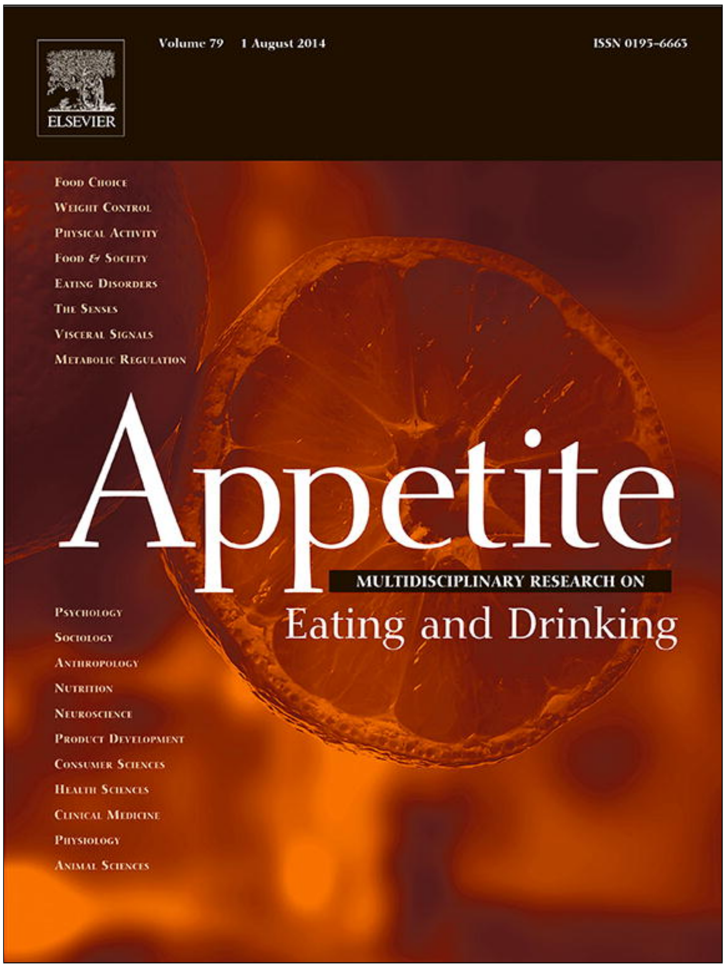
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Research report

Working for food you don't desire. Cues interfere with goal-directed food-seeking ☆

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A B S T R A C T

Why do we indulge in food-seeking and eating behaviors at times when we are already fully sated? In the present study we investigated the hypothesis that food-associated cues in the environment can interfere with goal-directed action by eliciting food-seeking that is independent of the current desirability of the outcome. To this end, we used a computerized task in which participants learned to press keys for chocolate and popcorn rewards. Subsequently, we investigated whether satiation on one of these rewards would bias choice toward the other, still desirable, food reward. We found that satiation did indeed selectively reduce responding on the associated key in the absence of food-associated cues. In contrast, in a Pavlovian-instrumental transfer (PIT) test, satiation failed to reduce cue-elicited food-seeking: in line with our hypothesis, cues that had previously been paired with chocolate and popcorn led to increased responding for the signaled food reward, independent of satiation. Furthermore, we show that food-associated cues will not only bias choice toward the signaled food (outcome-specific transfer), but also enhance the vigor of responding generally (general transfer). These findings point to a mechanism that may underlie the powerful control that cues in our obesogenic environment exert over our behavior.

Introduction

We live in an environment that is full of cues that remind us of palatable, energy-dense food, whether these are commercials on the television or food displays at the supermarket. This 'obesogenic environment' is thought to encourage excessive food consumption and has been cited as a leading cause in the growing epidemic of obesity (Cohen, 2008; Johnson, 2013; Swinburn et al., 2011). Statistics from the Organisation for Economic Co-operation and Development suggest that across the 34 member countries, 18% of the population is now obese (OECD, 2013) – a condition with well-documented negative health consequences (Dietz, 1998; Finkelstein, Ruhm, & Kosa, 2005; Puhl & Heuer, 2009; Wyatt, Winters, & Dubbert, 2006). It is therefore of crucial importance to identify the processes by which the obesogenic environment affects food-motivated behaviors.

Although many factors may contribute to food-seeking and consumption, recent studies suggest that associative learning processes play an important role (Bouton, 2011). The obesogenic environment provides ample opportunities for associations to be formed between foods, cues and actions. For example, as a result of Pavlovian stimulus–outcome (S-O) conditioning, cues such as advertising logos or food packaging may come to elicit craving for certain unhealthy snacks. Indeed, previous research has shown that television commercials promoting unhealthy foods increase consumption of these types of foods in both children and adults (Halford, Gillespie, Brown, Pontin, & Dovey, 2004; Harris, Bargh, & Brownell, 2009). Furthermore, more direct reminders such as the sight and smell of food have also been shown to increase food craving as well as consumption (Jansen, 1998; Jansen et al., 2003; Temple et al., 2006), sometimes even despite explicit intentions to diet (Fedoroff, Polivy, & Herman, 1997). Therefore, Pavlovian processes undoubtedly play an important role in food-motivated behavior. However, there are many situations in which instrumental actions need to be carried out to gain access to food – in order to buy food for dinner, for example, you may walk a specific route home from work via the supermarket. These instrumental actions are often goal-directed, in the sense that they are mediated by the current desire for the anticipated outcome of the action. However, some dual-process theories suggest that Pavlovian cues can interfere with goal-directed

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action (de Wit & Dickinson, 2009; Hogarth, 2012; Hogarth & Chase, 2011; Huys et al., 2011). As a result of separate Pavlovian and instrumental conditioning processes, Pavlovian cues that remind one of food can indirectly trigger the associated instrumental action independently of the current motivation for the outcome. For example, seeing the golden arches of the McDonald's restaurant chain on a billboard may remind one of cheeseburgers, the thought of which triggers the action of going to McDonald's, even when one is already fully sated. This interaction between Pavlovian cues and instrumental behavior – known as 'Pavlovian-instrumental transfer' (PIT) – may be a mechanism by which our obesogenic environment, saturated with reminders of food, biases our food-seeking behaviors and causes overconsumption.

To investigate the effect of Pavlovian cues on instrumental action, associative learning psychologists have developed the PIT paradigm. This paradigm has been adopted most extensively in animal studies (Colwill & Rescorla, 1988; Corbit & Balleine, 2005; Estes, 1948; Holland, 2004; Rescorla, 1994), but in recent years also in human studies (Allman, DeLeon, Cataldo, Holland, & Johnson, 2010; Bray, Rangel, Shimojo, Balleine, & O'Doherty, 2008; Hogarth, 2012; Hogarth & Chase, 2011; Lovibond & Colagiuri, 2013; Nadler, Delgado, & Delamater, 2011; Prévost, Liljeholm, Tyszka, & O'Doherty, 2012; Talmi, Seymour, Dayan, & Dolan, 2008). The classic PIT paradigm assesses the effect of a previously established Pavlovian cue on ongoing instrumental behavior. For example, in an animal study by Corbit, Janak, and Balleine (2007), a clicker cue was always followed by the delivery of food pellets and a tone cue by sucrose solution. During this Pavlovian (S-O) conditioning phase, the rats gradually learned to anticipate the delivery of food rewards when the cues were presented. In a separate instrumental (response–outcome; R-O) conditioning phase, two levers were inserted into the operant chambers and the rats now had to learn to perform instrumental actions to gain access to the food rewards. For example, they learned to press a left lever in order to gain food pellets, and a right lever to gain a drop of sucrose solution. Finally, to assess the effect of Pavlovian cues on instrumental action, the critical transfer test was conducted. During this test, the animals were once again given the opportunity to freely respond on the two levers, but for the first time the Pavlovian cues (the clicker and the tone) were occasionally presented. As expected, the Pavlovian cues biased responding toward the food that they signaled; in the presence of the clicker, rats increased responding on the left lever, while they increased responding on the right lever in the presence of the tone. Importantly, the Pavlovian cues had never been trained with the instrumental actions – so their effect on instrumental responding is thought to be mediated by the cue-evoked outcome anticipation in an S-O-R associative chain. It should be noted that the transfer test is conducted in extinction (no rewards are actually given) to ensure that direct experience with the outcomes does not influence behavior during the test.

This 'outcome-specific transfer' effect is robust and plays a role in many domains of instrumental action: in animals it has been replicated using different food rewards (and drugs), and in humans it has been demonstrated with rewards such as cigarettes, food and money as well as purely symbolic outcomes. Importantly, several studies provide evidence that the outcome-specific transfer effect is insensitive to motivation. Animal studies have shown that Pavlovian cues for food will bias instrumental actions even when rats have been sated on the signaled food reward (Holland, 2004; Rescorla, 1994) or on their daily maintenance chow (Corbit et al., 2007). Rescorla (1994) first trained rats to expect a food pellet in the presence of a light cue, and a drop of sucrose in the presence of a tone. In the instrumental training phase rats then learned to press a lever for the food pellet and pull on a chain for the sucrose. To reduce the motivational value of one of the food outcomes, either the food pellet or the sucrose was paired with lithium chloride (to induce illness). In the transfer test that followed, the light and tone cues biased responding toward the food that they signaled, regardless of the desirability of that food outcome. In related studies in humans, Hogarth and colleagues (Hogarth, 2012; Hogarth & Chase, 2011) have shown that presenting smokers with pictures of cigarettes while they make instrumental choices for those rewards biases choice toward the pictured outcome. In line with the animal studies, this effect was not reduced by exposure to health warnings about cigarettes (Hogarth & Chase, 2011), nor by a dose of nicotine (Hogarth, 2012). Further highlighting the role of outcome-specific transfer in drug-seeking behavior, cues associated with cigarettes have been shown to prime actual smoking behavior (Hogarth, Dickinson, & Duka, 2010) as well as craving for cigarettes (Hitsman et al., 2013; Hogarth et al., 2010). These cue-elicited effects were observed independently of satiety induced by smoking (Hogarth et al., 2010) or by administration of varenicline – a nicotine agonist prescribed for smoking cessation (Hitsman et al., 2013). It seems feasible that this transfer effect may also play a role in food-seeking behaviors. Interestingly, in two studies (Hogarth, 2012; Hogarth & Chase, 2011), a similar pattern of results was observed for chocolate pictures in a control condition, which also appeared to bias responding independently of current motivation. The aim of the present study is to extend this animal and human research to investigate more thoroughly the role of the outcome-specific transfer effect in the domain of food-seeking in humans.

We investigated whether indirect reminders of food (such as seeing the golden arches of McDonald's in our previous example) would bias instrumental responding independently of satiation. To this end, we adopted a computerized task with the classic PIT design, consisting of separate Pavlovian and instrumental training phases, using two food rewards (Smarties and popcorn), two cues (abstract pictorial cues on a computer screen) and two responses (right and left keyboard presses). Following training, we induced 'specific satiety' for one of the two food rewards by asking participants to consume a large amount of this food. One group of participants was sated on Smarties, the other group on popcorn, and a third control group did not receive the satiation manipulation. Subsequently, participants received a noncued and a cued test. In the noncued test, instrumental choice between the two key presses was assessed in the absence of the Pavlovian cues. We expected performance to be goal-directed during this test, meaning that the Smarties-satiation group should prefer the popcorn key, and the popcorn-satiation group the Smarties key (but no difference in the no-satiation group). In the cued (PIT) test, we expected that occasional presentations of Pavlovian cues would interfere with goal-directed action by eliciting the response for the signaled food reward regardless of specific satiety. To discourage an explicit strategy in the noncued test, we instructed participants to ignore the Pavlovian cues. We also employed a 'nominal extinction' procedure and told participants that they were still winning food rewards but they would find out at the end how many they had won – this kept participants motivated during the test phase while preventing further learning (see e.g., Hogarth & Chase, 2011).

Next to assessing outcome-specific PIT, we also assessed the general motivating effect of the Pavlovian cues on instrumental behavior. In the domain of food, several animal studies (and one human study: Prévost et al., 2012) have provided evidence for this 'general PIT' effect, by showing that a Pavlovian cue for food will invigorate responding generally (i.e. not just for the food-outcome that is signaled). To investigate general transfer, we included two more Pavlovian cues in our design: one for a third food outcome (cashew nuts) and one for no-outcome. Neither of these outcomes was associated with an instrumental response. General transfer would be evident if participants responded more vigorously (on the keys associated with the chocolate and popcorn rewards) during the cashew nuts cue relative to the no-outcome cue. We tested whether satiety

Table 1
Sample characteristics. Group means are displayed with standard deviations in brackets. Groups did not differ significantly on any relevant dimensions at the beginning of the experiment.

	Smarties satiation (n = 32)	Popcorn satiation (n = 34)	No satiation (n = 65)	One-way ANOVA $F(2,128)$
Age (years)	21.8 (2.5)	21.9 (3.8)	21.7 (2.7)	<1
% of males	28%	26%	22%	N/A
BMI	22.6 (3.5)	22.9 (3.5)	22.3 (3.2)	<1
Hunger T1 (%)	62 (21)	62 (18)	60 (22)	<1
Popcorn wanting T1(%)	56 (24)	66 (25)	55 (26)	=2.0, $p = 0.14$
Smarties wanting T1 (%)	67 (21)	66 (24)	61 (25)	<1
Cashew wanting T1 (%)	53 (24)	56 (24)	54 (24)	<1
TV clip rating (%)	76 (25)	83 (17)	75 (19)	=1.92, $p = 0.15$
BIS impulsivity	67 (9)	68 (11)	66 (10)	<1
DEBQ restrained eating	2.8 (0.8)	2.9 (0.9)	2.6 (0.8)	=1.0, $p = 0.20$
SSRT (ms)	212 (33)	219 (37)	216 (36)	<1

T1, time point 1; BIS, Barratt Impulsivity Questionnaire; DEBQ, Dutch Eating Behavioral Questionnaire; SSRT, Stop Signal Reaction Time.

(on chocolate or popcorn) would affect this general motivating effect of the cashew nuts cue. On the basis of a study by Corbit et al. (2007), that showed that general transfer with food rewards only occurs when animals are tested in a hungry state, we expected that participants who had been sated on Smarties and popcorn would show an attenuated general transfer effect relative to the no-satiation group.

To summarize, the main aim of the present study was to assess whether Pavlovian cues interfere with the ability to reduce responding for food rewards on which people have already been sated. Evidence for this hypothesis would be observed if a cue previously associated with a certain food reward would trigger responding on the associated key even if the desire for this food had been reduced as a consequence of specific satiety. Next to this outcome-specific transfer effect we also assessed the general motivating effect of food-associated cues on the vigor of responding.

Methods

Participants

A total of 144 subjects were recruited from the University of Amsterdam. Advertisements highlighted that the study involved eating popcorn, chocolate Smarties, and cashew nuts. Following 13 exclusions (see results section) 131 participants between the ages of 18 and 40 years (mean = 21.8 years; SD = 3.0 years), 24% males, with BMIs ranging from 16.5 to 32.4 (mean = 22.5, SD = 3.4), remained in the study. All sample demographics can be seen in Table 1. Participants received €12 or course participation credits for taking part. Participants were assigned to one of three experimental groups (no satiation, popcorn satiation, Smarties satiation). An attempt was made to ensure that males and females were spread equally across the three experimental groups. In addition, because this experiment concerned cued instrumental responding for food outcomes, we measured eating restraint and impulsivity to ensure that there were no differences between the three experimental groups. All participants were asked to refrain from eating for at least 2 hours before the experiment began. The Psychology Ethics Committee of the University of Amsterdam approved the study.

Stimuli and materials

A computerized PIT task similar to that used by Prévost et al. (2012) was programmed in presentation and run on a laptop. The task consisted of instrumental and Pavlovian training phases followed by noncued and cued test phases. The task design is depicted in Fig. 1 and described in the procedure section. Four images of black and white patterns were used as Pavlovian cues (during the

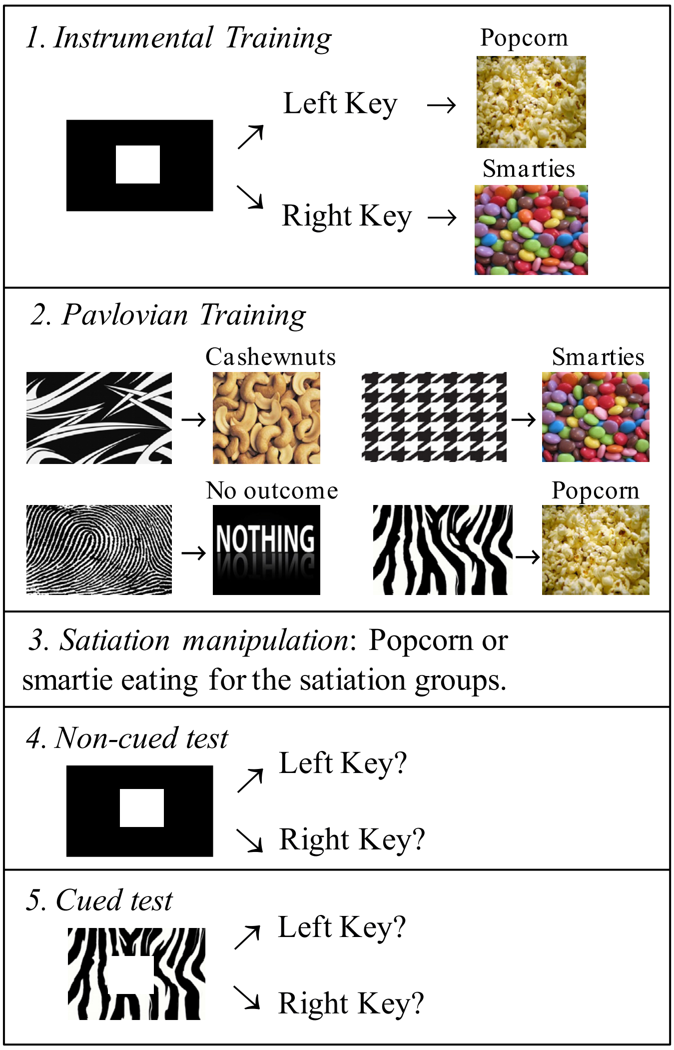

Fig. 1. *Procedure*. Participants learned the relationships between two keys and chocolate Smarties and popcorn outcomes. They then learned the relationships between four Pavlovian cues and popcorn, Smarties, cashew nuts and no-outcome. During a 10-minute TV watching phase, half the participants were asked to eat 100 g of either popcorn or Smarties. The order of the noncued test and cued test were counterbalanced across participants. In both tests participants were instructed to try and win popcorn and/or Smarties. In the cued test, Pavlovian cues were presented on the screen (participants were told they could ignore them).

Pavlovian training and the cued test phase) and were always presented full-screen. Popcorn and Smarties photographs were used in both training phases and in addition, during the Pavlovian training phase, a photo of cashew nuts and the word 'nothing' were also used (see Fig. 1). These images were approximately one-fifth of the screen size and presented in the center of the screen. Real food outcomes were used during the experiment – these were mini chocolate Smarties (Nestle, 471 calories per 100 g), salted popcorn (Albert Heijn, 525 calories per 100 g) and unsalted cashew nuts (Albert Heijn, 625 calories per 100 g). The experiment took place in two separate rooms – a plain lab room for the PIT-task and a TV-room for the satiation manipulation. In the TV-room, the lights were dimmed and the participants sat in a comfortable chair. By mimicking the home environment we aimed to make participants feel more comfortable about eating a large amount of snack food during the satiation treatment. During 10 minutes, the first half of Series 1 Episode 2 of a popular American TV show *"Modern Family"* was shown to participants during the TV-watching (satiation) phase.

Likert scales

At various times during the experiment, different Likert scales were used (see procedure). Participants were asked to rate their hunger on a 10-cm Likert scale marked with the anchors: not at all hungry (1), neutral (5) and very hungry (10). Furthermore they were asked to report how much they wanted to eat each of the foods on a 10-cm Likert scale marked with the anchors: not at all (1), neutral (5) and very much (10). In addition, participants were asked to rate how much they enjoyed watching the TV clip on a 10-cm Likert scale marked with the anchors: not at all (1), neutral (5) and very much (10).

Dutch eating behavioral questionnaire

To ensure that the groups were matched on eating restraint, the Dutch Eating Behavioral Questionnaire (DEBQ; van Strien, Frijters, Bergers, & Defares, 1986) was used in this study. The DEBQ consists of 33 items scored on a 5 point Likert-scale, of which 10 items make up the restrained eating subscale. An example of an eating restraint item is "when you have eaten too much, do you eat less than usual the next day?" Internal consistency and reliability of the restrained eating subscale is good (Banasiak, Wertheim, Koerner, & Voudouris, 2001; van Strien et al., 1986).

Barratt impulsivity questionnaire

To ensure that the groups were matched on impulsivity, the Barratt Impulsivity Scale (BIS-11; Patton, Stanford, & Barratt, 1995) was used to measure impulsivity. The BIS-11 consists of 30 items scored on a 4 point Likert-scale, with higher scores indicating impulsivity. The total BIS score is derived from scores on three subscales (1) attentional impulsiveness, (2) motor impulsiveness and (3) nonplanning impulsiveness. The BIS has good internal consistency and test–retest reliability (Stanford et al., 2009).

Stop signal reaction time task

To ensure that the groups were matched on response inhibition, the stop signal reaction time (SSRT) task detailed by Logan, Schachar, and Tannock (1997) was used, with the only difference being that our task version consisted of four blocks of 64 trials. As usual, a staircase-tracking procedure was used to ensure that participants were able to inhibit on approximately 50% of trials. Following successful stopping the stop signal delay was increased by 50 ms, whereas following unsuccessful stopping the delay was decreased by 50 ms. Longer SSRTs indicate greater difficulty to inhibit one's responses.

Procedure

At the start of the experiment, participants were asked to sample each of the three foods used in the experiment and to rate on the Likert scales how much they desired to eat each food (T1). Two small bowls containing Smarties and popcorn were placed to the side of the laptop corresponding to the nondominant hand. The Smarties bowl was always placed closest to the participant.

Participants then completed the *instrumental training phase* of the PIT Task, in which they could earn popcorn and chocolate Smarties. Upon presentation of a white box in the center of the screen (the availability window), participants could press on two keyboard keys (the 'I' and '[' keys) using one finger of their dominant hand. One of these two keys was assigned to popcorn and the other to chocolate Smarties. This response–outcome relationship was counterbalanced across participants. On each trial, participants were instructed that only one of the two food outcomes would be available and that they would have to work out which food outcome that was by trial and error. They were told to continue trying both keys until they won something – as would be evidenced by the appearance of either a popcorn or Smarties image on the screen. Participants were told that they should try and learn the relationships between the keys and the food outcomes and that occasionally they would be tested on what they had learned. A variable ratio schedule of 10, between five and 15 key presses, determined the amount of specific key presses needed for the image of the food outcome available on that trial to appear. The food image remained on the screen for 1 s and the ITI was 1.5 s. Every fourth time that a specific food image was presented, there was also a 'ding' sound signaling that the participant should take one piece of that food (either a piece of popcorn or a chocolate Smarties) using their nondominant hand and consume it immediately. In order to allow the participants time for the consumption of the food outcome, the ITI was 6 s after 'eating' trials. The instrumental training phase consisted of four blocks in which the two different food outcomes were both available three times, in random order (24 trials in total). At the end of the second and fourth instrumental blocks, a block of four *instrumental query trials* was inserted to test the participants on their knowledge of the relation between the two keys and the two food outcomes. On each query trial a picture of either popcorn or Smarties was presented, upon which the participant was asked to press the key that previously yielded that food outcome (thus testing response–outcome knowledge). As soon as participants had pressed a key, they received feedback on their choice by presentation of the words 'correct' or 'incorrect' for 2 s, which was followed by a 0.5-s ITI. Each food outcome was presented twice in random order during each query block.

Following the instrumental training phase, a bowl of cashew nuts was placed between the two other bowls, for the *Pavlovian training* phase. Pavlovian training involved learning the relationships between four Pavlovian cues (black and white patterns) and four different food outcomes (popcorn, Smarties, cashew nuts, or no-outcome). The relationships between the Pavlovian cues and outcomes were counterbalanced across participants. During this training phase, participants passively viewed the screen and were not required to make any responses. They were told that they should pay attention because they would be occasionally tested on their knowledge of the relationships between the patterns and the food outcomes. During each trial, one of the four Pavlovian cues was presented for 2 s, and was then overlaid with the picture of the food (or "nothing") outcome for 1 s. The ITI was 1.5 s. Every fourth time that a specific food outcome picture was presented, there was also a 'ding' sound signaling that during the subsequent 6-s ITI the participant should consume a piece of that food. The Pavlovian training phase contained four blocks, during each of which the four cues were presented twice in random order (32 trials in total). At the end of the second and fourth block, a block of four *Pavlovian query* trials was inserted to test the participants on their knowledge of the cue–outcome contingencies. On each query trial, one of the Pavlovian cues was presented, upon which the participant had to use the mouse to select the picture of the outcome that had followed this cue. Participants received feedback by presentation of the words 'correct' or 'incorrect' for 2 s along with the image of the correct food outcome that had been signaled by the cue.

Following these training phases, participants filled in the hunger and food wanting ratings for the second time (T2) and were guided to the TV-room for the *satiation manipulation*. For participants in the satiation conditions, there was a bowl filled with 100 g of either salted popcorn or chocolate Smarties on the table next to the chair. These participants were asked to try and eat the whole bowl while watching the TV show. There were no snacks for the participants in the no-satiation group. As the show began, the experimenter left the room. After returning to the main room, the participants completed the hunger and food wanting ratings again (T3) and rated how much they enjoyed watching the show.

Participants then performed the test phase of the PIT task during which they were free to respond on the popcorn and Smarties keys as often as they liked in order to win these food outcomes. No food was in sight during this phase of the task. During the *noncued test*, we assessed choice behavior in the absence of Pavlovian cues to see whether participants would respond in a goal-directed manner (i.e. try to win food outcomes they had not been sated on). During the *cued test*, we assessed whether presentation of the different Pavlovian cues would bias responding on different keys and influence vigor of responding. The order of the two tests was counterbalanced across participants, with a pause between the two tests. At the beginning of the test phase participants received the instruction that the white box would be presented on the screen for 3 s and that during this time (the availability window) they could push on either key as often as they liked in order to win popcorn or chocolate Smarties. They were told that, as before, only one of the two food outcomes would be available on each trial but that this time they would not be told after each trial which food they had won. Instead they would find out at the end of the phase how many Smarties or pieces of popcorn they had earned and they would then eat these, while they filled in questionnaires (nominal extinction). After receiving these instructions participants received two demo trials. During these trials participants could press either key as often as they liked during the 3-s presentation of the white box (in order to win popcorn and Smarties). The ITI was 1 s. After the demo trials they were asked to confirm that they understood the instructions. The *noncued test* was exactly the same as the demo trials and consisted of 10 trials. Before the *cued test* began, participants were given the additional instruction that they would occasionally see patterns appear on the screen but that they should ignore these and pay attention to the white box signaling that they had 3 s available to respond in order to win popcorn or Smarties. During cued test trials, one of the Pavlovian cues was presented for 3 s, overlaid with the white 'availability window' box (see Fig. 1). The cued test consisted of five blocks with two presentations of each of the Pavlovian cues, in random order (40 trials in total). The number of presses on each key was recorded, as was the RT of the first key press. Finally, after the two tests had been completed, a block of four *instrumental query trials* tested whether the participants had remembered the instrumental response–outcome relationships from the instrumental training session. The timings were the same as has been reported previously, but the participants did not receive feedback on these query trials.

Finally, participants performed the SSRT task and completed the DEBQ and BIS questionnaires. Weight and height were then measured and BMI calculated.

Results

Participants

In total, 13 participants were excluded from the analysis (six from the no-satiation group, two from the popcorn-satiation group and five from the Smarties-satiation group). Six were excluded because they scored at or below 50% chance level on the final instrumental query trials, indicating that they had failed to learn about the response–outcome contingencies between the two response keys and the popcorn and Smarties outcomes. Five other participants were excluded because they did not push any keys in at least 25% of the cued test trials. One further participant did not push any keys during the noncued test and one participant reported during testing that she had a popcorn allergy. Of the remaining 131 participants, 65 were in the no-satiation condition, 32 were in the Smarties-satiation condition and 34 were in the popcorn-satiation condition. One-way ANOVAs demonstrated that the groups did not differ in age, BMI, impulsivity, restrained eating, SSRT, reported hunger and food wanting ratings at T1, or reported enjoyment of the TV show (see Table 1).

Satiation manipulation

During the TV watching phase of the experiment, participants in the Smarties-satiation group ate on average 71 g of chocolate Smarties (SD: 28 g) and those in the popcorn-satiation group ate on average 41 g of popcorn (SD: 18 g). The food wanting and hunger ratings from one participant in the Smarties-satiation group were missing. For the remaining participants, repeated measures ANOVA of the Smarties and popcorn wanting ratings *before* versus *after* the TV watching phase (T2 versus T3), revealed a significant three-way interaction between food, time and satiation group, $F(2,127) = 46.8$, $MSE = 187.8$, $p < 0.001$. Repeated measures ANOVA were, therefore, repeated separately for the three satiation groups. The analysis confirmed that the manipulation was successful and that participants reported reduced wanting ratings for the specific food they had been sated on. As can be seen in Fig. 2, participants in the no-satiation group reported no differences in food wanting ratings for popcorn or Smarties at either T2 or T3 (all $Fs < 1.1$, $ps > 0.29$). Participants in the Smarties-satiation group showed a significant time and food type interaction, $F(1,30) = 18.2$, $MSE = 419.6$, $p < 0.001$, Smarties were rated significantly lower than popcorn after the satiation manipulation, $t(30) = 3.9$, $p < 0.001$, but not before, $t(30) = -0.80$, $p = 0.43$. Likewise for the popcorn-satiation group the interaction was significant, $F(1,33) = 51.8$, $MSE = 191.6$, $p < 0.001$, after the manipulation popcorn was rated significantly lower than Smarties, $t(33) = -6.7$, $p < 0.001$, but not before, $t(33) = 0.25$, $p = 0.8$.

Furthermore, hunger ratings at T3 (after satiation) were significantly lower for participants who had been sated on either Smarties or popcorn (mean = 30%, SD = 23%) compared with the no-satiation group (mean = 58%, SD = 22%; $t(128) = 7.1$, $p < 0.001$).

Training phases

Average accuracy of R-O knowledge was 99% (SD = 0.04%) during the last block of instrumental training query trials and average accuracy of S-O knowledge was 98% (SD = 0.09%) on the last block of Pavlovian training query trials. One-way ANOVA revealed no significant differences in performance between the three satiation groups on the last block of instrumental query trials, $F(2, 128) = 1.1$, $p = 0.34$, nor on the Pavlovian query trials, $F < 1$.

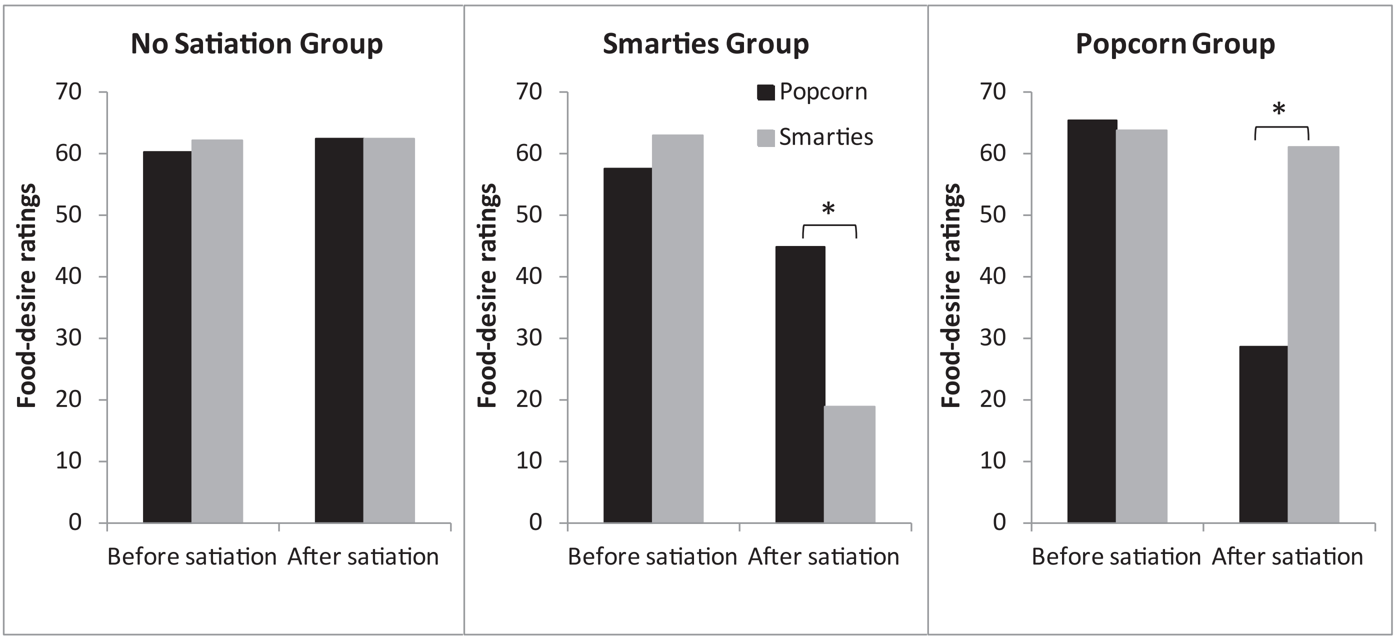

Fig. 2. *Food-wanting ratings.* Wanting ratings for popcorn and Smarties both before and after the TV watching (satiation) phase. Eating popcorn or Smarties resulted in a specific-satiety effect. $^{*}p < 0.001$.

Noncued test

To examine Smarties and popcorn choices in the absence of any Pavlovian cues, the mean percentage of Smarties presses was calculated (number of presses on the Smarties key divided by total number of presses) and this was compared between the three groups with one-way ANOVA. Participants in the no-satiation group responded about 50% of the time on the Smarties key – indicating that they pushed about equally often for popcorn and Smarties outcomes. As expected, participants in the popcorn and Smarties-satiation groups pushed less frequently on the keys for the food outcomes on which they had been sated (see Fig. 3; main effect of satiation group, $F(2,128) = 6.7$, $MSE = 197.4$, $p = 0.002$). Participants in the Smarties-satiation group responded significantly less often for Smarties (and therefore more often for popcorn) compared with the no-satiation group, $t(95) = 2.5$, $p = 0.03$. Likewise, participants in the popcorn-satiation group responded significantly more often for Smarties (and therefore less often for popcorn) compared with the no-satiation group, $t(97) = 2.0$, $p = 0.04$.

Cued test – outcome specific PIT

To examine whether the Pavlovian cues would bias responding for particular food outcomes, repeated-measures ANOVA was used to compare the mean percentage of Smarties presses across the four different trial types (trials with the Pavlovian cue associated with either popcorn, Smarties, cashew nuts or no food-outcome). First of all, as can be seen in Fig. 4, all three groups showed evidence for outcome-specific transfer, in that the Pavlovian cues biased responding toward the signaled outcome. In line with this observation, statistical analysis yielded a main effect of trial type, $F(3,384) = 117.6$, $MSE = 518.6$, $p < 0.001$, but no interaction between this factor and satiation group, $F(6,384) = 1.7$, $MSE = 518.6$, $p = 0.14$. As can be seen in Fig. 4, during trials when the cue for either cashew nuts or no-outcome was shown, participants in all three groups pushed about equally often on the two keys (on average 50% on the Smarties key). When the cue for Smarties was shown, participants pushed significantly more frequently on the Smarties key (on average ~80%) compared with the no-outcome and nut cues, $ts(130) = 10.2$ an 11.9, $ps < 0.001$. In contrast, when the cue for popcorn was shown, participants pushed significantly less frequently on the Smarties key (on average ~20%), compared with the no-outcome and nut cues, $ts(130) = -10.7$ and -10.5, $ps < 0.001$. Those results of the t-tests were replicated in three separate group analyses (with t-values between 3.73 and 9.06, and all $ps \leq 0.001$).

Although the analysis failed to yield evidence for motivational modulation of the outcome-specific PIT effect, the ANOVA did reveal

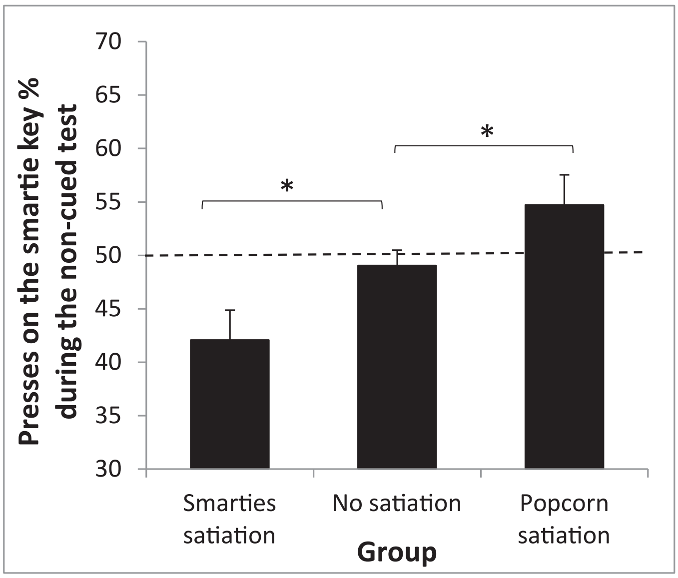

Fig. 3. *Noncued test.* In the absence of Pavlovian cues participants showed goal-directed behavior by responding less often for the food that they had been sated on. The horizontal axis crosses at 50% – representing equal responding on the Smarties and popcorn keys. Values above this line indicate more responding on the Smarties key and values below more responding on the popcorn key. Error bars represent standard error of the mean. $^{*}p < 0.05$.

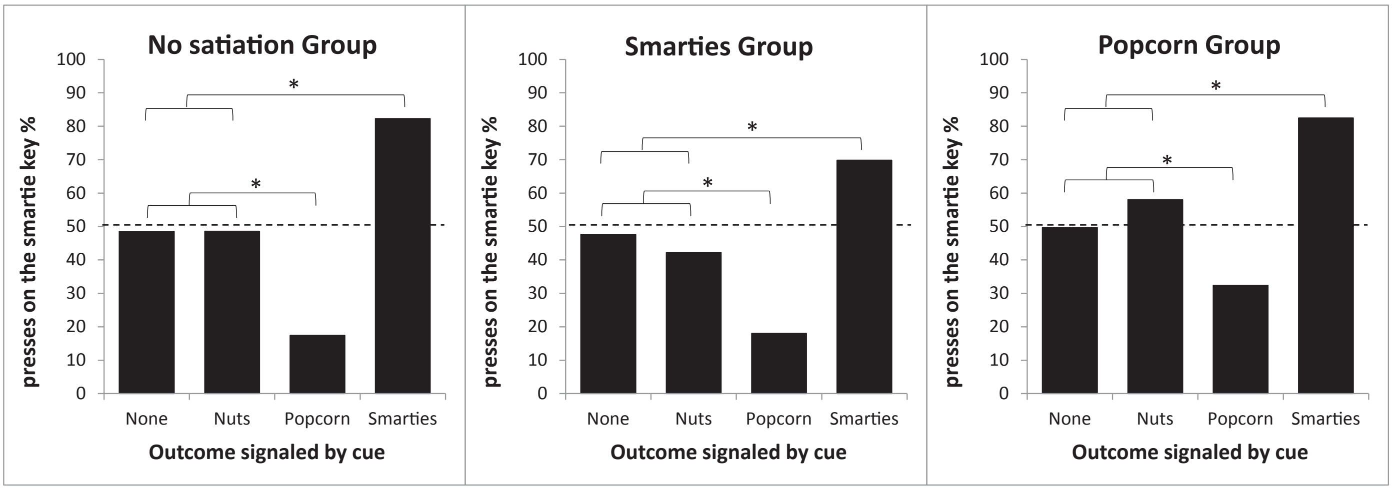

Fig. 4. *Cued test – Outcome-specific transfer.* Pavlovian cues that had previously been paired with Smarties and popcorn biased responding for those outcomes (outcome-specific transfer). Fifty percent represents equal responding on the Smarties and popcorn keys. Values above this line indicate more responding on the Smarties key and values below more responding on the popcorn key. The data are shown separately for the three groups. $^{*}p < 0.001$.

a main effect of satiation group, $F(2,128) = 7.7$, $MSE = 547.7$, $p = 0.001$. It seems, therefore, that during the transfer test participants still showed evidence for a specific reduction in responding for the food they had been sated on. Separate *t*-tests confirmed that participants in the Smarties-satiation group pushed the Smarties key significantly less often overall than the no-satiation group, $t(95) = 2.0$, $p = 0.046$. Participants in the popcorn-satiation group, on the other hand, pushed the Smarties key significantly more often overall than the no-satiation group, $t(97) = 2.7$, $p = 0.007$.

To further explore the lack of motivational modulation of the transfer effect in the satiation groups with a more in-depth analysis, we calculated the percentage of presses on the valuable key when the cue for the valuable reward was shown (mean = 82%; SD = 17%). A *t*-test showed that this was significantly greater than the percentage of presses on the devalued key when the cue for the devalued reward was shown (mean = 68%, SD = 27%), $t\ (65) = 3.94$, $p < 0.0001$, suggesting that indeed satiation did play a role in overall key choice. This finding, however, is to be expected, given that we found a difference between the groups in baseline responding for valuable versus devalued rewards. As a more sensitive analysis, therefore, we examined whether satiation modulated the ability of the cue to augment responding above baseline response rates for valuable and devalued outcomes. To this end we first calculated a baseline measure of responding by taking the mean response rates during the nuts and no outcome trials. During these trials, mean responding on the valuable and devalued keys was 54% and 46% (SD = 18%). We then subtracted these baseline response rates from the percentage of presses on the valuable or devalued keys when the cues for these outcomes were signaled. These difference scores are depicted in Fig. 5. Importantly, the difference score for still-valuable outcomes was not different than that for the devalued outcomes, $t\ (65) = 1.05$, $p = 0.30$. Therefore, the ability of the cues to augment responding for the signaled outcome (i.e. the outcome-specific transfer effect), was not diminished by satiation.

Cued test – general PIT

General PIT was examined by comparing the vigor of responding on trials during which the Pavlovian cue that signaled nuts was presented with trials in which the Pavlovian cue that signaled no-outcome was presented. To this end, we calculated the average total number of key presses on each trial with the nuts versus no-outcome cue, collapsed across both response keys. In line with our hypothesis, we found that participants pushed more vigorously when the nut cue was shown (mean of 9.7 key presses per trial, SD: 3.5) compared with the no-outcome condition (mean 9.4 key presses per trial, SD: 3.6). Although the difference in vigor was numerically small, repeated measures ANOVA revealed that this was significant, $F(1,128) = 6.88$, $MSE = 0.748$, $p = 0.01$. Therefore, our results provide evidence for the general motivating effect of Pavlovian cues on instrumental responding.

Although we did not prefeed the general food outcome (cashew nuts), the general PIT effect could still be attenuated by reduced hunger in the satiation groups relative to the no-satiation group. The ANOVA did not provide support for this possibility as there was no main effect of satiation group ($F < 1$) nor an interaction between cue and satiation group, $F(2,128) = 1.14$, $MSE = 0.748$, $p = 0.33$. As there was substantial individual variability in the reduction of hunger in

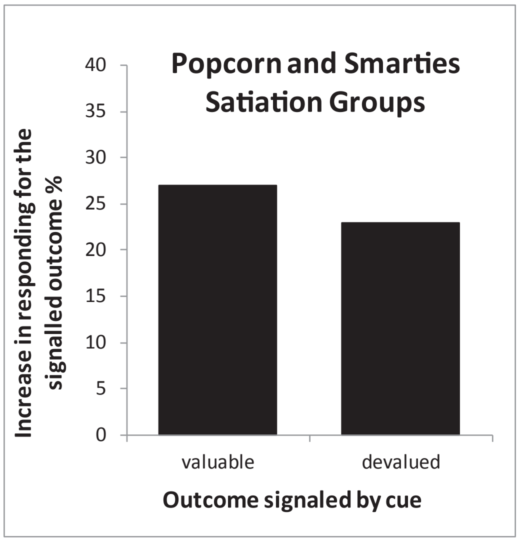

Fig. 5. *Cued test – Effect of satiation on outcome-specific transfer.* Plotted in this graph are difference scores that highlight the extent to which Pavlovian cues for valuable versus devalued outcomes augmented responding for that outcome over and above the baseline percentage of responding (which was the average percentage of responding for those outcomes during the no-outcome and nut cues). These difference scores did not differ significantly, indicating that satiation failed to reduce the outcome-specific transfer effect.

the (popcorn and Smarties) satiation groups, we ran an exploratory correlation between reported hunger at T3 and the general PIT effect (difference score for total number of presses during the nut cue minus no-outcome cue) for participants in the satiation groups. A significant positive correlation, $r\ (63) = 0.26$, $p = 0.036$, provides preliminary evidence that satiation did attenuate the general motivating effect of the cashew nut cue on response vigor. By comparison, no such relationship was observed between hunger at T3 and the magnitude of the outcome-specific transfer effect e.g. the mean percentage of responding on the popcorn key during trials when popcorn was signaled and responding on the Smarties key during trials when Smarties were signaled, $r\ (63) = 0.20$, $p = 0.12$.

Individual differences – exploratory analyses

One previous study with food rewards reported a negative correlation between motor impulsivity (as measured with the BIS) and the reduction in responding for a devalued reward (relative to a presatiation baseline phase; Hogarth, Chase, & Baess, 2012). To investigate whether we would observe a similar relationship we correlated the percentage of responses for the devalued food outcome during the noncued test, with the BIS motor impulsivity score. However, this correlation was not significant ($r\ (64) = -0.185$, $p = 0.14$). Across all participants, we also examined whether motor impulsivity and the SSRT would correlate with the magnitude of the outcome-specific transfer effect. We therefore calculated the mean percentage of responding on the popcorn key during trials when popcorn was signaled and responding on the Smarties key during trials when Smarties were signaled. However, this measure of outcome-specific transfer did not correlate with motor-impulsivity ($r\ (129) = -0.05$, $p = 0.56$) or SSRT ($r\ (129) = 0.01$, $p = 0.90$).

Although the participants were drawn from a student population with relatively homogenous BMI, we sought to explore whether there was any relationship between BMI and responding for food rewards. There was no correlation between BMI and the percentage of responses for the devalued food reward during the noncued test, $r\ (64) = 0.004$, $p = 0.98$. The strength of the outcome-specific transfer effect was also not correlated with BMI, $r\ (129) = -0.153$, $p = 0.08$. Finally, we examined whether the magnitude of the general PIT effect (difference score for total number of presses during the nut cue minus no-outcome cue) would correlate with BMI – however this was also nonsignificant, $r\ (129) = -0.051$, $p = 0.56$.

Discussion

This study demonstrates that Pavlovian cues can interfere with goal-directed action in the domain of food-seeking. When participants were tested in the absence of any cues, satiation on a specific food reward led to preferential responding for the other, still desirable, food reward. However, the presentation of food-associated cues biased choice toward the signaled food rewards even when the current desirability of that food had been reduced through specific satiety. In other words, satiation failed to reduce cue-elicited food-seeking. We propose, therefore, that outcome-specific Pavlovian-instrumental transfer contributes to excessive food-motivated behaviors in our obesogenic environment in which cues – such as advertisements – constantly remind us of the availability of food. To consider our real-life example, seeing the golden arches of McDonald's may trigger a trip to McDonald's, even when we are already fully sated.

Our findings support the idea that Pavlovian cues can conflict with goal-directed action by biasing responding toward an associated outcome via an S-O-R associative chain. In line with previous PIT studies, this absence of flexible motivational modulation of cue-elicited behavior was observed even after only limited training (Hogarth, 2012; Hogarth & Chase, 2011; but see for a notable exception, Allman et al., 2010). In that sense, Pavlovian-instrumental interactions do not appear to correspond with habits that result from extensive behavioral repetition. Indeed, the stimulus–response (S-R) reinforcement mechanism that is commonly thought to underlie such gradual habit formation is fundamentally different from that mediating PIT, in that the habitual response is thought to be elicited directly by environmental stimuli through a S-R association (Adams, 1982; de Wit & Dickinson, 2009; Neal, Wood, & Quinn, 2006; van't Riet, Sijtsema, Dagevos, & De Bruijn, 2011). The role of habitual, repetitive behavioral patterns in everyday eating behaviors has been well documented (see for review: van't Riet et al., 2011) and although the different roles of PIT and S-R habits in inflexible food-motivated behaviors remain to be determined, the current findings point to the pervasive influence that environmental cues have on our ability to act in line with current needs and desires. Whereas S-R habits may require extensive repetition to be evoked by certain stimuli, it seems that PIT provides a mechanism whereby these behaviors can readily generalize to cues and contexts that are associated with the same food rewards. For example, the S-R mechanism may readily account for the gradual formation of the habit of visiting McDonald's upon seeing the golden arches, but the PIT mechanism can explain that this habit then transfers to other McDonald's commercials or other situations in which one is reminded of the cheeseburgers. A related issue that deserves attention is the potentially differential effects of discrete versus more general contextual cues on the motivational modulation of instrumental behavior. Whereas most animal over-training studies have examined habit formation against a consistent contextual background, PIT studies – including the present one – usually adopt discrete stimuli to signal the instrumental outcome.

Dual-process models are influential in the decision-making and addiction literature (Balleine, Daw, & O'Doherty, 2008; Clark, Hollon, & Phillips, 2012; de Wit & Dickinson, 2009; Dayan, Niv, Seymour, & Daw, 2006; Everitt, Dickinson, & Robbins, 2001; Wiers & Stacy, 2006). Some dual-process models propose that both goal-directed and habitual "controllers" operate in parallel, summing together to determine the final course of action (Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1995; Hogarth, 2012; Hogarth & Chase, 2011; Huys et al., 2011). In this way, freely elected behavior is goal-directed, but reward-associated cues in the environment can elicit reward-seeking that is independent of the current desirability of the outcome. Indeed in the current study, participants demonstrated that they were perfectly well capable of directing their actions away from food rewards that they had been sated on but the effect of food-associated cues on instrumental choice was insensitive to satiety. Even though this outcome-specific transfer effect was not attenuated by satiety, participants still showed evidence for a specific reduction in responding for the food they had been sated on, when collapsing across all trial types in the cued test. The fact that these two effects did not interact with one another is in line with suggestions that these mechanisms operate in an additive manner (Dickinson et al., 1995; Hogarth, 2012; Hogarth & Chase, 2011; Huys et al., 2011).

This is the first human study to examine the general transfer effect within the context of a food satiety manipulation. We replicated previous studies showing general transfer in humans (Nadler et al., 2011; Prévost et al., 2012) by demonstrating that compared with a baseline (no-outcome) condition, anticipation of cashew nuts increased the vigor of responding for other food outcomes. As discussed in the introduction, on the basis of a previous study in animals, we expected that satiation would abolish general transfer (Corbit et al., 2007). However, although the satiation manipulation in the current study was effective in reducing hunger ratings overall in the groups who had been sated (on Smarties and popcorn) relative to the nonsated group, we failed to find evidence for an attenuation of the general PIT effect. An exploratory analysis did reveal, however, that the substantial individual variability in the success of the satiation manipulation in reducing hunger was related to the size of this transfer effect: in line with our hypothesis, participants who reported lower hunger levels also showed a weaker general PIT effect. It appears, therefore, that – in contrast to outcome-specific PIT – the general motivating effect of Pavlovian cues on the vigor of food-motivated behavior is sensitive to motivational state. We propose that future studies should further investigate these different sensitivities of outcome-specific and general PIT to motivation. To reduce individual variability in hunger, these studies could extend the duration of the satiation phase or ask participants to eat a fixed, large amount of the food rewards. Conversely, to achieve high levels of hunger in the nonsated group, participants could be asked to not eat for more than just 2 hours preceding the experiment. Finally, it should be noted that although the general PIT effect was statistically reliable in our study, the size was numerically rather small. It is possible that employing a palatable food reward other than cashew nuts would lead to a stronger effect. Furthermore, future studies that focus on comparing motivational modulation of outcome-specific and general PIT should counterbalance the assignment of different food types to these conditions.

The PIT effect was originally discovered by animal researchers, but the present study adds to recent evidence that this mechanism also plays an important role in human behavior. However, such translational research into the role of associative learning mechanisms in human behavior does pose certain challenges. It is difficult, if not impossible, to rule out the possibility that participants use explicit strategies when making decisions on how to respond during the transfer test. However, in the current study, participants were actively discouraged from using such explicit strategies, by telling them that they should pay attention to the availability window and ignore the Pavlovian cues in the background. Furthermore, prior to the test phase they received the instruction that they would have to eat any winnings form the transfer test at the end of the experiment. In light of their decreased self-reported desire to eat more of the food that they had been sated on, their persistent responding for that same food in the transfer test seems to preclude that their performance was driven solely by an explicit strategy. In addition, the fact that the human data model the animal data so closely suggests that this PIT effect may be a more general mechanism underlying behavior. This certainly makes sense from an evolutionary perspective. Throughout most of evolution, food was scarce and it was adaptive therefore to develop a mechanism that leads to automatic responding to cues that signal the availability of food. More recently, however, food has become abundant, and consequently this mechanism may now turn against us. In an environment that is saturated with food-associated cues, Pavlovian-instrumental interactions that are insensitive to satiety may contribute to excessive food-seeking and consequently to the recent rise in obesity.

In the present study, we assessed cue-elicited behavior in an extinction test, to replicate previous demonstrations in animal research that Pavlovian cues can interfere with an *immediate* and flexible adaptation to changes in the desirability of food rewards (Holland, 2004; Rescorla, 1994). The question remains as to whether presenting the no-longer-desirable food reward contingent upon responding would gradually reduce the strength of the original S-O-R associations underlying the PIT effect. It seems plausible that the Pavlovian cues would initially interfere with this learning process, but that participants would ultimately be perfectly capable of learning to redirect their responses toward the still-valuable food reward. In other words, we expect that in real life, the first response elicited by Pavlovian cues is insensitive to satiation, but that subsequent exposure to that food in a sated state should to some extent still allow us to adapt our behavior. However, in some cases it might be too late by then. Once we have successfully procured a certain food reward (for example buying a cheeseburger and milkshake at McDonald's), we usually persist in consuming it.

Previous research investigating food-cue exposure and reactivity has tended to use more direct food cues such as the sight and smell of food (Fedoroff et al., 1997; Jansen, 1998; Jansen et al., 2003; Temple et al., 2006) or pictures of food (Hogarth, 2012; Hogarth & Chase, 2011). In contrast, in our PIT study, we associated novel, abstract cues with food outcomes during the Pavlovian training phase. Given that these cues are more distal from the actual food reward, they may provide useful targets for behavioral weight-loss interventions (Lovibond & Colagiuri, 2013). However, we should point out that results from animal studies suggest that these mechanisms are extremely persistent (Bouton, 2011; Delamater, 1996; Todd, Winterbauer, & Bouton, 2012). Delamater (1996), for example, demonstrated that after extended Pavlovian training, neither cue exposure nor cue counterconditioning reduced the ability of the cue to elicit the associated instrumental response. This highlights the obstacles faced by individuals trying to lose weight and suggests that these associative mechanisms likely contribute to the reportedly high weight-loss failure rate (Tsai & Wadden, 2005; Wing & Hill, 2001). Relatedly, previous investigations of PIT in smokers have shown that cue-induced cigarette-seeking was insensitive to health warnings (Hogarth & Chase, 2011) and pharmacotherapy (Hitsman et al., 2013; Hogarth, 2012). An alternative approach may be to encourage people to form intention implementation "if–then" plans, in which they learn to identify critical environmental cues and plan healthier courses of action (Gollwitzer & Sheeran, 2006; Luszczynska, Sobczyk, & Abraham, 2007). These implementation intentions may lead to automatic performance of the desired behavior upon encountering those critical cues, thereby facilitating the formation of healthier eating habits. Future research should investigate the efficacy of such an approach in the context of Pavlovian-instrumental interactions. In any case, from research so far it is clear that once associations between cues, responses and food outcomes have been formed, it is challenging to override or extinguish these (Bouton, 2011; Delamater, 1996; Hogarth & Chase, 2011; Todd et al., 2012). The most effective course of action is of course to not learn them in the first place. It follows then, that policy makers should focus their efforts on prevention, by, for example, protecting children from excessive (unhealthy) food advertisements. Indeed this matter has already received interest from some policy makers, with a number of countries increasing regulation of food advertising aimed at children (Hawkes & Lobstein, 2011; Matthews, 2008).

To summarize, the present study provides evidence that food-associated cues can interfere with goal-directed food-seeking that is sensitive to satiation. In the absence of cues, participants were perfectly capable of directing their actions away from (Smarties or popcorn) food rewards on which they had been sated. However, presentation of cues that had previously been paired with these food rewards led to increased responding for the signaled reward, independent of satiation. In addition to providing evidence for the role of this outcome-specific PIT effect in human food-seeking, we also show that food-associated cues will enhance the vigor of responding generally. The latter effect may be more sensitive to satiation, but this remains to be further investigated. In conclusion, we provide evidence that Pavlovian-instrumental interactions provide a mechanism whereby the obesogenic environment, that constantly reminds of available and palatable food, leads to excessive food-seeking. This fundamental, associative mechanism may consequently contribute to the recent rise in obesity. This study furthers our understanding of maladaptive food-seeking behaviors and may have important clinical and policy implications.

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