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Cognitive processing of food rewards

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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

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