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## ABSTRACT

Cues associated with tasty foods, such as their smell or taste, are strong motivators of eating, but the power of food cues on behaviour varies from moment to moment and from person to person. Variation in the rewarding value of a food with metabolic state explains why food cues are more attractive when hungry. However, cognitive processes are also important determinants of our responses to food cues. An urge to consume a tempting food may be resisted if, for example, a person has a longer term goal of weight loss. There is also evidence that responses to food cues can be facilitated or inhibited by memory processes. The aim of this review is to add to the literature on cognitive control of eating by reviewing recent evidence on the influence of working memory and episodic memory processes on responses to food cues. It is argued that processing of food information in working memory affects how much attention is paid to food cues in the environment and promotes the motivation to seek out food in the absence of direct contact with food cues. It is further argued that memories of specific recent eating episodes play an important role in directing food choices and influencing when and how much we eat. However, these memory processes are prone to disruption. When this happens, eating behaviour may become more cue-driven and less flexible. In the modern food environment, disruption of cognitive processing of food reward cues may lead to overconsumption and obesity.

## 1. Introduction

Food reward processes underlie the motivation to seek out and consume certain foods (Berridge, 1996). We learn that some foods are good to eat, in that they evoke a pleasurable hedonic response (they are "liked"). As a result of this learning, cues associated with those foods (e.g. the sight and the smell of the food) acquire the ability to attract our attention and the foods become sought after (they become "wanted") (Berridge, 1996). Recent investigations of the role of food cues on eating behaviour suggest that they increase both food specific and general desire to eat, as well as enhancing hedonic responses to food when it is eaten (Fedoroff et al. 2003; Ferriday & Brunstrom, 2011; Johnson, 2013). Just seeing an advert of a tasty food can trigger the urge to seek out something to eat and increase our enjoyment of eating.

Much progress has been made in identifying the neural substrates of food reward (Richard, Castro, DiFeliceantonio, Robinson, & Berridge, 2013). Brain opioid, GABA, cannabinoid and orexin systems mediate "liking" via coordinated activity in a network of hedonic hotspots in the nucleus accumbens, ventral pallidum and brainstem (e.g. Peciña & Berridge, 2005; Mahler, Smith, & Berridge, 2007; Higgs, Williams, & Kirkham, 2003; Higgs & Cooper, 1996; for a review see Castro & Berridge, 2014). Whereas, the mesolimbic dopamine system is crucial for food "wanting" (e.g. Pecina, Cagniard, Berridge, Aldridge, & Zhuang, 2003; Tindell, Berridge, Zhang, Pecina, & Aldridge, 2005; Wyvell & Berridge, 2000; for a review see Castro & Berridge, 2014).

How we respond to food cues varies according to a number of factors. Food is more attractive and tastes better when we are hungry and becomes less appealing when have just eaten (Cabanac, 1971). Evidence has accumulated to suggest that the neural systems of food reward interact with circuits that respond to changes in metabolic state (homeostatic networks), thus providing a mechanism via which food deprivation or repletion affects eating pleasure and desire (Berthoud, 2011). Food reward waxes and wanes depending on metabolic state but also according to individual differences: people who are obese respond more strongly to food cues than do lean people when satiated (Castellanos et al., 2009). It has been suggested that differences in the brain mechanisms of both food "wanting" and "liking" might underlie this differential responding (Berridge, Ho, Richard, & DiFeliceantonio, 2010). For example, genetic differences in opioid and dopamine signalling may promote responsiveness to food rewards leading to

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compulsive eating (Davis et al., 2010). However, our response to food cues also depends on higher level cognitions such as expectations about how eating a food will make us feel. The aim of this paper is to review the literature on cognitive processes and food reward responding, with a particular focus on recent work which suggests a role for working memory and episodic memory processes in responses to food reward cues. The implications of this research for our understanding of overeating will also be discussed.

## 2. Cognitive processes and food reward

### 2.1. Goal directed learning, expectations and habits

The sight of a tasty food may elicit appetitive behaviours, such as a desire to eat, but it will also generate predictions (expectations) about the consequences of eating a food and its associated reward value based on past experience of similar outcomes (Balleine & O'Doherty, 2009; Dickinson, 2012). In this type of learning, associations are made between the act of eating a particular food and the outcome of eating. On encountering the same food again, eating will be facilitated if the predicted outcome is a desired goal at that moment (Dickinson, 1985). For example, imagine you are deciding whether to buy a chocolate cake or an apple. If you have not eaten for a long time and are very hungry, then buying the chocolate cake may be the favoured action because you have learnt in the past that an energy dense option is more satisfying when hungry. Specific actions such as buying a chocolate cake from a particular shop might also be favoured if you have learnt from repeat purchases that the chocolate cake from that shop is very tasty. Such goal directed behaviour is flexible in that the action that leads to the best outcome can be chosen from a range of possibilities (de Wit & Dickinson, 2009). However, over time, behaviour may become more habitual and automatic (Dickinson, 1985). If we get used to eating chocolate cake with our lunch then that context may elicit the response of buying chocolate cake even if eating the cake ended up not being that enjoyable because we were already quite full.

### 2.2. Short versus long-term goals: the role of dietary restraint

There are both immediate and longer term consequences of eating a particular food that are considered when responding to food cues (Rangel, 2013). Immediate consequences are hedonic pleasures associated with tasting a palatable food and delayed consequences might include understanding of the effects of overconsumption of certain foods on health or dieting goals. Both these types of consequences are taken into account when making food choices (Rangel & Hare, 2010). A person who takes into account longer term health consequences of eating choices is less likely to respond to a palatable food cue by choosing to eat it than a person who does not take the delayed consequences into account (Hare, Camerer, & Rangel, 2009). In this way, eating behaviour is adaptable to circumstance: if we have a longer term goal of, say, avoiding fattening foods, then an urge to consume a tempting food may be resisted.

These data are consistent with the notion that dietary restraint relies on higher level cognitive control to inhibit immediate appetitive response to palatable food cues (Polivy & Herman 1985). Various models of self-control suggest that the ability to resist an immediate reward in favour of a longer term goal depends on balanced activation in two neural systems: 1) an executive decision system involved in impulse control that is associated with activity in lateral and medial regions of the prefrontal cortex and; 2) a system for computing reward value of an outcome that is associated with activity in areas such as the orbitofrontal cortex/ventromedial prefrontal cortex and striatum (e.g. Heatherton & Wagner,

2011; Koffarnus, Jarmolowicz, Mueller, & Bickel, 2013). In support of these models, there is evidence that attributes relating to the healthiness of a food may be incorporated into decision making only when there is modulation of reward-related signals computed in ventro-medial prefrontal cortex (vmPFC) by the dorsolateral prefrontal cortex (dlPFC) (Hare et al., 2009, 2011). Further, it has been argued that the balance between impulse control and reward systems is prone to disruption if there are other competing cognitive demands (e.g. Ward & Mann, 2000), or if there are repeated self-control efforts (e.g. Vohs & Heatherton, 2000), perhaps explaining why restrained eaters may engage in counter-regulatory behaviour and dieting attempts often fail (Herman & Mack, 1975; Herman & Polivy, 2004).

An imbalance between inhibitory control mechanisms and reward processes may explain why some people are more prone to overeating and gaining weight than are others (Carr, Daniel, Lin, & Epstein, 2011; Price, Higgs, & Lee, 2015). Obese individuals have been reported to be less good at inhibiting responding to cues that signal an action that should be withheld than are lean individuals (e.g. Nederkoorn, Smulders, Havermans, Roefs, & Jansen, 2006). Failure of response inhibition is a facet of impulsive behaviour and is linked to overconsumption of palatable foods (Hall, 2012; Hofmann, Friese, & Roefs, 2009). Obese individuals are also less willing to delay receipt of a smaller monetary reward in favour of a larger monetary reward, which may relate to both enhanced reward responding generally, but also reduced inhibitory control over reward-related responses (Bickel et al., 2014; Jarmolowicz et al., 2014; Weller, CookAvsar, & Cox, 2008). However, it remains unclear whether difficulties with response inhibition predict increases in body weight or whether reduced control over food-related responding is a consequence of obesity or repeated dieting attempts.

### 2.3. External cues modulate expectations

Expectations about foods can be altered by external information such as logos, labels and even social context. It has been reported that just labelling a food as "healthy" reduces expected liking for that food (Raghunathan, Naylor, & Hoyer, 2006; Wansink, 2003). This probably reflects cognitive modulation of computation of reward value (Grabenhorst, Schulte, Maderwald, & Brand, 2013). In a similar fashion, other types of external information, such as price, affects responses to food products via changes in processing of reward value (McClure et al., 2004; Plassmann, O'Doherty, Shiv, & Rangel, 2008). Labels may also promote attention to longer term goals such as health or weight concerns (Papies, 2012) and may promote greater self-control via changes in reward-related processing of food cues. A recent study found that red traffic light food labels increased coupling between dlPFc and vmPFC (Enax, Hu, Trautner, & Weber, 2015), a pattern of brain activation seen during successful dietary self-control (Hare et al. 2009).

We have reported that providing information about the food preferences of others affects liking expectations (Robinson & Higgs, 2012). After exposure to information suggesting that other students do not much like orange juice, participants tended to believe that they themselves liked orange juice less than a group of participants who were exposed to neutral social information about orange juice. This effect was item specific in that information about liking of orange juice had no effect on liking for a similar drink (apple juice). The effect was also specific to the type of social information provided because expected liking for orange juice was significantly lower only when participants were provided with information about the preferences of an in-group and not when the information came from an out-group. One explanation for these results is that social norms modulate expectations about the consequences of

consuming that food (Higgs, 2015a).

### 2.4. Expectations affect actual food liking

Expectations affect food choices but also influence liking of a food once it is consumed (Grabenhorst, Rolls, & Bilderbeck, 2008). Expecting a food to taste good can enhance the eating experience (Cardello & Sawyer, 1992). For example, the presentation of visual cues previously associated with a sweet drink enhances liking for less sweet drinks (Kuenzel, Zandstra, Deredy, Blanchette, & Thomas, 2011). This phenomenon, known as assimilation, probably helps us deal with ambiguous stimuli by taking advantage of past experience to resolve uncertainty. If we are unsure whether we will like a food based on how it looks or smells, our expectations strongly influence our responses in the direction of the expectation. An experimental illustration of this point is that the hedonic evaluation of an odour (a component of food flavour) can be highly liked if the expectation is that it emanates from cheese rather than body odour (de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005). However, when a large difference between the expected and actual stimulus is perceived, this generates surprise, which leads to a contrast effect rather than assimilation (Deliza & MacFie, 1996). For example, Yeomans and colleagues found that when a frozen salmon mousse was presented as an ice-cream, leading to expectations of sweetness, actual liking for the mousse was much less than when the same mousse was presented as a frozen savoury mousse. In other words, the large discrepancy between the expected sweetness and actual fishy taste resulted in an exaggerated dislike response (Yeomans, Chambers, Blumnethal, & Blake, 2008). Hence, the same food can produce different hedonic responses depending upon what the consumer brings to the eating occasion in terms of their expectations.

### 2.5. An expanded view of cognitive processes in appetite

Research to date suggests that responses to food cues are governed by prior learning about the consequences of eating. Cognitions such as expectations and goals affect our responses to food cues via changes in the reward value assigned to food. Memory processes are integral to learning about the rewarding consequences of eating. Stored associations of the relationships between food cues, eating behaviours and the consequences of eating acquired over repeated experiences underpin our responses to food cues. However, there is growing interest in the role of other types of memory processes in appetite control. There is now evidence that working memory is important in determining the attention we pay to food cues. There is also evidence that memory for specific eating episodes (episodic memory) affects food choice and decisions about how much and when to eat.

## 3. Working memory processes and responses to food cues

### 3.1. Attention to food-related cues

We have hypothesised that maintenance of food-related information in working memory guides attention to food cues, meaning if people are already thinking about food, they are more likely to notice food cues in the environment and may be more responsive to those cues than if they were not thinking about food. Soto and colleagues reported that holding information about an object in working memory affects visual attention. Information held in working memory, and forming a mental image of an object, caused attention to be drawn to similar stimuli presented as part of a visual search task (Soto, Heinke, Humphreys, & Blanco, 2005). These data suggest that attentional biases towards food could be mediated by

food-related cognitions. In support of this idea, we have reported that when participants are asked to memorise a food picture (an experimental induction to increase food-related thoughts) they subsequently show an attentional bias towards food pictures (Higgs, Robinson, & Lee, 2012). Guidance of attention by the contents of working memory may be adaptive in allowing us to more efficiently detect objects that are relevant to current behavioural goals, for example being better at locating food when hungry.

We further found that thinking about food was more effective in guiding attention than thinking about neutral stimuli was, which is consistent with the high motivational significance of food (Higgs et al., 2012). The suggestion that food stimuli are strongly represented in working memory is supported by evidence from brain imaging studies. We found that electrophysiological measures of attention and memory (the P3, LPP and SPCN components) were larger when food was kept in working memory than when non-food items were memorised (Rutters, Kumar, Higgs, & Humphreys, 2014). These data suggest that inhibition of food thoughts may be challenging because food-related stimuli have privileged access to working memory. This could be especially problematic for people who are preoccupied with thoughts of food because they could be over-responsive to food cues. Indeed, attentional biases towards energy dense palatable food cues food cues have been linked to increased food intake and weight gain (Calitri, Pothos, Tapper, Brunstrom, & Rogers, 2010; Polivy, Herman, & Coelho, 2008).

### 3.2. Food cravings

Once a food cue is attended to, this can bring to mind intrusive thoughts about food, especially if one is hungry (Berry, Andrade, & May, 2007). The extent to which these intrusive thoughts influence behaviour has been suggested to depend on how they are elaborated in working memory (Kavanagh, Andrade, & May, 2005). While food cues may stimulate appetitive behaviour, conscious urges and plans to obtain and consume food depend on further cognitive processing of cues in working memory. For example, the sight of a chocolate bar might elicit a desire for chocolate. However, it is the mental embellishment of the initial thought, for example, extending thoughts about wanting the chocolate bar to how it will taste, that transforms it into a craving for the target of the thought. This processes is different from unconscious "wanting" processes but is likely triggered by "wanting" processes (Robinson & Berridge, 1993). A function of the maintenance of elaborated food imagery in working memory may be the facilitation of food seeking in the absence of direct contact with specific cues (Kavanagh et al., 2005).

Support for the idea that mental elaboration in working memory underlies food cravings comes from studies in which participants are asked to perform a cognitive task while imagining food. Performance of such tasks reduces working memory capacity and is associated with reduced reports of food craving (e.g. Kemps, Tiggemann, Woods, & Soekov, 2004). Conversely, if imagination of eating is the primary task, then performance on a concurrent cognitive task is reduced, which provides support for the idea that maintenance of food imagery in working memory consumes cognitive resources (Green, Rogers, & Elliman, 2000; Higgs, 2007).

Some individuals appear to be more sensitive than others are to food-related intrusive thoughts, including those with a higher BMI and dieters (Israel, Stolmaker, & Andrian, 1985 Kemps & Tiggemann, 2005). It may be that failure to inhibit the elaboration of intrusive thoughts about food results in a reduced ability to dampen responses to food cues, for example when in a satiated state, which could explain tendencies towards overeating in the absence of hunger (Martin & Davidson, 2014). This suggests that manipulating the contents of working memory could provide a

basis for interventions to reduce food cravings. There is evidence to suggest that trying not to think about food once a thought has been retrieved is very difficult, and may in fact be counterproductive in attempts to reduce food cravings, because suppression increases the frequency of the intrusive thoughts (Wegner, 1994). However, it has been reported recently that a simple intervention that interferes with working memory, which involves merely watching a flickering pattern of random black and white dots, can successfully reduce food cravings (Kemps & Tiggemann, 2013).

### 3.3. Implications

If food-related thoughts and memories are accessible, perhaps due to a current mind-set of food preoccupations, then an intrusive thought elicited in response to a food cue may be more likely to be elaborated in working memory, which could enhance food cravings and attention paid to food cues in a reinforcing cycle: greater attention to food may increase thoughts of food which further enhances attention to food and the likelihood of consumption. Therefore, individual differences in the level of food preoccupation or how food thoughts are elaborated in working memory are likely to affect responses to food cues. Indeed, we have found that dieting traits moderate the effects on attentional selection of holding food-related information in working memory (Higgs et al., 2015). Unsuccessful dieters appear to be easily primed by food stimuli and show strong attentional guidance from working memory to food stimuli, whereas successful dieting is associated with inhibition of food cues in working memory and reduced guidance of attention to food cues via memory. This pattern of results may be explained by differences in the types of thoughts that are activated when food cues are held in working memory. Successful dieting has been associated with the activation of health-related goals rather than hedonic thoughts related to food stimuli (Fishbach, Friedman, & Kruglanski, 2003; Papies, Stroebe, & Aarts, 2008a, 2008b), which may affect how attention to food is guided by working memory. The neural response to food cues of obese women has also been shown to be affected by current mind-set. Obese women showed greater activity in reward-related brain areas than did lean women when they focused on the taste of the pictured foods but showed less activation when they merely viewed the pictures (Frankort et al. 2012).

## 4. Episodic food memories, expected enjoyment and food choice

When we see a food we have an expectation of how it will taste based on accumulated past experiences stored in memory, but we may also recall memories of eating that food in a specific context and at a specific time, such as remembering enjoying a meal in a particular restaurant or the last time we ate an apple (Kahneman, Krueger, Schkade, Schwarz, & Stone, 2004; Robinson & Clore, 2002). There is evidence that these episodic memories influence the food choices we make (Higgs et al. 2012). The reason for this may be that we use episodic memories to mentally simulate the outcomes of specific choices, which allows the best outcome for that moment to be selected (Daw & Shohamy, 2008; Lengyel & Dayan, 2008). For example, when considering what to order from a restaurant menu we may rely on our experience of eating in that restaurant to play out the consequences of alternative choices. If the memory of eating a particular dish in that context is very positive then this might bias our decision. Interestingly, it has been further argued that these mental simulations based on memory occur automatically when faced with a choice and generally without conscious awareness (Wang, Cohen, & Voss, 2015). The idea that many of the cognitive processes that underpin appetite

control operate without conscious awareness may explain why eating appears as if it is a "mindless" process (Wansink, 2006), when in fact there is a high level of cognitive processing involved in every day dietary decisions (Herman & Polivy, 2014).

### 4.1. Episodic recall and expected liking and intake

Two studies have investigated the effect of episodic recall on later food choice. Recall of a specific occasion when vegetables were eaten and enjoyed led to increases in expected enjoyment of eating vegetables and an increase in vegetable choice (Robinson, Blissett, & Higgs, 2011a). The effect of recalling a specific vegetable eating episode was compared with the effects of recalling eating another "healthy" food item (to control for experimental demand effects), the effects of visualising someone else eating carrots (to control for priming effects) and a neutral control condition. Only recall of a specific eating episode affected expected liking, which suggests that participants may have been using the content of the memory to predict how enjoyable it would be to eat vegetables, which resulted in them choosing vegetables to eat.

### 4.2. Manipulating episodic food memories: effects on remembered enjoyment and food choice

In another two studies, we examined the effect that manipulating the memory of an eating episode had on remembered enjoyment and choice of the same food the next day (Robinson, Blissett, & Higgs, 2012). We reasoned that if decisions about what to eat are influenced by recent experiences of eating that same food, then manipulating post-meal consolidation of that food memory would affect later choice and intake. In the first study, participants in the experimental group ate a meal and immediately afterwards were asked to write down their thoughts on the enjoyable aspects of the meal they had just eaten. This rehearsal was predicted to affect consolidation of hedonic aspects of the meal memory. Another group of participants wrote down their thoughts about enjoyable aspects of a meal they had eaten the previous day. This was to control for the effects of thinking about eating enjoyment per se. A final group of participants wrote down their thoughts about neutral aspects of the meal. This condition controlled for rehearsing the meal without concentrating on its enjoyable aspects. We found that the actual meal enjoyment was the same for all groups, but remembered enjoyment differed according to condition. When participants rehearsed what was enjoyable about the meal immediately after eating, they later remembered it to be much more enjoyable than did participants in the control groups. The second study was similar but here we also assessed the effect of the memory manipulation on food choice and intake the day after the memory manipulation. The study was presented as an investigation of the effects of food on mood. At the first test session, the participant ate the target meal and the meal memory was manipulated, via post-meal rehearsal of the eating episode. To reduce demand characteristics, this session was presented as a screening day to test for eligibility. When the participants returned the next day, ostensibly for a different study, they were offered a buffet lunch that included the food they had eaten the previous day. They were asked to choose what they would like to eat for lunch from the buffet. No participants guessed the aims of the study, but the group that had rehearsed the positive aspects of the meal the previous day, chose and ate twice as much of that food at the buffet than did a group that had rehearsed neutral aspects of the meal (Robinson et al., 2012). Taken together, the data from these studies suggest that remembered enjoyment of a food can be altered and that this has effects on later food choice and intake.

### 4.3. When do episodic memories affect expected liking?

The extent to which our responses to food are affected by recent episodic memories of eating those foods depends on the familiarity of the food item and the recency of the experience (Robinson, Blissett, et al., 2013; Robinson, Daley, et al., 2013; Robinson, Higgs, et al., 2013). We have reported that expected liking can be reduced if a person consumes a food that they expect to enjoy but actually enjoy less than they expected (Robinson, Blissett, et al., 2013; Robinson, Daley, et al., 2013; Robinson, Higgs, et al., 2013). When a food is familiar, a recent disappointing hedonic experience reduces expected liking for that food assessed the next day, but this effect is short-lived because if expected liking is assessed a week after the disappointing experience, then no effect of the disappointing consumption episode is evident. When a food is less familiar, the effects of the disappointing eating episode are more long lasting and expected liking is reduced at least one week after the disappointing experience. One explanation for these findings is that liking expectations are affected by specific memories when they are highly accessible, which is the case when the experience is recent (Conway, 2009). When episodic memories are less accessible, people may be more likely to rely on semantic-knowledge and intuitive theories about frequently consumed foods when making judgements (Robinson & Clore, 2002). However, the extent to which such semantic knowledge about food is used to predict liking will depend upon how familiar someone is with a food. People are likely to have built up knowledge about familiar foods and may revert to using that information more quickly for familiar foods than for less familiar foods, for which such information is has yet to be accumulated (Robinson, Blissett, et al., 2013; Robinson, Daley, et al., 2013; Robinson, Higgs, et al., 2013).

### 4.4. What factors influence the encoding of episodic food memories?

How episodic memories influence decisions about food choice and intake will depend upon what is encoded in memory. Memory for an event is far from an exact replica of what was actually experienced because there is selectivity in encoding (Conway, 2009). This means that enjoyment of an experience, such as a holiday, is often much better in the telling than the reality because specific moments, such as the most pleasant or most recent, have a disproportionate influence on memory (Ariely & Carmon, 2000; Redelmeier & Kahneman, 1996). The same appears to be true of eating experiences. There is evidence that how much participants report having enjoyed eating a food is influenced by the final few moments of the experience and the peak level of enjoyment (Robinson, Blissett, & Higgs, 2011b). Interestingly, the final moments of an eating experience have also been reported to be the best predictor of repeat purchase of a food product (Garbinsky, Morewedge, & Shiv, 2014). However, memory is also dependent upon the type of food eaten and characteristics of the eater such as their level of dietary restraint (Robinson, 2014; Robinson et al., 2011b) and so there may be no simple rules that dictate what will be remembered about eating a food. Nevertheless, these data, along with similar results from studies of painful experiences (Kahneman, Fredrickson, Schreiber, & Redelmeier, 1993), indicate that it is the remembered experience rather than the actual experience that is more strongly associated with future choices. An implication of this idea is that healthy food choices could be promoted by changing what is remembered about a food rather than its physico-sensory properties (Higgs, 2011).

## 5. Memory for recent eating, satiety and reward

We are able to recall from memory how enjoyable a food was to eat was but we also encode in memory other attributes relating to how much has been eaten. These memories allow us to predict the physiological after effects of eating. There is now a significant body of evidence suggesting memory for recent eating is factored into decisions about how much to eat (Higgs, 2002; for reviews see Higgs, 2008; Higgs et al., 2012). Of course, both information about current physiological state and the memory of recent consumption influence appetite, but in line with the view that an important function of memory is to be able to more reliably predict the future by utilising past experience, the memory of the perceived energy content or size of a meal may be more effective in inhibiting subsequent intake than are the internal signals produced by the meal itself (Brunstrom et al., 2012). Using memory for recent eating rather than a read out of current physiological state to predict the effects of future consumption is advantageous because prior knowledge about the satiating effects of foods can be taken into account.

### 5.1. Manipulating memory for recent eating affects later food intake

Boosting memory for recent eating by facilitating recall or enhancing encoding of food memories decreases later intake (Higgs, 2002; Higgs, Williamson, & Attwood, 2008; Higgs & Donohoe, 2011; Higgs, Williamson, Rotshtein, Humphreys, 2008; Robinson, Kersbergen, & Higgs, 2014). Importantly, the effect of meal recall is dependent on the time delay between eating the lunch and recalling the meal: there is a bigger effect of recall when more forgetting of the meal has occurred, suggesting the involvement of memory processes (Higgs, Williamson, & Attwood, 2008; Higgs, Williamson, Rotshtein, et al., 2008a). There is also some evidence that enhancing chewing of a food at lunch may decrease later intake via an increase in lunch memory (Higgs & Jones, 2013). Encoding of episodic food memories can be disrupted if participants are required to engage in a secondary activity, such as watching TV or playing a computer game, while eating (Higgs & Woodward, 2009). The effect of distraction at a meal to increase later intake has been replicated many times and is related to measures of meal memory (Higgs, 2015b; Mittal, Stevenson, Oaten, & Miller, 2011; Moray, Fu, Brill, & Mayoral, 2007; Oldham-Cooper, Hardman, Nicoll, Rogers, & Brunstrom, 2011). Moreover, amnesic patients who are unable to recall recent eating will eat multiple meals in quick succession, suggesting that memory of recent eating usually inhibits responses to food cues after eating (Hebben, Corkin, Eichenbaum, & Shedlack, 1985; Higgs, Williamson, & Attwood, 2008; Higgs, Williamson, Rotshtein, et al., 2008; Rozin, Dow, Moscovitch, & Rajaram, 1998).

### 5.2. What are the underlying mechanisms?

The hippocampus may be involved in the inhibitory effects of recent eating on subsequent consumption. Amnesic patients who eat multiple meals share common damage to the hippocampus, which is thought to account for their memory deficits (Higgs, Williamson, & Attwood, 2008; Higgs, Williamson, Rotshtein, et al., 2008). They also have damage to other areas of the brain such as the amygdala, which means it is difficult to attribute the eating problems to specific damage to the hippocampus. However, rats with selective lesions to the hippocampus show similar disruption to their eating, including disturbance of meal patterns and overeating (Clifton, Vickers, & Somerville, 1998; Davidson & Jarrard, 1993; Davidson, Kanoski, Tracy, et al., 2005; Davidson, Kanoski, Walls, et al., 2005). Furthermore, temporary inactivation

of the hippocampus of rats accelerates the onset of the next meal (Henderson et al., 2013). It has been proposed that memories of recent eating encoded in the hippocampus may inhibit eating by signalling whether eating is likely to be followed by rewarding post-ingestive consequences (Davidson, Sample, & Swithers, 2014; Higgs, 2005).

Davidson and colleagues have theorised that cues associated with nutritional status influence eating behaviour by modulating associations between food-related conditioned stimuli and the post-ingestive consequences of eating (Davidson, Kanoski, Schier, Clegg, & Benoit, 2007, 2014). Importantly, they note that in relation to eating, the same food cues are associated with rewarding consequences on some occasions, for example at the start of meal, but may be associated with a lack of rewarding consequences or even aversion on others, for example at the end of a meal. Hence, both excitatory and inhibitory associations are formed between food cues and post-ingestive outcomes. The ambiguous nature of the associations between food-related cues and consequences means that additional signals must be used to predict when eating will be followed by positive rewarding consequences and when these consequences will be absent. Rats can learn that the presence of certain states, such as those arising from different levels of food deprivation, predict whether further eating will result in positive consequences (Benoit & Davidson, 1996; Bouton, 2004; Davidson et al., 2005; Kanoski, Walls, & Davidson, 2007). For example, a satiated state promotes the inhibitory connection between food cues and post-ingestive outcomes, thereby reducing conditioned responses to food cues. Theoretically, any discriminative cue that signals whether an event will be followed by a rewarding stimulus could function in the same way to inhibit eating (Davidson et al., 2014). This raises the possibility that the memory of the most recent eating episode inhibits eating by providing information about the consequences of future consumption (Higgs, 2005).

An outstanding question about the role of memory for recent eating in appetite is the nature of what is encoded in memory that is important for inhibiting intake. There is some evidence that information related to perceptions of the amount of food consumed may be critical. For example, Mittal et al. (2011) found that distraction during a meal affected the amount of food that participants recalled eating. Similarly, Brunstrom et al. (2012) found that a manipulation that altered participants' perception of the amount of soup they had eaten affected later intake. However, there are other possibilities that remain to be tested such as the influence of memory for bodily state feelings at the end of the meal on later intake. It may be that information about how much food was consumed is combined with information about internal state at the end of the meal to make a prediction about future satiety, which then modulates responses to food cues.

### 5.3. Implications

Episodic food memories contribute to flexible and adaptive responding to food cues because they provide a basis for predicting the value of a food in a particular context, thus allowing behaviour to be tailored to current needs. For example, a flexible response to a food cue would be adapting our decision about whether to buy a chocolate cake on seeing it in a shop, based on knowledge that while we generally like chocolate cake, the cake from that particular shop was remembered as disappointing the last time we ate it. Or, not choosing chocolate cake from a dessert trolley in a restaurant, because eating it is likely to lead us to feel uncomfortably overfull. An intriguing hypothesis is that a tendency to overeat may result from an imbalance between flexible cognitive control over eating (that relies to some extent on episodic memory) and habitual responses that are driven by the mere presence of food cues (e.g. Furlong, Jayaweera, Balleine,

& Corbit, 2014), perhaps due to impaired episodic food memories. In other words, reduced cognitive control over eating may bias someone towards an automatic response to choose chocolate cake if it is available, regardless of the predicted outcome. In the context of an environment that is replete with food cues, disruption to cognitive control could lead to weight gain over time if there is no compensation for the additional calories. Indeed, given evidence that the physiological signals that underpin our ability to compensate engage learning and memory processes, a reduced ability to compensate would be predicted if these processes are disrupted (Davidson et al., 2007, 2014). In support of this idea, there is evidence that overweight and obesity are associated with learning and memory problems (for reviews see Smith, Hay, Campbell, & Trollor, 2011; Prickett, Brennan, & Stolwyk, 2014; Coppin, Nolan-Poupart, Jones-Gotman, & Small, 2014). However, whether obesity is caused by impaired cognitive control of appetite, or, obesity, and/or dietary patterns associated with obesity, impair cognitive control, is unclear. In fact, it has been argued that both associations exist (Martin & Davidson, 2014). Furthermore, the extent to which impaired cognitive control of eating accounts for different types of obesity is not known. Overly habitual responding to food cues may be more associated with later onset obesity and less associated with obesity that is co-morbid with binge eating disorder, although this is speculative and warrants investigation. The specific idea that episodic memory deficits may be linked with reduced flexibility in responding to food cues, overeating and obesity, also requires evaluation, not least because attention to food cues has been reported to be elevated in obesity (Castellanos et al., 2009; Yokum, Ng, & Stice, 2011) and this might be expected to enhance memory encoding. To understand these relationships better it will be important also to consider how attention and memory interact in obesity (Martin & Davidson, 2014). For example, it is possible that enhanced reactivity to food cues is related to a more general deficit in inhibiting unwanted thoughts, leading to food preoccupations (Ebneter, Latner, Rosewall, & Chisholm, 2012), which may interfere with episodic memory formation to promote overeating. If this is the case, then strengthening episodic food memories could help people avoid overeating in response to the presence of food cues that would normally promote consumption (Robinson, Daley, Jolly, et al., 2013). This could be achieved by using external cues such as photographs to remind people of previous eating (Robinson, Higgs, Daley, et al. 2013).

### 6. Conclusions

Taken as a whole, the data reviewed here suggest that high level cognitive processes, such as working memory and episodic memory processes, affect eating by modulating our responses to food reward cues. If these cognitions are disrupted, then eating behaviour may become less flexible and more habitual. Greater appreciation cognitive processing of food reward cues will be important in understanding the unique flexibility of human food choices and the conditions that might promote overeating.

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