Fig. 1. Experiment 1: Sucrose as the reinforcer. Mean flavor preference ratios (\pm SEM) for the flavor vs. water choice test are shown separately by flavor (A, intended blocking flavor; B, intended blocked flavor) and by group.

Table 1
Mean flavor and water consumption [grams (SEM)] for the tests of flavor B vs. water in experiments 1, 2, and 3.

	Group	Flavor	Water
Exp 1	PA	3.1 (.8)	2.1 (.7)
	UP	4.5 (.5)	1.1 (.3)
Exp 2	PA(malt)	3.8 (.7)	1.2 (.2)
	UP(malt)	4.8 (.6)	1.3 (.3)
	PA(fruct)	3.0 (.3)	1.1 (.2)
	UP(fruct)	3.4 (.6)	1.1 (.2)
Exp 3	PA(malt)	5.4 (.8)	2.2 (.5)
	UP(malt)	4.9 (.7)	2.3 (.8)
	PA(fruct)	3.3 (.6)	1.7 (.3)
	UP(fruct)	2.7 (.4)	1.7 (.7)

Note: PA = paired; UN = unpaired; malt = maltodextrin; fruct = fructose.

of blocking of a conditioned flavor preference based on sucrose can be readily obtained with the procedures used here.

Experiment 2

As we have noted, the preference generated when using sucrose as the reinforcer may be attributed to flavor–taste learning, flavor–nutrient learning, or to the simultaneous occurrence of both. The aim of this experiment was to identify the separate contributions of these two forms of learning and to assess the susceptibility of each to the blocking phenomenon. To do this, we repeated the essential design of Experiment 1, but changed the nature of the reinforcer. For one pair of groups, PA(fruct) and UP(fruct), the reinforcer was fructose which, we have argued, generates a preference by way of its palatable taste. For a second pair of groups, PA(malt) and UP(malt), the reinforce was maltodextrin, thought to produce a preference by way of its nutritive properties. Previous work (Dwyer et al., 2011) has produced results indicating that blocking can be obtained with maltodextrin (and thus in flavor–nutrient learning). Is this the sole source of the effect observed when sucrose is used as the reinforcer, or does blocking of flavor–taste learning also play a role?

Method

Subjects and apparatus

The subjects were 32 experimentally naive male Wistar rats with a mean body weight of 397 g (range 360–432 g) at the start of the experiment. Housing, general maintenance, and apparatus were the same as in Experiment 1, with the exception that the reinforcer was a 10% (wt/vol) maltodextrin (Maltodextrin white pure, Applichem, Darmstadt, Germany) solution for one pair of groups, or a 10% (wt/vol) fructose (D[–]-Fructose, Panreac, Barcelona, Spain) solution for the other pair.

Procedure

Animals were weighed and allocated to four weight-matched groups ($n = 8$): PA(malt) and UP(malt), PA(fruct), and UP(fruct). As in Experiment 1, the PA groups received simultaneous conditioning of flavor A over the course of eight sessions, whereas the UN groups received the flavor and the reinforcer separately. As before, a preference test of A was given after the first phase of training. Testing of B followed the phase of conditioning with the AB

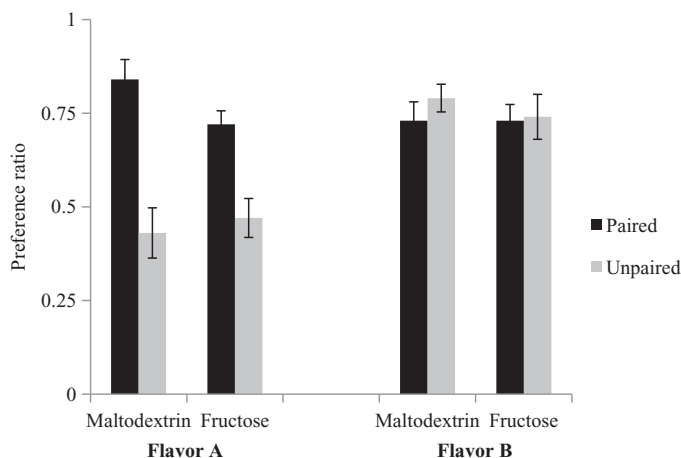


Fig. 2. Experiment 2: Maltodextrin and fructose as the reinforcers (standard blocking procedure). Mean flavor preference ratios (\pm SEM) for the flavor vs. water choice test are shown separately by flavor (A, intended blocking flavor; B, intended blocked flavor), group (Paired and Unpaired) and reinforcer.

compound. In respects not specified here, the procedure was the same as that described for the previous experiment.

Results and discussion

During the first phase of training, the rats in groups PA(malt) and PA(fruct) drank means of 4.4 g and 4.3 g, respectively of the reinforced flavor A solution. Groups UP(malt) and UP(fruct) each drank 3.9 g of the unreinforced flavor A solution, and 4.4 and 4.3 g of maltodextrin and fructose solutions, respectively. There were no differences among the groups on these measures ($F_s < 1$). Mean scores for consumption of the reinforced AB compound were PA(malt) 5.0 g, UP(malt) 4.9 g, PA(fruct) 4.8 g, and UP(fruct) 4.8 g. Again there were no differences among these scores (largest $F < 1.30$).

The results (preference scores) for the test with flavor A are shown on the left of Fig. 2. Neither of the UP groups showed a preference for A over water, but both PA groups did so, and to approximately the same extent. A two-way ANOVA with training procedure (PA vs. UP) and reinforcer type (malt vs. fruct) as the variables revealed a significant effect of the training variable, $F(1, 28) = 31.35$, but no effect of reinforcer, $F < 1$, and no reliable interaction between the variables, $F(1, 28) = 1.82$.

Preference scores for the test of flavor B conditioning are shown on the right of Fig. 2 (absolute scores are given in Table 1). All groups showed a positive preference, and, for both reinforcers, this was as marked in the PA as in the UP groups; that is, there was no indication of a blocking effect either with fructose or with maltodextrin. A two-way ANOVA with training procedure and reinforcer type as the variables confirmed this impression; neither main effect nor the interaction was significant, $F_s < 1$. The average preference ratio was .74, which differed significantly from .50, $t(31) = 10.59$.

On the face of things these results suggest that neither flavor–taste nor flavor–nutrient learning is susceptible to blocking, in contrast to a preference based on both forms of learning (as we assume was produced by using sucrose as the reinforcer in Experiment 1). As we have noted, the absence of a blocking effect in flavor–taste learning might be expected according to some theoretical perspectives; but the lack of an effect with maltodextrin as the reinforcer is unexpected, particularly in the light of the results previously reported by Dwyer et al. (2011). Given this discrepancy, we thought it appropriate to conduct a further experiment to investigate the generality and reliability of the results obtained in Experiment 2.

Experiment 3

The procedure used by Dwyer et al. (2011) in their studies of blocking differed in a number of respects from that used here. The experiment most similar to ours in other respects (their Experiment 1C) differed most obviously in that, instead of giving a first phase of A+ sessions followed by the AB+ sessions, there were sessions of conditioning to the compound (AB+) intermixed with flavor-A conditioning sessions (A+) before the preference test with flavor B. It is possible that this is a more sensitive procedure than the two-phase procedure used in our experiments (which may be capable of detecting the effect with sucrose as the reinforcer but not when using reinforcers that promote preferences based of only one, instead of two, reinforcing properties). Accordingly, in the present experiment we replicated the essential features of Experiment 2, but conditioning consisted of a single phase in which A+ and AB+ trials were intermixed. Will this procedure allow us to confirm the blocking effect with the maltodextrin reinforcer? And will blocking still be absent with fructose in these circumstances?

Method

Subjects and apparatus

The subjects were 32 experimentally naive male Wistar rats with a mean body weight of 400 g (range 386–412 g) at the start of the experiment. Housing, general maintenance, and apparatus were the same as in Experiment 2.

Procedure

The rats were weighed and allocated to four weight-matched groups ($n = 8$): PA(malt), UP(malt), PA(fruct), and UP(fruct). During conditioning, the PA groups received alternate presentations of A+ and AB+. The UN groups received the same AB+ trials, but A and the reinforcer were presented separately on the alternate days. There were 8 days of training, and thus four trials of each type; this is a change from Experiments 1 and 2, in which there was more training with A than with the AB compound, but it follows the arrangement of Dwyer et al. (2011) who gave equal numbers of the two trial types. After this phase of training, all subjects received preference tests, first for flavor B, and the next day for flavor A. Details not specified here were the same as those described for Experiment 2.

Results and discussion

In this experiment, in contrast to Experiment 2, there was some sign of a difference in the consumption of fructose and maltodextrin. During the AB+ trials of training, group means for consumption of the compound were PA(malt) 4.3, UP(malt) 4.1, PA(fruct) 3.8, and UP(fruct) 3.8 g. An ANOVA, with reinforcer type (malt vs. fruct) and training procedure (PA vs. UP) as the variables, revealed a significant effect of reinforcer type, $F(1, 28) = 14.89$ (other $F_s < 1.30$). Similarly, rats in group PA(malt) drank more of the reinforced flavor A solution (mean 4.2 g) than did those in group PA(fruct) (mean 3.8 g); $F(1, 14) = 20.02$. Groups UP(malt) and UP(fruct) drank 3.6 g and 3.4 g of the unreinforced flavor A solution, and 4.2 g and 4.1 g of maltodextrin and fructose solutions, respectively. On neither of these measures did the groups differ ($F_s < 2.33$).

The results of the preference test with A vs. water are presented on the left of Fig. 3. Preference ratios for the maltodextrin groups were somewhat higher than those for the fructose groups, but in both cases the preference was greater in the PA than in the UN group. An ANOVA with training procedure and reinforcer type as the variables yielded significant effects both of procedure, $F(1, 28) = 21.34$, and of reinforcer, $F(1, 28) = 8.24$; the interaction was not significant ($F < 1$).

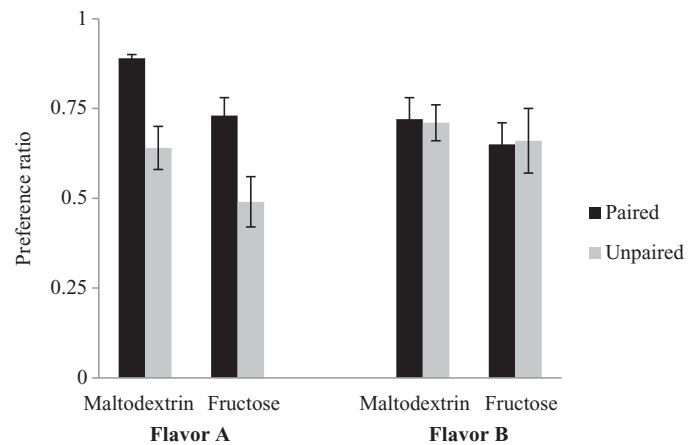


Fig. 3. Experiment 3: Maltodextrin and fructose as the reinforcers (intermixed blocking procedure). Mean flavor preference ratios (\pm SEM) for the flavor vs. water choice test are shown separately by flavor (A, intended blocking flavor; B, intended blocked flavor), group (Paired and Unpaired) and reinforcer.

The test results for flavor B are shown on the right of the figure (with absolute scores being presented in Table 1). It is evident that all groups showed a substantial preference for B over water, and that the size of this preference did not differ among the groups. An ANOVA with reinforcer type and training procedure as the variables revealed no significant effects ($F_s < 1$). The average preference ratio for flavor B was .68, which differed significantly from .50, $t(31) = 5.63$. Thus, just as in Experiment 2, a training procedure that was effective in producing conditioning to flavor A had no effect on the ability of conditioning trials with AB to establish a preference for B; that is, in contrast with the results obtained for sucrose in Experiment 1, blocking was not found with fructose or maltodextrin as the reinforcer. The wider implications of these results will be taken up in the General Discussion, but we should note here that the discrepancy between our results with maltodextrin and those of Dwyer et al. (2011) is not to be explained in terms of training schedule (intermixed vs. two-phase) that is used. It must lie in some other procedural difference (for example in the nature of the flavors used as the stimuli – Dwyer et al. used flavors that are nonpreferred by rats, whereas ours are accepted readily), or even in the exact composition of the maltodextrin used (there can be differences in the proportion of mono- and disaccharides they contain). These are possibilities that need further experimental work. Our present results show, in summary, that under conditions that produce blocking of a preference based on flavor–nutrient and flavor–taste learning (sucrose), a conditioned flavor preference based either on flavor–nutrient (maltodextrin) or flavor–taste (fructose) does not show blocking.

Given that blocking is an exceedingly robust phenomenon, demonstrated for a wide range of conditioning procedures, its absence in this case may seem surprising. There are however, a number of instances of failures to obtain blocking from studies using stimuli similar to those used here. The result reported by Capaldi and Hunter (1994) has already been mentioned; and a number of studies of aversion learning (Batsell & Batson, 1999; Batsell, Paschall, Gleason, & Batson, 2001) have demonstrated that pretraining with a taste or an odor can actually augment learning about the other cue when both are subsequently trained as a simultaneous compound. Explanations for these effects have focused on the possible role of within-compound (i.e., odor–taste) associations, or on the possibility that odor and taste together might be perceived as a unique configural cue, rather than as two separate elements. Thus, for example, Capaldi and Hunter (1994) have suggested that taste and

odor together will form a configural cue that is more similar to the odor alone than to the taste. Pretraining with the taste will have no relevance for subsequent training with the compound, and since there will be good generalization from the compound to the odor, responding to the odor alone on test will not show evidence of blocking. Whether an analysis of this sort could be developed for the stimuli used in our experiments (two, rather similar, odors, presented in a fully counterbalanced design) may be doubted. And more critically, this sort of analysis cannot accommodate the fact that blocking was found in Experiment 1, which used just the same stimuli as those used in the present experiment. If interaction between the two odors is responsible for the absence of blocking in this experiment then the same interaction should have precluded the occurrence of blocking in Experiment 1. We conclude that our stimuli are quite appropriate for generating the blocking effect, and that its presence or absence is determined by the nature of the substance used as the reinforcer.

General discussion

The experiments reported in this paper were designed to analyze the conditions under which the cue-competition effect of blocking may be found in flavor-preference conditioning. Replicating previous findings (e.g., Balleine et al., 2005), Experiment 1 showed that a flavor established as a cue for the availability of sucrose was able to block conditioning of a second flavor when this was subsequently reinforced in compound with the first. A preference supported by conditioning with sucrose can be the product of both flavor-taste and flavor-nutrient learning. Experiments 2 and 3 were intended to determine if both these forms of learning were susceptible of blocking. To achieve this, maltodextrin and fructose were used as reinforcers, under the assumption that the first will produce flavor-nutrient (but not flavor-taste) learning, and the second flavor-taste (but not flavor-nutrient learning). In neither case, however, was blocking found, in spite of the fact that conditioning to the first flavor was well established during the first stage of training. Note that the absence of blocking means that a conditioned preference was readily established for the added flavor; that is, our “null result” is in fact the presence of a preference. And because clear evidence of blocking was obtained in Experiment 1, the failure to find the effect in Experiments 2 and 3 cannot be attributed to a lack of sensitivity in our general training and testing procedures. Taking together these data suggest that blocking can be easily obtained with sucrose but not with either fructose or maltodextrin, at least at the concentrations and under the conditions used in this study.

As a sucrose-based preference shows blocking, one would expect that at least one of the components assumed to be responsible for this preference (i.e., either flavor-taste or flavor-nutrient learning) would show the effect. One possibility to consider is that both of these forms of learning might show blocking to some small extent, but that the effect can only be detected when the reinforcer is one that allows both effects to exert an influence on test performance. But there is nothing in our results to support this suggestion – that is, we found no evidence for even a small degree of blocking in Experiments 2 and 3. As Figs. 2 and 3 show, conditioning with maltodextrin and with fructose produced a preference for B in the blocking groups that was as strong as that seen in the control groups.

Another, related, possibility is suggested by the fact that initial conditioning to the pretrained flavor A was as effective with maltodextrin and with fructose in Experiments 2 and 3 as it was with sucrose in Experiment 1. This suggests that the chosen concentrations of fructose and of maltodextrin that were used in Experiments 2 and 3 made them particularly effective reinforcers, each being able to generate a preference as great as that produced by the combined effects of flavor-taste and flavor-nutrient learning responsible for the preference seen with sucrose. The implication is

that both of the associations assumed to be formed with sucrose as the reinforcer were relatively weak, compared with those established by fructose and maltodextrin. But although this complicates the direct comparison of sucrose with the other reinforcers, it does not supply any obvious explanation for the differing blocking effects – provided the magnitude of the reinforcer is not changed between phases (see, e.g., Dickinson, Hall, & Mackintosh, 1976), blocking is found as readily with a strong as with a weak reinforcer.

From one point of view, however, the absence of blocking with fructose as the reinforcer is not unexpected. Blocking is a core phenomenon of predictive associative learning in which learning about a cue fails to occur when an outcome is already predicted by another cue. But, as we discussed in the Introduction, flavor-taste learning may not be associative in this sense; that is, the preference for the flavor may be acquired by another mechanism – by a change in the hedonic value of the flavor rather than by its acquiring the ability to act as a signal for a consequence. In this case blocking would be expected only for a preference based on the ability of the flavor to signal upcoming (nutritive effects) and would this occur with sucrose, but not with fructose. From this perspective it is only the absence of blocking with maltodextrin that remains problematic. This matter will not be resolved until further work has clarified the source of the discrepancy between our findings and those of Dwyer et al. (2011). We may add, however, that our results might be taken to challenge the assumption that maltodextrin (which after all has a distinctive flavor and is palatable to rats, see, e.g., Dwyer, 2008; Nissenbaum & Sclafani, 1987; Ramirez, 1994a) generates a preference solely or principally by way of its nutritive properties.

We began by asking whether the blocking procedure might be effective as a means of limiting unwanted learning about food-related cues; our conclusion must be that its scope is limited. Blocking does occur in some circumstances (as with sucrose) but in others it is quite absent. The hypothesis that it might be found reliably when the reinforcer is the nutritive consequence of a food is undermined by our studies with maltodextrin. And the failure to find blocking with fructose fits in well the results of other procedures investigating the properties of flavor-taste learning. None of the learning phenomena (e.g., extinction, latent inhibition, blocking), which limit the conditioned responding controlled by a cue in standard associative learning, seems to be reliably active in flavor-sweetness learning. This may explain why “hedonic” eating is so powerful and persistent. The advice is straightforward: to reduce the effects of flavor-taste learning it is necessary to eliminate the opportunity for experiencing the critical events together. Little that is done before, during, or after a flavor-taste pairing seems capable of reducing a conditioned preference.

References

- Albertella, L., & Boakes, R. A. (2006). Persistence of conditioned flavor preferences is not due to inadvertent food reinforcement. *Journal of Experimental Psychology: Animal Behavior Processes*, *32*, 386–395.
- Anderson, G. H. (1997). Sugars and health. A review. *Nutrition Research*, *17*, 1485–1498.
- Baeyens, F., Crombez, G., Van den Bergh, O., & Eelen, P. (1988). Once in contact, always in contact. Evaluative conditioning is resistant to extinction. *Advances in Behaviour Research and Therapy*, *10*, 179–199.
- Balleine, B. W., Espinet, A., & González, F. (2005). Perceptual learning enhances retrospective reevaluation of conditioned flavor preferences in rats. *Journal of Experimental Psychology: Animal Behavior Processes*, *31*, 341–350.
- Batsell, W. R., & Batson, J. D. (1999). Augmentation of taste conditioning by a preconditioned odor. *Journal of Experimental Psychology: Animal Behavior Processes*, *25*, 374–388.
- Batsell, W. R., Paschall, G. Y., Gleason, D. I., & Batson, J. D. (2001). Taste preconditioning augments odor-aversion learning. *Journal of Experimental Psychology: Animal Behavior Processes*, *27*, 30–47.
- Boakes, R. A. (2005). Persistence of acquired changes in the properties of odors and flavors for both humans and rats. *Chemical Senses*, *30*(Suppl. 1), i238–i239.
- Bouton, M. E. (2011). Learning and the persistence of appetite. Extinction and the motivation to eat and overeat. *Appetite*, *103*, 51–58.
- Capaldi, E. D. (1996). Conditioned food preferences. In E. D. Capaldi (Ed.), *Why we eat what we eat* (pp. 53–82). Washington, DC: American Psychological Association.

- Capaldi, E. D., & Hunter, M. J. (1994). Taste and odor in conditioned flavor preference learning. *Animal Learning & Behavior*, *22*, 355–365.
- Capaldi, E. D., Myers, D. E., Campbell, D. H., & Sheffer, J. D. (1983). Conditioned flavor preferences based on hunger level during original flavor exposure. *Animal Learning & Behavior*, *11*, 107–115.
- Cohen, D. A., & Babey, S. H. (2012). Contextual influences on eating behaviours. Heuristic processing and dietary choices. *Obesity Reviews*, *13*, 766–779.
- De la Casa, L. G., Márquez, R., & Lubow, R. E. (2009). Super-latent inhibition of conditioned taste preference with a long retention interval. *Learning and Motivation*, *40*, 329–342.
- Delamater, A. R. (2007). Extinction of conditioned flavor preferences. *Journal of Experimental Psychology. Animal Behavior Processes*, *33*, 160–171.
- Delamater, A. R. (2011). Partial reinforcement and latent inhibition effects on stimulus-outcomes associations in flavor preference conditioning. *Learning & Behavior*, *39*, 259–270.
- Dickinson, A., & Brown, K. J. (2007). Flavor-evaluative conditioning is unaffected by contingency knowledge during training with color-flavor compounds. *Animal Learning & Behavior*, *35*, 36–42.
- Dickinson, A., Hall, G., & Mackintosh, N. J. (1976). Surprise and the attenuation of blocking. *Journal of Experimental Psychology. Animal Behavior Processes*, *2*, 313–322.
- Drucker, D. B., Ackroff, K., & Sclafani, A. (1994). Nutrient-conditioned flavor preference and acceptance in rats. Effects of deprivation state and nonreinforcement. *Physiology & Behavior*, *56*, 701–707.
- Dwyer, D. M. (2008). Microstructural analysis of conditioned and unconditioned response to maltodextrin. *Learning & Behavior*, *36*, 149–158.
- Dwyer, D. M. (2009). The effects of midazolam on the acquisition and expression of fructose- and maltodextrin-based flavor preferences. *Pharmacology, Biochemistry and Behavior*, *91*, 503–510.
- Dwyer, D. M., Haselgrove, M., & Jones, P. M. (2011). Cue interactions in flavor preference learning. A configural analysis. *Journal of Experimental Psychology. Animal Behavior Processes*, *37*, 41–57.
- Dwyer, D. M., & Quirk, R. H. (2008). Context conditional flavor preferences in the rat based on fructose and maltodextrin reinforcers. *Journal of Experimental Psychology. Animal Behavior Processes*, *34*, 294–302.
- Elizalde, G., & Sclafani, A. (1988). Starch-based conditioned flavor preferences in rats. Influence of taste, calories and CS-US delay. *Appetite*, *11*, 179–200.
- Fedorchak, P. M. (1997). The nature and strength of caloric conditioning. In M. E. Bouton & M. S. Fanselow (Eds.), *Learning, motivation and cognition. The functional behaviorism of Rober C. Bolles* (pp. 255–269). Washington, DC: American Psychological Association.
- García-Burgos, D., González, F., & Hall, G. (2013). Motivational control of latent inhibition in flavor preference conditioning. *Behavioural Processes*, *98*, 9–17.
- Gibson, E. L., & Brunstrom, J. M. (2007). Learned influences on appetite, food choice and intake. Evidence in human beings. In T. C. Kirkham & S. J. Cooper (Eds.), *Appetite and body weight. Integrative systems and the development of anti-obesity drugs* (pp. 271–300). Billington, MA: Academic Press.
- González, F., García-Burgos, D., & Hall, G. (2012). Associative and occasion-setting properties of contextual cues in flavor-nutrient learning in rats. *Appetite*, *59*, 898–904.
- Harris, J. A., Shand, F. L., Carroll, L. Q., & Westbrook, R. F. (2004). Persistence of preference for a flavor presented in simultaneous compound with sucrose. *Journal of Experimental Psychology. Animal Behavior Processes*, *30*, 177–189.
- Holder, M. D. (1991). Conditioned preferences for the taste and odor components of flavors. Blocking but not overshadowing. *Appetite*, *17*, 29–45.
- Jansen, A. (1998). A learning model of binge eating. Cue reactivity and cue exposure. *Behaviour Research and Therapy*, *36*, 257–272.
- Jansen, A. (2010). Obesity needs experimental psychology. *The European Health Psychologist*, *12*, 48–51.
- Jenkins, D. J. A., Wolever, T. M. S., Taylor, R. H., Barker, H., Fielden, H., Baldwin, J. M., et al. (1981). Glycemic index of foods. A physiological basis for carbohydrate exchange. *The American Journal of Clinical Nutrition*, *34*, 362–366.
- Kamin, L. J. (1969). Predictability, surprise, attention and conditioning. In B. A. Campbell & R. M. Church (Eds.), *Punishment and aversive behavior* (pp. 279–296). New York: Appleton-Century-Crofts.
- Livesey, G., & Tagami, H. (2009). Interventions to lower the glycemic response to carbohydrate food with a low-viscosity fiber (resistant maltodextrin). Meta-analysis of randomized controlled trials. *The American Journal of Clinical Nutrition*, *89*, 114–125.
- Lubow, R. E. (1989). *Latent inhibition and conditioned attention theory*. New York: Cambridge University Press.
- Malik, V. S., Schulze, M. B., & Hu, F. B. (2006). Intake of sugar-sweetened beverages and weight gain. A systematic review. *The American Journal of Clinical Nutrition*, *84*, 274–288.
- Nissenbaum, J. W., & Sclafani, A. (1987). Qualitative differences in polysaccharide and sugar tastes in the rat. A two-carbohydrate taste model. *Neuroscience & Biobehavioral Reviews*, *11*, 187–196.
- Papachristou, H., Nederkoorn, C., Beunen, S., & Jansen, A. (2013). Dissection of appetitive conditioning. Does impulsivity play a role? *Appetite*, *69*, 46–53.
- Ramirez, I. (1994a). Glucose polymer taste is not unitary for rats. *Physiology & Behavior*, *55*, 355–360.
- Ramirez, I. (1994b). Sucrose and fructose have qualitatively different flavors to rats. *Physiology & Behavior*, *56*, 549–557.
- Reppucci, C. J., & Petrovich, G. D. (2012). Learned food-cue stimulates persistent feeding in sated rats. *Appetite*, *59*, 437–447.
- Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning. Variations in the effectiveness of reinforcement and nonreinforcement. In A. H. Black & W. F. Prokasy (Eds.), *Classical conditioning II. Current research and theory* (pp. 64–99). New York: Appleton-Century-Crofts.
- Sclafani, A. (1991). Conditioned food preferences. *Bulletin of the Psychonomic Society*, *29*, 256–260.
- Sclafani, A., & Ackroff, K. (1994). Glucose and fructose c-conditioned flavor preferences in rats. Taste versus postingestive conditioning. *Physiology & Behavior*, *56*, 399–405.
- Stevenson, R. L., Boakes, R. A., & Wilson, J. P. (2000). Resistance to extinction of conditioned odor perceptions. Evaluative conditioning is not unique. *Journal of Experimental Psychology. Animal Behavior Processes*, *26*, 423–440.
- Tappy, L., & Lê, K. (2010). Metabolic effects of fructose and the worldwide increase in obesity. *Physiological Review*, *90*, 23–46.
- Todd, T. P., Winterbauer, N. E., & Bouton, M. E. (2012). Contextual control of appetite. Renewal of inhibited food-seeking behavior in sated rats after extinction. *Appetite*, *58*, 484–489.
- Urcelay, G. P. (2012). Exposure techniques. The role of extinction learning. In P. Neudeck & H.-U. Wittchen (Eds.), *Exposure therapy. Rethinking the model. Refining the method* (pp. 35–63). New York: Springer.
- Van den Akker, K., Jansen, A., Frenzt, F., & Havermans, R. C. (2013). Impulsivity makes more susceptible overeating after contextual appetite conditioning. *Appetite*, *70*, 73–80.
- Van Gucht, D., Baeyens, F., Hermans, D., & Beckers, T. (2013). The inertia of conditioned craving. Does context modulate the effect of counterconditioning? *Appetite*, *65*, 51–57.
- Van Gucht, D., Baeyens, F., Vansteenwegen, D., Hermans, D., & Beckers, T. (2010). Counterconditioning reduces cue-induced craving and actual cue-elicited consumption. *Emotion*, *20*, 688–695.
- Van Gucht, D., Vansteenwegen, D., Beckers, T., & Van den Bergh, O. (2008). Return to experimentally induced chocolate craving after extinction in a different context. Divergence between craving for and expecting to eat chocolate. *Behaviour Research and Therapy*, *46*, 375–391.
- Van Gucht, D., Vansteenwegen, D., Van den Bergh, O., & Beckers, T. (2008). Conditioned craving cues elicit an automatic approach tendency. *Behaviour Research and Therapy*, *46*, 1160–1169.
- Ventura, A. K., & Mennella, J. A. (2011). Innate and learned preferences for sweet taste during childhood. *Current Opinion in Clinical and Metabolic Care*, *14*, 379–384.
- Yeomans, M. R. (2010). Understanding individual differences in acquired flavor liking in humans. *Chemosensory Perception*, *3*, 34–41.
- Yeomans, M. R., Leitch, M., Gould, N. J., & Mobini, S. (2008). Differential hedonic, sensory and behavioral changes associated with flavor-nutrient and flavor-flavor learning. *Physiology & Behavior*, *93*, 798–806.