Research report

Associative and occasion-setting properties of contextual cues in flavor–nutrient learning in rats ☆

Felisa González [a,*], David Garcia-Burgos [a], Geoffrey Hall [b,c]

[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, United Kingdom
[c] School of Psychology, University of New South Wales, Sydney, NSW 2052, Australia

ABSTRACT

This article studied the role of contextual cues, present at the time flavor conditioning occurs, on intake behavior in rats. In three experiments animals were given flavor–sucrose pairings in one distinctive context (Context A) whereas the flavor was presented unreinforced in an alternative context (Context B). Experiments 1 and 2 used a simple Pavlovian discrimination procedure (A: X+, B: X−) and tested consumption of flavor X in each context. Consumption of the flavor was higher in Context A than in Context B. In Experiment 2 rats were given a treatment (exposure to water in the context) designed to extinguish associations between the context and the reinforcer. This procedure did not affect the ability of the context to control intake of flavor X. Experiment 3 used a biconditional discrimination procedure (A: X+, Y−; B: X−, Y+; where X and Y were different flavors) in which no single context or flavor predicted reinforcement. The rats learned this discrimination, consuming more of each flavor in the context in which it had previously been reinforced. The results are interpreted in terms both of the effects of direct associations between context and events presented in them, and in terms of the modulatory or occasion-setting properties of the context.

© 2012 Elsevier Ltd. All rights reserved.

Introduction

Eating behavior is, in part, the consequence of learned responses to food cues. Consumption of a given substance depends on its look, smell, and, importantly, on its flavor (an emergent property based on taste, oral somatosensory, and retronasal olfactory cues; see Stevenson, 2009). Flavor cues are susceptible to the effects of conditioning, can form associations with the reinforcing properties of foods, and thus influence intake when the flavor is encountered subsequently. It is well established that pairing a neutral flavor with a food substance such as sucrose will increase subsequent acceptance of that flavor (i.e., willingness to consume it), and produce a preference for it in a choice test (see, e.g., Capaldi, Campbell, Sheffer, & Bradford, 1987; Fedorchak & Bolles, 1987; Harris, Gorrissen, Bailey, & Westbrook, 2000; Mehiel & Bolles, 1984). Although the reinforcing power of the sucrose in this procedure appears to derive both from its palatable taste and also from

its nutritive post-ingestive consequences, we will refer to the phenomenon simply as flavor–nutrient learning.

Conditioning is not confined to the cues provided by discrete cues, such as flavors, directly associated with food. Contextual cues (by which is meant the set of varied properties, e.g., spatial, olfactory, auditory, identifying a particular place) that are present when food is consumed may also enter into associations, and serve not only to locate and identify food (e.g., Maes & Vossen, 1993; Shishimi & Nakajima, 2007), but also to determine food preference and intake. For instance, it has been shown that contexts can serve as conditioned cues that potentiate eating in rats, and this cue-enhanced eating can be relatively specific to the food used during training (Petrovich, Ross, Gallagher, & Holland, 2007; but see Boggiano, Dorsey, Thomas, and Murdaugh (2009) for evidence of a generic increase in food consumption). Again, Albertella, Harris, and Boakes (2008) have shown that, during conditioning of flavor preferences, the training context may acquire value as a signal for food and affect the expression of the preference. In general, learning processes may play an important role in determining how contexts affect food intake and contextual influences should be considered as environmental risk factors for obesity and for poor dietary habits (see, e.g., Jansen, 2010) from which individuals may need the kind of protection that falls under the mission of public health (e.g., Cohen & Babey, 2012).

The mechanisms by which contextual learning might come to influence food intake remain to be determined. One possibility is to attribute it to the formation of simple associations between the context and the (palatable) food, in the manner described by Petrovich et al. (2007) and Boggiano et al. (2009). Another possibility is that the context acts not as a simple conditioned stimulus (CS), but as an occasion setter (e.g., Holland, 1992); that is, the context in which food is consumed might come, independently of its own direct association with the food unconditioned stimulus (US), to signal that a particular flavor CS, which is otherwise without consequence, will be followed or accompanied by the US. It should be noted that these possibilities (i.e., direct association and conditional control) are not mutually exclusive alternatives. It has been shown that a discrete stimulus can serve both as a CS and as an occasion setter at the same time (e.g., Holland, 1992; Urcelay & Miller, 2010), and it has been argued (Bouton, 2010) that the same will apply for contextual cues.

Previous work investigating these issues has provided evidence that the context can acquire an occasion-setting function in flavor–nutrient learning, at least under some circumstances of training. Occasion setting was demonstrated by Dwyer and Quirk (2008), who used a biconditional discrimination design involving two flavors and two contexts. During training flavor X was paired with a US (e.g., fructose or maltodextrin) in context A, whereas flavor Y was not; in context B, Y was paired with the US and X was not. The rats successfully learned the discrimination, showing context-dependent preferences on test (i.e., preferring X over Y in A, and Y over X in B). As the design ensured that the direct association with the US would be the same for both contexts, this outcome may be attributed to the acquisition of occasion-setting powers by the contexts. Campbell, Capaldi, Sheffer, and Bradford (1988) used a similar biconditional design, but a procedure in which the presence of a given flavor signaled what consequence would follow. Thus in context A, X signaled that sucrose would shortly become available whereas Y signaled that quinine would be available; the assignments were reversed in context B. Campbell et al. recorded the latency to approach the bottle containing the consequence, taking a short latency to indicate expectancy of a positive outcome (sucrose). This behavior exhibited conditional control with the rats showing short latencies after presentation of flavor X in context A, but after flavor Y in context B. Interestingly, however, conditioned preference, as assessed by a two-bottle choice test between flavors X and Y, did not show a context-specific effect.

Consuming food in a particular place may provide the opportunity for different types of learning to occur: flavor–nutrient learning, context conditioning, and contextual occasion setting. The experiments to be reported here investigate the relation among these forms of learning. There is little evidence directly addressing the question of whether the association of a context with a nutrient—paired itself with a flavor—will make that context capable of influencing preference for (or degree of acceptance of) the flavor. Thus, in the first experiment to be reported here, we sought to demonstrate that a context in which flavor–sucrose conditioning has occurred can acquire the power to enhance consumption of the flavor when presented subsequently unreinforced. We made use of a discrimination procedure in which rats were allowed to drink a compound solution made of flavor X and sucrose (X+) in one context (context A) whereas the solution was presented unreinforced (X−) in another context (context B). When this discrimination had been acquired we tested consumption of flavor X in both contexts and demonstrated, to anticipate, that it was greater in context A than in context B. In Experiment 2 we used an extinction manipulation to investigate the extent to which this effect was determined by direct associations (excitatory for context A and inhibitory for context B) between contextual cues and the US used in training. The possibility that occasion-setting may also contribute to the effects seen with

the contexts, flavors, and motivational conditions used in the present experiments was tested in Experiment 3, which employed the biconditional discrimination procedure.

Experiment 1

In Experiment 1 rats received flavor–sucrose pairings in context A (A: X+) whereas the flavor was presented unreinforced in context B (B: X−). The contexts differed in their visual, auditory, and tactile properties. Because flavor preferences based on a nutrient appear to be enhanced by food deprivation (Fedorchak & Bolles, 1987; see also Balleine, Espinet, & González, 2005; Harris et al., 2000; Yiin, Ackroff, & Sclafani, 2005), food was removed from the home cages before the test sessions. Afterwards, rats had the opportunity of consuming flavor X (unreinforced) in each of the two contexts to test for contextual control over consumption of the trained flavor.

Methods

Subjects

The subjects were 16 experimentally naive male Wistar rats with a mean weight of 283 g at the start of the experiment (range 269–293 g). They were housed in individual home cages and kept in a large colony room located in the laboratory of the University of Granada under a 12-h light/12-h dark schedule (lights coming on at 0800 h). The rats were water deprived, as detailed below, but had continuous access to food throughout the experiment, with the exceptions mentioned below. The home cages measured 50 cm long × 26 cm wide × 14.5 cm high; the walls and floors were made of translucent plastic, and the roof of wire mesh that held food and a water bottle (when available); a layer of wood shavings covered the floor. Training sessions took place twice a day at approximately 0900 h and 1500 h.

Apparatus

Two sets of cages, each distinct from the home cage, served as the experimental contexts. The first set of cages (Type 1) was located in a separate room dimly lit by a single 40-W red bulb positioned in a corner close to the cages. This room contained a speaker supplying constant background white noise with an intensity of 70–75 dB measured close to the cages. The cage walls and floor were made of opaque grey plastic and the roofs were made of wire mesh, containing a hole through which a drinking spout could be inserted. The cages were 32 cm long × 22 cm wide × 12 cm high. The floor was covered with commercially obtained cat litter. The cages in the second set (Type 2) were 20.5 cm long × 20.5 cm wide × 23 cm high, and were located in a separate brightly lit room. The floors and walls of these cages were made of white wood, and the wire mesh roofs included a section through which a drinking spout could be inserted. The floor was covered with a clean piece of white paper.

Fluids using during training and tests were administered in an inverted 50-ml plastic tube with a rubber stopper fitted with a stainless steel ball-bearing tipped spout. Fresh solutions were made daily with tap water and administered at room temperature. Consumption was measured by weighing the tubes before and after fluid presentation to the nearest 0.1 g. The US was a 10% (w/v) sucrose solution. The target flavor X was a 2% (v/v) almond solution (SuperCook, Leeds, UK).

Procedure

Water bottles were removed from the home cages 24 h before the start of the experiment. Rats were given 3 days to accommodate to water deprivation, with access to water restricted to two periods of 30 min (morning and afternoon sessions). The next

4 days constituted the training phase of the experiment. Twice a day, in the morning and in the afternoon, rats were moved from the home cages to the appropriate context where they spent 30 min. In one of the sessions they were offered 10 ml of the reinforced flavored solution (a simultaneous compound of almond and sucrose) in context A, whereas in the alternative session they drank 10 ml of the unreinforced almond solution in context B. For half of the animals, context A consisted of Type 1 cages and context B of Type 2 cages, whereas for the rest of the animals this assignment was reversed. The reinforced solution was presented in context A during the morning sessions on the Days 2 and 3 of training, and during the afternoon sessions on Days 1 and 4. After the last session of training, in the afternoon of the fourth day, food was removed from the home cages. During the rest of the experiment rats were given access to food and water in the home cage for 90 min following the morning session, and to an additional 30-min access to water in the afternoon. Before starting the test phase, rats spent 3 days in the home cages to get used to the new regime of feeding. After this period consumption of flavor X in each context was evaluated during the morning sessions of two consecutive days. Subjects had free access to flavor X for 30 min, half of the animals were tested in context A on the first day and in context B on the second; for the other half this order was reversed.

All the experimental procedures were approved by the University of Granada Ethics Committee, and were in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC).

Results and discussion

During training the rats consumed flavor X readily, although intake of the compound containing sucrose was higher than of X alone. Mean consumption over all trials with each was 8.8 ml for the reinforced X and 7.9 ml for the unreinforced flavor. This difference was statistically reliable, $t(15) = 4.02$ (the rejection level adopted for this and for subsequent analyses was $p < .05$).

Figure 1 shows the mean consumption of the conditioned flavor (X) in each context on test. Consumption of the flavor was greater in the trained context, A, than in context B, $t(15) = 7.18$. This result shows that the rats can discriminate between the contexts, consuming flavor X according to the training reinforcement schedule that had been in force in the context. It does not, however, allow us to identify the mechanism responsible. One possibility is that direct associations (between context A and the US, context B and the absence of the US) operate to modulate the consumption of
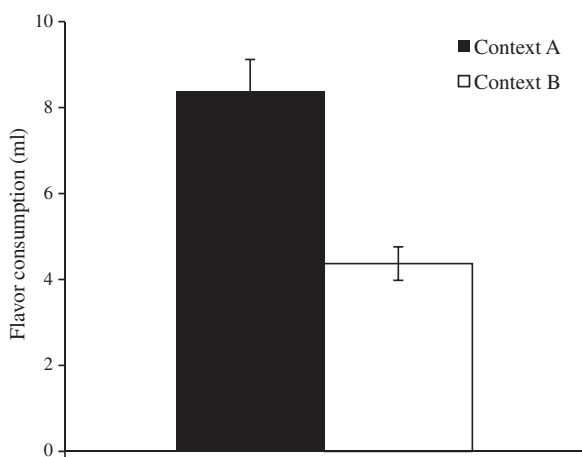

Fig. 1. Experiment 1: Mean flavor X consumptions (±SEM) on tests in Context A and B. During training flavor X was reinforced in Context A and unreinforced in Context B.

fluids presented in the contexts. Occasion-setting effects, by contrast, are usually assumed to be independent of the direct associations with the US. Thus, further experimental analysis is required to determine the mechanism responsible for the results obtained in this experiment. Experiment 2 was designed to allow assessment of the role of direct associations.

Experiment 2

In this experiment rats were trained on the discrimination used in Experiment 1 but, prior to the test phase, they received a treatment designed to allow extinction of excitatory associations governed by the contexts. Specifically, the subjects in the extinction (Ext) group received a series of exposures to the contexts in which water was made available, but no flavor or sucrose was presented. If the control of flavor consumption by context in Experiment 1 was due to the excitatory properties of context A, such control should be abolished or attenuated by extinction. On the other hand, if contextual control depends on an occasion-setting mechanism, this should not be influenced by the extinction manipulation, as the occasion-setting function of a cue has been shown to be independent of its direct associations with other events (e.g., Holland, 1983, 1989; Rescorla, 1986). It should also be acknowledged that the control by context seen in Experiment 1 could, in principle, reflect the acquisition of inhibitory properties by context B. Since inhibition, like occasion setting, appears to be immune to the effects of a simple extinction procedure (Zimmer-Hart & Rescorla, 1974), this mechanism too can predict that the discrimination might be maintained in group Ext.

Method

Subjects

The subjects were 32 experimentally naive male Wistar rats with a mean weight of 326 g at the start of the experiment (range 270–406 g). They were obtained, housed, and maintained as in the previous experiment, apart from the exceptions mentioned below.

Apparatus

The contexts and flavor were the same as in the previous experiment.

Procedure

After the schedule of water deprivation had been established all subjects received discrimination training in which flavor X was paired with sucrose in context A, and presented alone in context B, as in Experiment 1. They were then divided into two equal-sized groups matched in average body weight and flavor consumption. Over the next 6 days, Group Ext continued to receive two 30-min sessions each day, one in context A and one in context B. Water was available during these sessions. The context sequence during the morning sessions was ABABBA; the alternative context was presented in the afternoon sessions (i.e., BABAAB). Animals in the other group (Group NonExt) remained in their home cages during this phase, receiving water at the same times. After the last afternoon trial of this phase food was removed from the home cages of all subjects. After 3 days to allow the rats to become accustomed to the feeding schedule, tests for consumption of flavor X was given in both contexts. Any details not specified here were the same as those described for Experiment 1.

Results and discussion

As in Experiment 1, the rats consumed flavor X readily during the discrimination training phase, especially when it was mixed

with sucrose. Group means for consumption over all trials of this phase were 9.0 ml for the reinforced solution and 7.5 ml for X alone. These scores differed reliably, $t(31) = 6.67$.

Water consumption during the extinction phase was assessed in the hope of detecting differences that would reveal changes in the associative properties of the contexts under the assumption that excitatory and inhibitory food cues might increase and decrease intake behavior, respectively. Consumption was generally low in the afternoon sessions of the extinction phase. Accordingly, only consumption during the morning sessions for Ext group (Context A: Sessions 1, 3, and 6; Context B: Sessions 2, 4, and 5) was analyzed, comparison being made with the amounts consumed at the equivalent times by the NonExt group that remained in the home cage. The results are summarized in Fig. 2. They show that consumption was lower in context B than in the home cage; an analysis of variance comparing these conditions yielded $F(1, 30) = 10.68$. This result is consistent with the context having inhibitory properties. It should be noted, however that consumption was also generally lower in context A than in the home cage, $F(1, 30) = 8.49$, allowing the simple explanation that rats are more likely to drink at home than in a less familiar context.

Potentially more interesting is the fact that consumption of water by the Ext group in context A declined over trials, whereas consumption by the NonExt group appeared to be more stable. This impression was confirmed by an ANOVA comparing the groups over days which yielded a significant Group × Day interaction, $F(2, 60) = 4.80$. Further repeated-measure ANOVAs conducted for each group showed that consumption changed over days in group Ext, $F(2, 30) = 5.35$, and post hoc Tukey's test revealed a difference between the first and the last extinction days, but that consumption did not change over days in group NonExt, $F(2, 30) = 1.52$. This result is consistent with the idea of a progressive reduction in con-
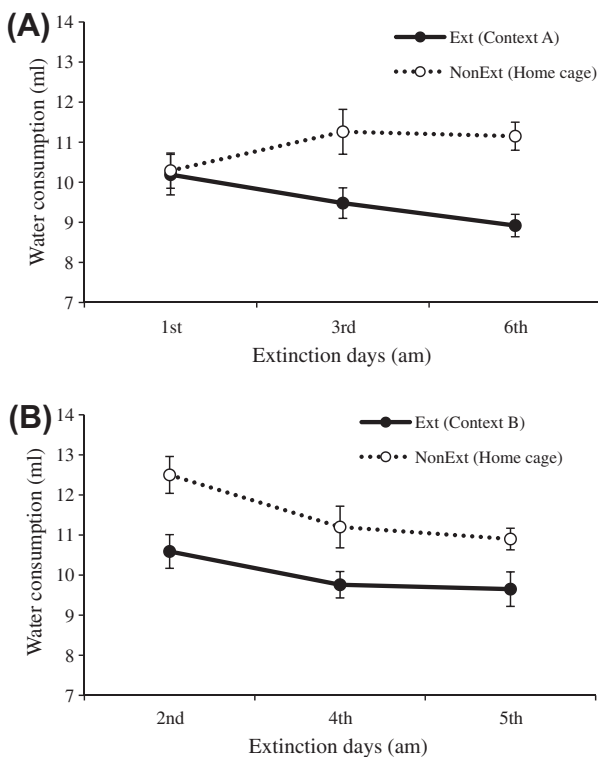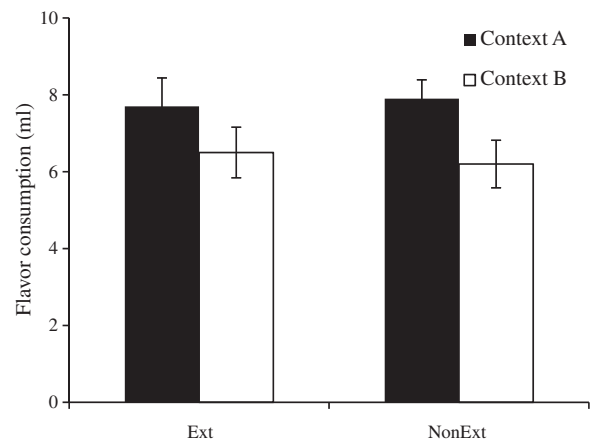
Fig. 3. Experiment 2: Mean flavor X consumptions (±SEM) on tests in Context A and B collapsed across groups Ext and NonExt. During training flavor X was reinforced in Context A and unreinforced in Context B.

sumption produced by experience of the absence of the nutrient in context A. That consumption by the Ext group in context B remained relatively stable, and consistently lower than that shown by the NonExt group, is to be expected if the properties of this context derived from an inhibitory relation with the US established during the training phase.

Figure 3 shows the results of the final test with flavor X in each of the contexts for each group. The critical finding was that consumption of the flavor was greater in the trained context, context A, than in context B, irrespective of the extinction treatment. Confirming this impression, a repeated-measures ANOVA conducted on the consumption of flavor X in each of the contexts revealed a main effect of Context, $F(1, 30) = 5.45$, but there was no significant effect of Group (Ext vs. NonExt) and no significant Group × Context interaction, $F_s < 1$.

The results of the extinction phase of this experiment follow from the suggestion that discriminative training (X+ trials in context A; X− trials in context B) endows those contexts with associative properties that allow then to control consumption of other substances. In particular water was consumed readily in context A at the start of the phase, but consumption then declined, consistent with the proposal that experience of the context, in absence of both the flavor and the nutrient, allowed extinction of the associations formed during training. In spite of this, the final test with the target flavor showed no difference between groups Ext and NonExt, both drinking more of the flavor in context A than in context B. If direct associations contribute to this effect (see Loy, Alvarez, Rey, & Lopez, 1993) then we must conclude that the inhibitory properties of B are sufficient to produce it. Alternatively, it may be that the control shown by the contexts depends on the acquisition of occasion-setting properties. To demonstrate these unambiguously requires a different experimental design.

Experiment 3

In this experiment two flavors rather than one were used in a biconditional discrimination procedure. Flavor X was reinforced in context A and nonreinforced in context B, whereas flavor Y was presented along with sucrose in context B but alone in context A (A: X+, Y−; B: X−, Y+). This training schedule ensured that no single flavor or context signaled the presence of absence of reinforcement. In order to solve the discrimination rats had to combine context and flavor information. As both contexts served as positive and negative features, no differential context conditioning was expected. After training, the rats were food deprived and given two-

Fig. 2. Experiment 2: Mean water consumption (±SEM) for group Ext and NonExt during the morning sessions (am) of the extinction phase. During the 1st, 3rd, and 6th days group Ext received water in Context A, whereas on days 2nd, 4th, and 5th rats drunk water in Context B. Animals in group NonExt had access to water in their home cages.
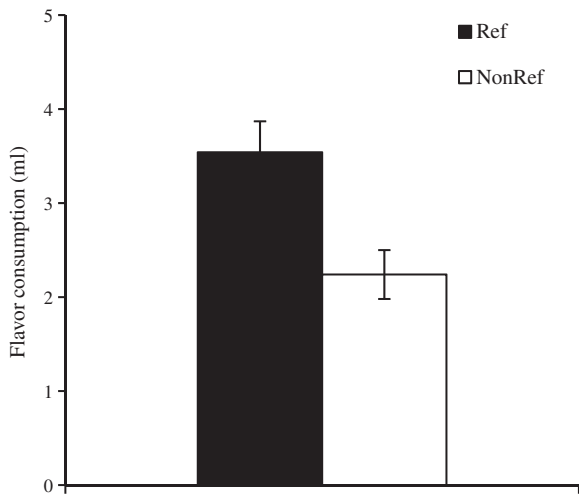
Fig. 4. Experiment 3: Mean reinforced (Ref) vs. unreinforced (NonRef) flavor consumption (±SEM) on tests collapsed across contexts. Animals were given a two-bottle choice test between flavor X (reinforced in Context A but unreinforced in Context B) and Y (reinforced in Context B but unreinforced in Context A) in each of the contexts.

bottle, X vs. Y, choice tests in each of the contexts, instead of the one-bottle test used in Experiments 1 and 2. The reason for this change was to enhance the sensitivity of the test, a choice procedure being able to detect even weak differences in preference for the two flavors by allowing direct comparison between them. If contexts A and B modulate flavor X–US and flavor Y–US associations respectively, it may be anticipated that animals will consume more of flavor X than of flavor Y in context A, and more of flavor Y than flavor X in context B. In summary, rats should show a higher consumption of the flavor that had previously been reinforced in each test context.

This pattern of results may be anticipated on the basis of the study by Dwyer and Quirk (2008), who also trained rats in flavor-preference biconditional discrimination with contexts as features and flavors as targets. There are a number of procedural differences, however, which may make that conclusion premature. The contexts used in the present series of experiments differed in their visual, auditory, and tactile (but not their olfactory) properties, whereas in the study by Dwyer and Quirk a different odor was added to each of the contexts; they used Kool-Aid flavored solutions that possessed both taste and odor components, and to which 0.1% saccharin was added, whereas we used plain odors as CSs without additional sweetener; also the critical effect obtained by Dwyer and Quirk (Experiment 3B) depended on having a dilute (2%) maltodextrin solution added to the CSs on test.

But perhaps the most relevant difference is that Dwyer and Quirk trained and tested their rats hungry, whereas in the experiment to be reported here (as in Experiments 1 and 2) the rats were deprived of food only for the test phase. There are reasons to think that conditional control might be difficult to establish under these training conditions. First, hunger during training might be expected to increase the salience of the nutrient and its incentive value, and thus potentiate learning. Specifically, it has been suggested that hunger cues can lower the threshold for activation of the postingestive (although not the orosensory) aspects of the US representation (Davidson, 1998). Therefore the absence of food deprivation during the biconditional discrimination phase in our experiment might lessen the likelihood of full activation of the postingestive US representation during training, making it harder to learn the biconditional discrimination. Second, it is has been argued that cues associated with food deprivation may form part of

the context in which the flavor–nutrient learning occurs. Changing these cues from training to the test might thus restrict the extent to which contextual control can be observed. It will be noted that contextual control was obtained in Experiments 1 and 2 in spite of the change of motivational condition from training to the test phase. But, as we have argued, the control observed in those experiments could be a consequence of direct associations between the contexts and events presented in them, involving a learning process that may be less sensitive to the effects of motivational change than the more complex discrimination required in the present experiment. It remains to be seen whether contextual control that requires some form of conditional learning can be generated under these training conditions.

Method

Subjects

Sixteen experimentally naive male hooded (Lister) rats with a mean weight of 469 g (range 410–535 g) at the start of the experiment, were housed in pairs and kept in a large colony room located in the laboratory of the University of York, with a 12-h light/12-h dark schedule (lights coming on at 0800 h); they were maintained in a similar way as the subjects in the previous experiments. In this experiment a different rat strain was used (hooded Lister instead of albino Wistar); but previous studies, both of conditioned taste aversion (e.g., De Brugada, Hall, & Symonds, 2004) and of flavor preference based on sucrose (e.g., Dwyer, Mackintosh, & Boakes, 1998), have also made use of these two different strains without finding any notable difference between them. It is true that absolute levels of fluid consumption may differ between strains, but the critical result in our experiments is within-subject difference (consumption by an individual rat across different contexts) so that strain differences in general levels of consumption should not prevent our making the relevant cross-experiment comparisons.

Apparatus

The home cages were made of opaque plastic and measured 35 cm long × 22 cm wide × 19 cm high. They had wire mesh roofs that held food and a water bottle (when available); a layer of wood shavings covered the floors. The first set of experimental cages (Type 1) was located in a separate small room dimly lit by a single 60-W red lamp and containing a speaker supplying constant background white noise with an intensity of 70–75 dB, measure close to the cages. The walls and floors of these cages were made of transparent plastic, and each cage measured 33 cm long × 20 cm wide × 19 cm high; the roofs were made of wire mesh, through which drinking spouts could be inserted. The floors were covered with commercially obtained cat litter. The cages in the second set (Type 2) were larger, each measuring 42 cm long × 35 cm wide × 16 cm high, and were located in a brightly lit colony room in a separate part of the laboratory. The floors and walls of these cages were made of translucent white plastic. For half of the animals context A consisted of Type 1 cages and context B of Type 2 cages, whereas for the rest of the animals this assignation was reversed. The US was a 10% (w/v) sucrose solution. Flavor X and Y were either almond or vanilla (SuperCook, Leeds, UK) solutions at 2% (v/v), counterbalanced.

Procedure

Before the start of the experiment, the rats were water deprived for 3 days during which they had access to water for 30 min twice a day in their home cages. Training occurred over the next 8 days. The procedure was similar to that described for the previous experiments, with the exception that two target flavors were used. In context A, animals received flavor X reinforced, and flavor Y

unreinforced (i.e., A: X+, Y−); in context B flavor X was nonreinforced whereas flavor Y was presented reinforced (i.e., B: X−, Y+). On each day the rats received two trials, one in the morning and one in the afternoon, one in context A and one in context B. The sequence of contexts during the morning sessions was AABABBAB (the alternative context sequence in the afternoon); the flavor sequence was XYYXXYYX. After training, food was removed from the home cages after the last afternoon session and, as in Experiments 1 and 2, the rats were given 3 days to become accustomed to the feeding schedule. On the next 2 days, two-bottle choice tests were conducted; for half of the animals the test in context A occurred on the first day, and the test in context B on the second; this sequence was reverse for the remaining animals. On each test trial the rats spent 30 min in the context, in which they were offered two drinking bottles containing 30 ml of each flavor, X and Y. The position of the tubes containing the particular flavors (i.e., left or right) were counterbalanced by group and day. At the start of the test, the bottle of the right was positioned in the appropriate hole until the animal started drinking, and was then removed. The same operation was repeated with the other tube in the alternative hole, and then both tubes were inserted, remaining in place for the rest of the test session.

Results and discussion

Group means for consumption of flavors X and Y on the reinforced trials during training were 8.7, and 9.1 ml; equivalent scores for the nonreinforced trials were 6.3, and 7.2 ml. An ANOVA with flavor and reinforcement as factors showed that subjects consumed more of flavor Y than of flavor X, $F(1,15) = 8.48$, probably due to a lesser degree of neophobia, as it was the second flavor introduced. Generally, animals consumed more of the reinforced (8.9 ml) than of the nonreinforced solution (6.7 ml), $F(1,15) = 47.44$. The interaction of Context × Flavor was not significant, $F < 1$.

As contexts, flavors, and order of testing were fully counterbalanced, data from the two test sessions were collapsed. Figure 4 presents the average consumption of the flavor that had been previously reinforced in the test context (Ref in the figure), and that of the alternative flavor (NonRef). It shows that the rats consumed more of the former than the latter, a difference that was statistically reliable $t(15) = 2.64$. This pattern of results cannot be explained in terms of direct associations between the contexts and the events presented in them during training. Both flavors and contexts were equally reinforced and unreinforced, and neither was a more valid cue for predicting reinforcement. However, the specific combination of context and flavor (i.e., flavor X in context A and flavor Y in context B) provided information about the occurrence of reinforcement, suggesting that contextual cues exerted conditional control on flavor consumption, acting as a modulator of the flavor–sucrose association.

These results are essentially the same as those of Dwyer and Quirk (2008).The change in motivational state between training and testing phases (from water deprivation to food and water deprivation) did not seem to impair performance; neither did the absence of food deprivation affect the capacity of the rats to learn the biconditional discrimination during the training phase. Perhaps the mild level of hunger produced by water deprivation (water-deprived rats restrict their intake of dry food) may have been enough to activate the postingestive US representation during training. An alternative hypothesis is that rats do not need to experience any level of hunger to learn about the postingestive consequences of the nutrient and discriminate among cues that signal when the flavor will be reinforced. For instance, it has been shown that food restriction specifically enhances the expression, but not the acquisition, of nutrient-based flavor preferences (Yiin et al., 2005).

General discussion

Flavors and the behavior they evoke do not occur in a vacuum; they always occur in a context, most obviously the physical location where food is eaten, but perhaps also including the people with whom it is eaten, the food-preparation rituals that precede eating, and so on. All of them can be paired with eating and support conditioning (Jansen, 2010; see also Todd, Winterbauer, & Bouton, 2012). The results of the present experiments demonstrate that the contextual cues present when a flavor is paired with a nutrient exert control over the readiness with which that flavor will be subsequently consumed by rats. Thus the readiness to consume food depends not simply on the intrinsic or acquired properties of the foodstuff itself; contexts or places in which foods are consumed can also exert control of appetite and food intake behavior. They can do so through more than one mechanism.

In all three experiments the rats drank more of the flavored solution on test when it was presented—unreinforced—in the context in which it had been previously paired with sucrose. Regarding Experiment 3, with a biconditional discrimination design (i.e., A: X+, Y−; B: X−; Y+) in which no individual flavor or context was unconditionally valid as a predictor of reinforcement, the effect seems best explained as an example of occasion setting. But, as with other more familiar examples of the phenomenon, the precise mechanism responsible for the occasion-setting effect is debatable. We have so far considered only a general hierarchical account in which the context is assumed to modulate the effectiveness of a flavor–US association. If this account is adopted it remains to specify the exact nature of the modulation; for instance, the context could operate by lowering the threshold of the US activation, by facilitating the flow of activation between the CS and the US, or by means of an association between the occasion setter with the entire target CS–US association (see Bonardi, Bartle, & Jennings, 2012, for a recent exposition of these issues). The notion of configural learning provides a quite different explanation of the occasion-setting phenomenon. According to this, a context and flavor, presented together, will activate a configural representation that will not be activated when either the flavor or the context is presented alone (or when the CS is presented in some other context). The suggestion that the AX configuration becomes associated with reinforcememt and the AY configuration with nonreinforcement (similarly for BY and BX) is equally capable of explaining the results of Experiment 3. Further research will be needed to determine which of these accounts is better suited to explaining conditional control of learned flavor preference; it should be acknowledged, however, that the occasion-setting phenomenon may be multiply determined (see, e.g., Brandon & Wagner, 1998).

Contextual control was also evident in Experiments 1 and 2, which used a simpler discrimination training procedure (A: X+, B: X−). In this case the cues constituting context A were uniquely predictive of reinforcement, and might be expected to form a strong association with it. The test results could thus be explained if we assume that the direct association between context A and the nutritive US tended to increase acceptance of familiar substances presented in that context. These data are also congruent with other studies in which learned contextual cues related to food consumption have been found to potentiate eating, both in animals (e.g., Boggiano et al., 2009; Petrovich et al., 2007), and in humans (e.g., Birch, McPhee, Sullivan, & Johnson, 1989). Experiment 2 provided some evidence of such an effect in that consumption of unflavored water was found to decline over the trials in context A, perhaps as a result of extinction of the association between the context and the US. The contribution of context–US excitatory association can only have played a minor role in producing the test result however, as even after context extinction consumption of the flavored solution during the test was found to be greater in context A than in

context B. This result can be explained both by assuming that context B acquires and maintains inhibitory properties (which should be immune to extinction), and also by the suggestion that the feature-positive training procedure used here has endowed the contexts with occasion-setting properties. These are not mutually exclusive alternatives. Although several studies have shown that a context may act as occasion-setter without evidence of context conditioning (e.g., Bouton & Swartzentruber, 1986; Puente, Cannon, Best, & Carrell, 1988), there are many occasion-setting experiments involving a feature-positive discrimination in which the feature elicits responses directly in addition to acquiring the ability to occasion-set responding to the target (Bouton, 2010).

In summary, the present results suggest that appetite for and acceptance of a flavor may, under some conditions, be context-specific, and that the context can affect consumption through different and not mutually exclusive mechanisms. Contextual cues may control acceptance of a flavor directly by eliciting intake behavior—increasing and decreasing flavor consumption—when they differentially signal the presence or the absence of a nutrient. They can also control preference and intake by signaling whether or not a particular flavor will be associated with a nutrient. In this latter case context can engage eating behavior not by directly eliciting behavior, but by exerting conditional control over behavior.

To understand the role of contextual cues in controlling eating behavior is a matter of some practical and clinical importance. Human dietary behavior is, in large part, a consequence of automatic responses to contextual cues (Cohen & Babey, 2012), producing a state of food cue reactivity that can lead to overeating (Jansen, 2010), and obesity. Further experimental analysis of the role of context will help in the task of "dissecting the obesogenic environment" (Swinburn, Egger, & Raza, 1999), and, we may hope, suggest interventions for alleviating or eliminating its unwanted effects.

References

Albertella, L., Harris, J. A., & Boakes, R. A. (2008). Acquired flavour preferences. Contextual control of adaptation-level effects. *Quarterly Journal of Experimental Psychology, 61*, 227–231.

Balleine, B. W., Espinet, A., & González, F. (2005). Perceptual learning enhances retrospective revaluation of conditioned flavor preferences in rats. *Journal of Experimental Psychology. Animal Behavior Processes, 31*, 341–350.

Birch, L., McPhee, L., Sullivan, S., & Johnson, S. (1989). Conditioned meal initiation in young children. *Appetite, 13*, 105–113.

Boggiano, M. M., Dorsey, J. R., Thomas, J. M., & Murdaugh, D. L. (2009). The Pavlovian power of palatable food. Lessons for weight-loss adherence from a new rodent model of cue-induced overeating. *International Journal of Obesity, 33*, 693–701.

Bonardi, C., Bartle, C., & Jennings, D. (2012). US specificity of occasion setting. Hierarchical or configural learning? *Behavioural Processes, 90*, 311–322.

Bouton, M. E. (2010). The multiple forms of "context" in associative learning theory. In B. Mesquita, L. F. Barret, & E. R. Smith (Eds.), *The mind in context* (pp. 233–258). New York: Guilford Press.

Bouton, M. E., & Swartzentruber, D. (1986). Analysis of the associative and occasion-setting properties of contexts participating in a Pavlovian discrimination. *Journal of Experimental Psychology. Animal Behavior Processes, 12*, 333–350.

Brandon, S. E., & Wagner, A. R. (1998). Occasion setting. Influences of conditioned emotional responses and configural cues. In N. A. Schmajuk & P. C. Holland (Eds.), *Occasion setting. Associative learning and cognition in animals* (pp. 343–382). Washington, DC: American Psychological Association.

Campbell, D. H., Capaldi, E. D., Sheffer, J. D., & Bradford, J. P. (1988). An examination of the relationship between expectancy learning and preference conditioning. *Learning and Motivation, 19*, 162–182.

Capaldi, E. D., Campbell, D. H., Sheffer, J. D., & Bradford, J. P. (1987). Conditioned flavor preferences based on delayed caloric consequences. *Journal of Experimental Psychology. Animal Behavior Processes, 13*, 150–157.

Cohen, D. A., & Babey, S. H. (2012). Contextual influences on eating behaviours. Heuristic processing and dietary choices. *Obesity Reviews, 13*, 766–779.

Davidson, T. L. (1998). Hunger cues as modulatory stimuli. In N. A. Schmajuk & P. C. Holland (Eds.), *Occasion setting. Associative learning and cognition in animals* (pp. 223–248). Washington, DC: American Psychological Association.

De Brugada, I., Hall, G., & Symonds, M. (2004). The US-preexposure effect in lithium-induced flavor-aversion conditioning is a consequence of blocking by injection cues. *Journal of Experimental Psychology. Animal Behavior Processes, 30*, 58–66.

Dwyer, D. M., Mackintosh, N. J., & Boakes, R. A. (1998). Simultaneous activation of the representations of absent cues result in the formation of an excitatory association between them. *Journal of Experimental Psychology. Animal Behavior Processes, 24*, 163–171.

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.

Fedorchak, P. M., & Bolles, R. C. (1987). Hunger enhances the expression of calorie-but not taste-mediated conditioned flavor preferences. *Journal of Experimental Psychology. Animal Behavior Processes, 13*, 73–79.

Harris, J. A., Gorrissen, M. C., Bailey, G. K., & Westbrook, R. F. (2000). Motivational state regulates the content of learned flavor preferences. *Journal of Experimental Psychology. Animal Behavior Processes, 26*, 15–30.

Holland, P. C. (1983). Occasion-setting in Pavlovian feature positive discriminations. In M. L. Commons, R. J. Herrnstein, & A. R. Wagner (Eds.). *Quantitative analyses of behavior* (Vol. 4, pp. 183–206). New York: Ballinger.

Holland, P. C. (1989). Feature extinction enhances transfer of occasion setting. *Animal Learning & Behavior, 17*, 269–279.

Holland, P. C. (1992). Occasion setting in Pavlovian conditioning. In G. Bower (Ed.). *The psychology of learning and motivation* (Vol. 28, pp. 69–125). Orlando, FL: Academic Press.

Jansen, A. (2010). Obesity needs experimental psychology. *The European Health Psychologist, 12*, 48–51.

Loy, I., Alvarez, R., Rey, V., & Lopez, M. (1993). Context–US associations rather than occasion setting in taste aversion learning. *Learning and Motivation, 24*, 55–72.

Maes, J. R., & Vossen, J. M. (1993). Context conditioning. Positive reinforcing effects of various food-related stimuli. *Physiology & Behavior, 53*, 1227–1229.

Mehiel, R., & Bolles, R. C. (1984). Learned flavor preferences based on caloric outcome. *Animal Learning & Behavior, 12*, 421–427.

Petrovich, G. D., Ross, C. A., Gallagher, M., & Holland, P. C. (2007). Learned contextual cues potentiates eating in rats. *Physiology & Behavior, 90*, 362–367.

Puente, G. P., Cannon, D. S., Best, M. R., & Carrell, L. E. (1988). Occasion setting of fluid ingestion by contextual cues. *Learning and Motivation, 19*, 239–253.

Rescorla, R. A. (1986). Extinction and facilitation. *Journal of Experimental Psychology. Animal Behavior Processes, 12*, 16–24.

Shishimi, G., & Nakajima, S. (2007). Contextual control of rat's foraging behavior in a radial maze. *Behavioral Processes, 74*, 97–103.

Stevenson, R. J. (2009). *The psychology of flavour*. Oxford: Oxford University Press.

Swinburn, B., Egger, J., & Raza, F. (1999). Dissecting obesogenic environments. The development and application of a framework for identifying and prioritizing environmental interventions for obesity. *Preventive Medicine, 29*, 563–570.

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., & Miller, R. R. (2010). Two roles of the context in Pavlovian fear conditioning. *Journal of Experimental Psychology. Animal Behavior Processes, 36*, 268–280.

Yiin, Y. M., Ackroff, K., & Sclafani, A. (2005). Food deprivation enhances the expression but not the acquisition of flavor acceptance conditioning in rats. *Appetite, 45*, 152–160.

Zimmer-Hart, C. L., & Rescorla, R. A. (1974). Extinction of Pavlovian conditioned inhibition. *Journal of Comparative and Physiological Psychology, 86*, 837–845.