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Research review

Evolved to satisfy our immediate needs: Self-control and the rewarding properties of food

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Abstract

Evolutionary explanations of overeating in modern society emphasize that humans have evolved to eat to their physiological limits when food is available. The present paper challenges the idea that eating is driven by the availability of food only and proposes that it is regulated by strategic anticipatory behaviour in service of the most profitable long-term scenario as well. Our alternative explanation emphasizes the interaction between the reward system that regulates the liking and wanting of food and the role of self-control, which is involved in maintaining the best outcome in the long run.

Keywords: Evolution; Self-control; Reward; Overeating; Iowa gambling task

Contents

Introduction

It is widely acknowledged that an important stimulus for eating is not hunger but the anticipated pleasure of eating determined by the sensory qualities of palatable foods (Pinel, Assanand, & Lehman, 2000; Woods, Schwartz, Baskin, & Seeley, 2000). But does this also imply that humans have a tendency to gratify their immediate needs about eating without any consideration of the future consequences of immediate consumption whatsoever? Evolutionary accounts of overweight in modern society tend to answer this question in an affirmative way, as there may be no adaptive benefit in patience or waiting for other, better foods (Kacelnik, 2003). Such explanations emphasize that humans have evolved to eat more than is required to meet their immediate nutritional needs (Pinel et al., 2000). Whereas this behaviour was once adaptive in an environment characterized by scarce food supplies, it has become maladaptive in the modern environment in which a variety of foods with highly rewarding value are almost always available. Indeed, the human eating system did not evolve to cope with the continuous exposure to highly tempting foods such as French fries, hamburgers or

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chocolate cookies (Loewenstein, Hsee, Weber, & Welch, 2001; Pinel et al., 2000). The maladaptive response of overeating under conditions of abundance is often explained in terms of difficulties to resist the temptation of the immediately rewarding value of palatable foods. However, from an evolutionary perspective it seems more likely that humans (and other animals) would be able to attribute proper value to delayed rewards when it enhances the chance of maximizing their long-term gain. That is, that they would be able to exert self-control and deny immediate rewards in the interest of delayed but bigger rewards—in modern society: a slim body, physical health, and longevity (which may be quite different from the bigger food rewards our ancestors were expecting; we will deal with this issue later). The capacity for self-control has been regarded as "one of the defining features of human evolution, contributing some of the central abilities that have made human beings distinctively human" (Vohs & Baumeister, 2004, p. 3), which makes it a probable candidate for understanding in what way people deal with immediate gratification when this may turn against their long-term interests.

The view that self-control may have played an important role in human evolution of (eating) behaviour seems at odds with the dominant evolutionary explanation that immediate pleasure from food drives decisions about food intake. The issue we want to address in this paper is to what extent both views are compatible. When it is true that anticipated pleasure of eating has proven a powerful device to protect us from future famine, does this imply that the role of self-control or delaying the gratification of one's immediate needs is by definition limited? Or does it imply that under some conditions people may be able to exert self-control and benefit from it, even when confronted with the pleasure of highly rewarding foods? We discuss in what way self-control interacts with the system that deals with the rewarding properties of food and examine under which environmental conditions self-control may, or may not, attenuate the reward system with regard to food intake. Before we do so, we will first discuss the biological underpinnings of the reward system involved in the regulation of eating.

Rewarding properties of food

Two essential components of the reward system that regulates eating behaviour are the hedonic experience of eating and appetitive behaviour involved in attempts to obtain foods (Kelley, Baldo, Pratt, & Will, 2005). The hedonic experience or sensory pleasure of eating is determined by the palatability of foods and has been labelled as 'liking' (Berridge, 1996; Berridge & Robinson, 2003). 'Liking', under control of opioids, deals with the immediate appraisal of food items and has been shown to be active when subjects (rats) are more or less sated (Barbano & Cador, in press). When hungry (not sated) it appears that the specific qualities of food items are of less relevance than the mere consumption of food items per se, leading to the ingestion of large quantities of food regardless of their hedonic quality (Kelley et al., 2005). Opioid-induced overeating behaviour in sated subjects, especially of highly palatable and caloric food, serves to increase fat stores that promote survival under conditions of future famine. It may thus be hypothesized that the role of opioid-mediated 'liking' and consumption of foods becomes stronger when basic nutritional needs are met (Barbano & Cador, in press; Berthoud, 2004; Kelley et al., 2005).

The second component of the reward system relates to the degree to which anticipated pleasure is translated into action (Berridge, 1996; Berridge & Robinson, 2003). The disposition to act upon previously liked food items, also labelled as 'wanting', is under control of dopamine and involves the willingness to engage in activities to obtain desired foods (Van den Bos, Houx, & Spruijt, 2002; Van den Bos & Cools, 2003; Salamone & Correa, 2002; Spruijt, Van den Bos, & Pijlman, 2001). Animal studies of 'wanting' behaviour have shown that subjects (rats) show higher levels of anticipatory activity prior to the arrival of food when hungry than when they are sated—thus demonstrating the opposite pattern from 'liking' behaviour, which proved to be higher in sated subjects (Barbano & Cador, in press). Moreover, it appears that only when food items are relatively new or rare, or when the arrival of the standard meal has been recently changed under conditions of rendering it temporarily more palatable, anticipatory behaviour remains under control of dopamine and is thereby sensitive to environmental features (Barbano & Cador, in press; Kas, Van den Bos, Baars, Lubbers, Lesscher, Hillebrand et al., 2004). When standard or regular foods are involved, anticipatory behaviour remains under control of other (probably lower) systems in the brain and is thereby relatively insensitive to environmental features (Van den Bos & Cools, 2003). It seems plausible then that animals become more sensitive to new items or are willing to exert more effort for such items when a shortage exists in their current situation. This seems an adaptive response to a less than optimal condition.

Animals (including humans) may learn to appreciate (want and like) a great variety of different food items, which can be obtained at different locations and may vary in quality. An important issues therefore is how they select the best strategy of foraging, balancing the costs and benefits of different options, which calls for an examination of the role of environmental factors.

Uncertainty in the environment

Variation in environmental commodities, such as the quality of foods or the costs associated with obtaining foods, is a fact of everyday life for all animals (except perhaps humans living in modern society, but see later) and introduces a considerable amount of uncertainty about the prospects of obtaining food. Of course it is impossible to reduce this uncertainty to zero as animals would be required to spend all their efforts on getting information on their surroundings, which would run right against fulfilling nutritional needs. Ongoing behaviour, then, is a compromise between 'information gathering' and 'satisfying physiological needs': when subjects are hungry they should go to the easy-to-find sites with the lowest cost–benefit ratios, when they are not (or less) hungry they should explore, update information and eat while on the way. This is essentially what Inglis, Langton, Forkman, and Lazarus (2001) have described in their information primacy model of animal exploration and foraging behaviour in an uncertain environment.

Whereas the foregoing is especially relevant for animal behaviour, the same kind of reasoning may be applied to human eating behaviour too. When confronted with uncertainty in the expectancy of larger food rewards, humans tend to become less willing to wait for these bigger rewards (King & Logue, 1992). This finding suggests that, even though there is no absolute uncertainty about food supplies in modern society (quite the contrary, indeed), humans may experience relative uncertainty about when and where they will have access to food again. From an evolutionary viewpoint it has even been argued that humans continue to behave as if they are uncertain about the availability of food, which might explain their maladaptive response in the presence of sufficient food (Logue, 1988). It is also important to note that humans face uncertainty in terms of deciding about what is the most profitable long-term scenario: should they opt for immediate gratification of their needs with the risk of compromising their health in the long run; or should they invest in the best long-term options at the cost of denying their immediate needs? Thus, although different in nature from the type of decisions animals have to make about foraging, it may be argued that humans are confronted with considerable uncertainty in their decisions about the intake of food too.

As dealing with uncertainty is such a prominent feature in decisions about food, monitoring the attention paid to the internal budget on the one hand and exploratory activity on the other hand seems of utmost importance and gives credit to the assumption that some amount of self-control is required to decide about the efforts spend on immediate gratification and those spend on long-term scenarios. In the next section we will examine the role of self-control in more detail.

Self-control

Self-control is often referred to as the choice of a more-delayed outcome that is ultimately of more value over a less-delayed outcome that is ultimately of less value (Ainslie, 1974; Logue, 1988). Although this definition of self-control emphasizes the ability to restrain impulses for immediate gratification, it also incorporates elements of consideration of the future consequences of behaviour—thus emphasizing the strategic nature of self-control. Although self-control seems a feature that is unique to humans, many studies assert that animals are capable of self-control too, albeit to a lesser extent than humans (Ainslie, 1974). Despite its importance for engaging in the most profitable long-term scenario, animals and humans alike have difficulties in demonstrating self-control under uncertain conditions. As stated earlier, the inability for patience may have adaptive benefits when delayed rewards are not likely to occur. Nevertheless, the foregoing suggests that it may be worthwhile to examine how self-control affects decisions about immediate gratification against delayed gratification.

The Iowa Gambling task (IGT, Bechara, Damasio, Damasio, & Anderson, 1994) has proven a valid paradigm for examining the role of self-control when exposed to the temptation of immediate big rewards The IGT mimics the essential features of real-life decision making under conditions of uncertainty and requires participants to choose from four decks of cards that provide losses and gains in money: two decks have high gains but even higher losses, and two decks have low gains but lower losses. In the long run (within the time limits of the test) the high gain–high loss decks are disadvantageous, whereas the low gain–low loss decks are advantageous. It is generally found that as the task proceeds, normal subjects learn to choose from the 'good' decks and avoid the 'bad' decks (Bechara et al., 1994; Tranel, Bechara, & Damasio, 2000), thus demonstrating a capacity for self-control that involves the (implicit) recognition of long-term winning options. In people with a diversity of disinhibited behaviours such as substance dependencies or pathological gambling, IGT performance is generally poor, however, as these individuals tend to continue choosing from the disadvantageous decks—even when they realize that it compromises their performance on the task in the long run (Bechara & Martin, 2004; Goudriaan, Oosterlaan, De Beurs, & Van den Brink, 2005). Recently, it has also been demonstrated that overweight women (BMI $>$ 25) perform poorly on the IGT compared to lean individuals (Davis, Levitan, Muglia, Bewell, & Kennedy, 2004), demonstrating the relevance of this approach for understanding failures in the regulation of eating behaviour.

(Van den Bos and colleagues 2006; Van den Bos, 2004) have suggested that different brain systems are involved, depending on the stage of the test. In the early stage of the IGT the reward system is active, necessary for learning the best long-term options by assessing and integrating trial-by-trial wins and losses; but when the test proceeds the role of self-control becomes more apparent, aiding in maintaining the choice for options for which pay-off lies ahead in the future. Two recent studies using different but related paradigms (temporal discounting paradigm, McClure, Laibson, Loewenstein, & Cohen, 2004; Markov decision task, Tanaka et al., 2004) have confirmed the idea of two systems being involved in the regulation of behaviour at different time-scales: the fast-acting, immediate pay-off prone, dopamine-sensitive reward system and the slow-acting long-term pay-off prone, serotonin-sensitive self-control system (Daw, Kakade, & Dayan, 2002). In our lab, we have recently observed that individuals who are less inclined to discount the future (i.e., who are able to attribute proper value to delayed outcomes) perform better on the IGT, suggesting that both paradigms may assess the same underlying processes (Kuijer, De Ridder, Ouwehand, Houx, & Van den Bos, submitted for publication).

Interpreted in terms of the information primacy model (Inglis et al., 2001), these findings suggest that individuals initially explore the decks to learn their specific features in the context of the instruction to earn as much money as possible. Dopamine plays a role in facilitating to explore the environment, while sustaining a negative budget for a long period of time (Fiorillo, Tobler, & Schultz, 2003; Salamone & Correa, 2002; Spruijt et al., 2001). When the relevant task-features have been sufficiently explored and learned, the balance between budget and exploration is shifted towards maintaining a positive budget. Based upon the information gathered in the exploratory phase self-control helps in maintaining the once chosen advantageous options and dampens the tendency to respond to the risky, but tempting big rewards (Daw et al., 2002; Katz, 1999).

Overweight in modern society

The foregoing suggests that the reward system and self-control interact in such a way that optimal foraging behaviour is a balance between maintaining strategies that have proven to provide the best long-term benefit and remaining sensitive to environmental changes that are relevant to food. As stated earlier, the environment in which the reward system and self-control operate affects how the balance between both is maintained or compromised. How then does this relate to the epidemic of overweight in modern society? Until now, evolutionary accounts of failure to regulate eating in the midst of plenty have focused on the ‘liking’ part of the reward-system, emphasizing the pleasure of eating as a powerful mechanism to protect from future famine (Pinel et al., 2000; see also Mela, 2006). Yet, the ‘wanting’ part of the reward-system seems more sensitive to environmental variability as it directly relates to the amount of effort individuals are willing to (or must) spend to obtain food and is therefore a more promising candidate to explain maladaptive over-consumption from an evolutionary perspective—especially as this relates to an imbalance between the reward system and self-control.

Two factors seem especially relevant for understanding the ‘typical modern’ imbalance between the reward system and self-control. The first factor relates to the rewarding value of modern foods. The rewarding properties of modern food-items may be so powerful that ‘wanting’ is extremely activated and thus overrides self-control. In our own studies of the IGT we have observed that increasing the immediately rewarding value of the long-term loosing decks, while keeping the net losses per deck intact, increases the chance that participants will take more cards from these disadvantageous decks (Van den Bos, Houx, & Spruijt, 2006). Enhancing the rewarding properties of some items relative to others thus increases the chance that individuals cannot suppress responding to them, even though they know that this choice will turn out disastrous in the long run. The contrast between small and big rewards under conditions of uncertainty strongly enhances tonic activity in the dopaminergic system (Fiorillo et al., 2003), which may contribute to the observed increase in exploratory or risk-taking behaviour and concomitant loss of self-control (Van den Bos et al., 2006). One may argue that exposing humans to an environment with a large variety of foods that differ in rewarding value makes them extremely vulnerable to the strongly rewarding food items that are immediately available. The perceived reward of food has proven an important factor in self-control of humans: if they like the immediate food better they show more impulsiveness; if they like the delayed food better, however, they demonstrate self-control (Forzano, Porter, & Mitchell, 1997).

Whereas the presence of highly rewarding foods may make individuals vulnerable to the satisfaction of immediate needs, we have also found that people may become more sensitive to their long-term winning scenario. In one of our studies with the IGT in young women who were concerned about weight gain, we observed that implicitly reminding them of their long-term weight goals improved their performance on the IGT significantly compared to the performance of women who were not reminded of these goals (De Ridder, Kuijer, & Ouwehand, submitted for publication; Kuijer et al., submitted for publication; see also De Ridder & Kuijer, 2006). It also thus appears that more abstract health goals are relevant for deciding about the gratification of immediate needs against delayed rewards.

The second factor that is relevant for understanding an imbalance between the reward system and self-control relates to the role of stress. Although many studies have asserted that the experience of stress does not increase the consumption of food in non-restrained individuals (Greeno & Wing, 1994), a recent study suggests that even though stress does not affect the total amount of caloric intake it does increase the proportion of highly palatable ‘comfort foods’ ingested (Pecoraro, Reyes, Gomez, Bhagava, & Dallman, 2004). Also our own studies suggest that acute (but not chronic) stress increases the wanting of palatable food—which may act as a compensation for negative experiences and/or the restoration of the energy balance (Spruijt & Van den Bos, 2006). Whereas this compensatory mechanism may have been adaptive in an environment with relatively few palatable food items, it seems quite maladaptive in a society characterized by the abundance of such foods, making it very easy to compensate on each and every occasion of stress without few costs. Although the role of ‘comfort food’ is still under debate, the observation that stress is a precipitating factor for the addiction to many (classes of) substances and increases the wanting of these substances demonstrates that stress may be an important factor in compromising the delicate balance between the reward system and self-control (Volkow & Wise, 2005).

Conclusion

We have argued that it is likely that self-control plays a greater role in regulating eating behaviour than hitherto assumed. Humans and animals alike may not be driven by the rewarding value of food only as this would run right against maintaining a profitable long-term scenario in many cases. A dynamic interaction between the reward system and self-control seems a more plausible explanation of the way decisions are made about food intake under natural, thus uncertain conditions. For humans, there may be no uncertainty about the availability of food in modern society but they are still confronted with decisions about whether or not consuming food when available when this may run right against their long term benefits—thus introducing uncertainty about delayed rewards in terms of future health. As the abundance of food in our society is a reality, it may be the omnipresence of highly rewarding palatable foods that is an important factor in compromising a balanced decision about the trade-off between short-term gains and long-term gains.

That said, it is important to make two additional remarks. The first is that the findings on the dynamic interaction between the reward system and the cognitive control system mostly involved monetary rewards. Yet, a number of studies suggest that individuals may respond differently to food rewards than to money rewards in a way that food rewards tend to generate relatively more impulsive behaviour, probably related to the fact that its rewarding properties are time-constrained (Forzano & Logue, 1994).

The second, and even more important, remark is that most research in this domain involves decisions comparing immediate and delayed rewards of the same kind, i.e. small amounts of money versus bigger amounts of money or, for that matter, small portions of food versus bigger portions of food (Logue & King, 1991) This comparison may lack validity for the decisions individuals in modern society are required to make about food. The delayed reward for refraining from immediately available foods is not receiving a larger portion at a later time but a reward of a far more abstract nature requiring some reasoning that these rewards are worthwhile striving for, viz. good health (or at least the absence of illness). And even though humans, in contrast to other species, can understand that excessive consumption leads to obesity and ill health, and have the potential to prevent these problems by cognitively overriding the powerful attraction of highly rewarding foods (Pinel et al., 2000), research on restrained eating has proven that in most circumstances dieting is not a feasible strategy (cf. Polivy & Herman, 2006). Good health may not even be perceived as a reward at all but taken for granted (until one becomes ill, of course). This implies that declining immediate foods is not reinforced by a delayed reward but by avoiding future risk, which is quite a difficult task given that decisions on either or not engaging in risky behaviour are not guided by a consideration of the possible consequences (Loewenstein et al., 2001). Research employing a delay discounting paradigm confirms that people discount future health outcomes even steeper than money rewards (Chapman, 2003), which may be related to the fact that good health in the future, if regarded as a reward at all, may not be appreciated as a delayed reward but as a probalistic reward as refraining from food is not a guarantee of future health (cf. Holt, Green, & Myerson, 2003). Put in different terms, choosing the long-term benefit of (potential) good health is not equivalent to maximizing overall gains. As adult humans tend to prefer overall maximization instead of choosing long-term benefits (Logue, King, Chavarro, & Volpe, 1990), they may behave rationally if they opt for the gratification of some immediate needs as well. When there is a great uncertainty that they will ever receive the more delayed outcome, then there may be no point in waiting: the future is uncertain, eat dessert first (Fantino, 1995; cf. Kacelnik, 2003). With these remarks in mind it must be emphasized that our recent findings concerning the role of long-term health goals in performance on the IGT are promising because they demonstrate that people may be more prepared to delay gratification when they are made aware of these abstract goals.

In many aspects of our culture but especially with regard to food consumption, self-control is considered good and impulsiveness bad. However, such moral judgments are not appropriate as self-control is not inherently good and lack of control inherently bad. Sometimes the most profitable long-term scenario involves patience and self-control and sometimes it does not. Our analysis of the role of self-control in attenuating the rewarding properties of food does not imply that individuals who are overeating should be criticized for their impulsive behaviour. However, understanding the psychological and biological underpinnings of deciding about immediate rewards against long-term gains involved in the regulation of eating may contribute to the explanation of overweight in modern society.

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