

A Neuroeconomics Approach to Obesity

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Running title: A neuroeconomics approach to obesity

Keywords: Decision-making, reinforcement-learning, behavioral economics, intertemporal choice, uncertainty, energy balance

ABSTRACT

Obesity is a heterogeneous condition, affected by physiological, behavioral, and environmental factors. Value-based decision-making is a useful framework for integrating these factors at the individual level. The disciplines of behavioral economics and reinforcement learning provide tools for identifying specific cognitive and motivational processes that may contribute to the development and maintenance of obesity. Neuroeconomics complements these disciplines by studying the neural mechanisms underlying these processes. Here we survey recent literature on individual decision characteristics that are most frequently implicated in obesity: discounting the value of future outcomes, attitudes towards uncertainty, and learning from rewards and punishments. Our survey highlights both consistent and inconsistent behavioral findings. These findings underscore the need to examine multiple processes within individuals in order to identify unique behavioral profiles associated with obesity. Such individual characterization will inform future studies on the neurobiology of obesity, as well as the design of effective interventions that are individually tailored.

Value-based decision-making in obesity

Over the last 50 years, obesity rates in the United States have nearly tripled and 40% of American adults are now considered obese (1). Obesity has detrimental health consequences to the individual, and leads to tremendous costs to society (2). From a biomedical perspective, obesity results from sustained energy imbalance, with intake exceeding expenditure (3). This imbalance is affected by a myriad of factors, including both individual characteristics (genetic, neurobiological, and psychological) and environmental influences (cultural, economic, and public policy) (4). In recent years, there has been a growing understanding of the need to identify behavioral profiles that may be associated with obesity (5). A useful framework for integrating many of the signals influencing feeding behavior is that of value-based decision-making. In this framework, decisions about energy consumption and expenditure involve maximization of “subjective value” or the utility of the choice to the individual decision-maker. The subjective value of a food option can be computed by integrating over its different attributes (6) - including smell and taste (7), perceived health, (8) and nutritional content (9) - together with the decision-maker’s goals (e.g. losing or gaining weight) (10) and satiety level (11). Subjective values are also influenced by the same factors that affect virtually any decision we make: the balance between potential rewards and punishments (consuming highly palatable junk food at the cost of impaired health), likelihood estimates (the food is bound to be rewarding, but consuming it has uncertain health outcomes), and the temporal schedule of potential outcomes (the food is rewarding now, but may lead to impaired health in the future). While under some circumstances these individual characteristics can be modified (12), they are broadly considered stable traits (13,14). Individual differences in any of these processes may therefore play a role in the development and maintenance of obesity.

The disciplines of behavioral economics and reinforcement learning combine experimental designs that tease apart various decision characteristics with computational modeling, revealing otherwise unobservable latent variables. In behavioral-economics research, participants make a series of choices between options whose values vary parametrically across different attributes, such as the reward offered, the likelihood for reward, the time of receiving it, and the cost for obtaining it. In reinforcement learning paradigms, participants sample different available options, experience the outcomes of their choice, and learn to identify the better options. Behavior in those paradigms can be used to infer individual decision characteristics such as sensitivity to reward, aversion to uncertainty, discounting of future rewards, and the rate of learning associations between cues and outcomes. Neuroeconomics research combines these behavioral methods with neurobiological techniques to study the neural basis of value-based decision-making. The latent variables revealed by the behavioral

analysis are used in the neural analysis to identify biomarkers and functional patterns that relate to behavioral dimensions like risk and delayed rewards (15).

Neuroeconomics research implicates striatal and prefrontal regions in encoding the subjective value of available options (Figure 1). Activity in the ventral striatum and ventromedial prefrontal cortex (vmPFC) scales as a function of subjective value (16) across different domains (17), including food (18), and integrates over various nutritional attributes (19). These subjective value representations incorporate individual characteristics, such as attitudes towards uncertainty (20) and temporal discounting of future rewards (16). Striatal and prefrontal areas are both targets of midbrain dopaminergic inputs from the ventral tegmental area (VTA) and substantia nigra (21). Phasic activity of these dopamine neurons encodes reward prediction error – the discrepancy between expected and obtained reward (22).

In the case of food choices, value representations are likely modulated by homeostatic signals (18). Hormones such as leptin, ghrelin, and insulin control satiety, hunger, and fat levels by targeting neurons in the hypothalamus and brain stem, whose activity can promote or inhibit feeding behaviors and energy expenditure (23). Most relevant for the present review is the contribution of homeostatic signals to value computations. Rather than two separate pathways, the homeostasis and value systems work in concert to influence behavior (6,24).

A number of studies have applied the neuroeconomics approach to psychiatric research (25) and identified associations between specific symptoms and unique features of decision-making and learning across a wide range of disorders (26–30). Recent studies have begun to apply a similar approach to obesity, yielding interesting findings and mixed results. This review aims to highlight the potential of the neuroeconomics approach to provide an integrative perspective on obesity by surveying the literature and identifying directions for future research. In the following sections, we review studies that use behavioral economics and reinforcement-learning experimental paradigms to study decision-making in obesity (Supplementary Table 1). Our review focuses on human studies with healthy participants but is also informed by research on eating disorders and animal studies. We also examine to what extent these potential links are domain-specific (only occur in the food domain) or domain-general (occur in both monetary and food domains) (Figure 2).

We identify both consistent and variable findings across studies. In addition to methodological differences between studies, we suggest that these differences reflect the heterogeneous nature of obesity. Thus, we propose that longitudinal studies of multiple decision characteristics within individuals should be used to create an individualized behavioral profile as a basis for behaviorally informed neurobiological research.

Intertemporal preferences

Food choices have outcomes that extend beyond the present moment. In particular, options that are more immediately gratifying (such as high-calorie and high-fat food) are often more detrimental to our future health (Fig. 2.A). For most people, subjective values of future rewards diminish over time, a phenomenon known as temporal discounting (31). To estimate individual discount rates, economists typically ask participants to make a series of choices between rewards of different magnitudes that are received at different times (e.g., would you rather have \$20 now or \$40 in a month?).

Activation levels in the valuation system, including the vmPFC and the striatum, are influenced by the delay in receiving the reward and by individual discount rates (16). Subjective value representations may be modulated by indirect inputs from dorsolateral prefrontal cortex (dlPFC) (32). Activity in this area and its connectivity with vmPFC were higher for choices of delayed, compared to immediate, rewards and were predictive of individual discount rates (33); disruption of activity in the same area increased preference for immediate rewards (34). Consistent with this role, dlPFC activity may inhibit choices of immediate food rewards (35) by modulating vmPFC activity for tasty but unhealthy foods (36).

Discount rates are quite stable within individuals (14,37), suggesting that they may be a personality trait and a potential marker for unhealthy behaviors. Indeed, higher discount rates are associated with addictive behaviors (38), including drug use (39), smoking (40), and gambling (41). Similarly, unhealthy food choices lead to immediate food rewards, but future negative health outcomes (Fig. 2A). Several scholars have suggested a similar association between high discount rates and unhealthy diet, which in turn is associated with obesity (42–44).

Empirical results, however, are mixed. Studies that examine food decisions consistently report increased delay discounting in individuals with obesity (45). Most studies, however, examine monetary choices, and in that domain, findings are more varied. Some studies identify increased discount rates in individuals with obesity compared to their healthy-weight counterparts (46–64), while others do not (65–69). One small-sample study reported lower monetary discounting in individuals with obesity compared to relatives without obesity, but this was specific to individuals committed to weight loss (70).

Findings in eating disorders are also mixed. For example, there are reports of either decreased (71) or increased (72) discount rates for women with bulimia compared to controls, and reports of either higher (63) or similar (73) discount rates in binge-eating disorder (BED) compared to controls.

Methodological differences may account for some of the mixed results in the literature, including the use of real or hypothetical rewards and the modeling approach. A recent review (42) suggested that incentive-compatible paradigms, in which participants receive real rewards based on the choices they make, were more likely to show correlation between steeper discount rates and BMI. Studies also differ in sample size, demographic characteristics, and criteria for obesity status. Still, even after accounting for all these factors, substantial variability remains.

Uncertainty preferences

Ecological decision-making often involves uncertainty. Individuals' idiosyncratic attitudes towards uncertainty, and their ability to tolerate it, may therefore play important roles in decisions about food consumption and energy expenditure (Fig. 2.B). Behavioral economics provides useful tools for estimating individual uncertainty attitudes in the laboratory (74). The simplest form of uncertainty is *risk* – when probabilities for different outcomes are fully known (e.g. 50% chance for heads or tails on a coin toss (75)).

There is some evidence that individuals with obesity and overweight individuals tend to be more tolerant of risk in the monetary domain compared to healthy-weight individuals (53,76–78). Interestingly, some studies suggest that increased risk tolerance in obesity is specific to men, whereas in women with obesity it is reduced or unaltered (79,80). This willingness to accept greater uncertainty for potentially higher rewards may also play a role in eating behavior, where choosing unhealthy but gratifying foods is accompanied by uncertain health outcomes.

Outside of the laboratory, probabilities for different outcomes are seldom precisely known - rather, they are at least partly ambiguous (81). Individual risk and ambiguity attitudes are not strongly correlated across individuals (82–84) and make distinct contributions to psychopathology. For example, individuals with posttraumatic stress disorder (PTSD) show increased aversion to ambiguous, but not risky, losses (30), while individuals with antisocial personality disorder are more tolerant of ambiguity than healthy controls (85). Similarly, transient increases in tolerance to ambiguity, but not risk, predicted relapses in opioid users undergoing treatment (82). These studies suggest that examining both risk and ambiguity attitudes in obesity may be beneficial.

Another important aspect of probabilistic decisions is that they typically involve a trade-off between gains and losses. Loss aversion – favoring the avoidance of losses over the pursuit of gains – is a widely observed phenomenon (86,87). Studies that utilized the prospect theory formulation of loss aversion (75) and estimated the loss aversion parameter from behavior in risky-choice tasks did not find a significant difference between individuals with obesity and healthy-weight groups (53,88). There is

some evidence, however, for increased sensitivity to losses in individuals with obesity. Participants with obesity were more risk-seeking than healthy-weight individuals specifically in trials that did not incur large losses (76), and exhibited greater neural differences between losses and neutral outcomes (89). Considering its potential centrality for health-related decisions, more studies that specifically target loss aversion using behavioral-economic approaches are still needed to clarify its role in obesity.

Just like temporal delay, value representations in ventral striatum and vmPFC incorporate individual attitudes towards risk and ambiguity (20,90), as well as loss attitude (17). The level of uncertainty is reflected by activation patterns in several brain areas including posterior parietal cortex (PPC) (83), anterior insula (91–93), and the lateral orbitofrontal cortex (OFC) and ventrolateral prefrontal cortex (vlPFC) (83,93–95). Activity in PPC (83,96,97), as well as its structure (98,99), reflects individual risk attitudes. The structural and functional connectivity of the amygdala also reflects risk attitudes (100). These studies outline potential neural mechanisms for increased risk tolerance that may promote obesogenic decision-making.

Overall, existing evidence suggests that, in some individuals, obesity may be associated with decreased risk aversion and increased loss aversion. Health-promoting behaviors, such as exercising and healthy diets can be viewed as “losses” compared to a present lifestyle that does not include them; at the same time, the negative outcomes of engaging in unhealthy behaviors are uncertain. Heightened aversion to perceived losses in lifestyle, amplified by an increased tolerance to the risk associated with these choices, may thus promote obesity-inducing behaviors.

Learning from Rewards and Punishments

Altered reward learning has been associated with obesity across a number of studies (101). To quantify learning abilities, simple paradigms present participants with repeated choices between several cues that are predictive of different outcomes, such as higher or lower rewards. In these tasks, learning is assessed by the rate and magnitude of preference that participants develop towards better alternatives. In individuals with obesity, there is some evidence for impaired learning on such tasks with both food and monetary rewards (102,103), but also evidence for improved learning with food (104). In learning from passive observation of outcomes, without active choice, women with obesity rated both cues that predicted food, and those that did not, as highly predictive of food (103); no such generalization effect was observed in the monetary domain, where women with obesity acquired correct stimulus-reward associations and were able to flexibly change them (103).

The inappropriate generalization of food reward-learning in individuals with obesity may result from a failure to learn from negative prediction errors (105). This failure may be part of a general learning

abnormality in some individuals (89,102), but specific to food in others. In this framework, impaired learning could contribute to obesity as the association between unhealthy food choices and unhealthy (“negative”) outcomes is not properly learned. Impaired learning was also reported in participants with anorexia (106), especially when learned cue-food associations had to be updated (107). However, when participants were explicitly told that only one cue can be followed by reward at any phase of the experiment (precluding generalization), individuals with obesity exhibited better learning with food (but not money) compared to healthy-weight controls (104). This suggests that subtle changes in the structure of the environment may have substantial effects on attention and learning.

Accumulating evidence points to alterations in dopamine function in obesity (108). In rodents, high-fat diets lead to alterations in dopamine signaling (109,110). In humans, high-fat diets correspond with changes in binding potential of D2/D3 dopamine receptors (111–114), indicating changes in receptor availability or dopaminergic tone (115). OFC is also heavily implicated in value encoding (116–118) and its role may be specific to updating values with new information (119). Failure to properly update value representations in OFC has been shown in animal models of addiction (120) and may be similarly involved in overeating. In a small study, activity in OFC tracked prediction errors more accurately in healthy-weight women compared to women with obesity (121). Women with anorexia included in the same study showed stronger encoding of prediction errors in OFC compared to healthy controls (121), suggesting dissociable mechanisms for impaired learning in obesity and anorexia.

The simple paradigm utilized in many of these studies is helpful in identifying robust learning differences but is not sensitive to more subtle aspects of learning. Two-stage learning paradigms (122) allow distinction between two reinforcement learning strategies, model-free and model-based (123). While model-free learning relies on simple cue-outcome or action-outcome associations, model-based learning strategies incorporate the structure of the environment into the decision-making process. Model-based learning is more computationally demanding than model-free learning, but it allows for more flexible and context-specific decisions. Thus, model-based learning is considered more goal-oriented, in contrast to model-free learning which is linked to habit-formation (124). The tendency to utilize model-free learning increased with BMI (125) and was more pronounced in individuals with binge-eating disorder (126). Similarly, reduced goal-directed learning correlated with the degree of obesity (127,128), suggesting a link between obesity and the use of model-free strategies. Under model-free learning, it may be harder to adapt previously advantageous habits, developed to conserve energy, to changes in the environment (129).

Furthermore, the greater reliance on model-free learning may serve not only as the cause for obesogenic dietary choices, but also as the outcome of such choices. Obesity-related changes in dopamine function likely influence reward sensitivity and learning and may underlie the greater

reliance on model-free learning (130,131) as well as the reduced learning from negative prediction errors (89,105). Predicting the direction of these effects is not straightforward, however, because dopamine signaling is affected by multiple direct and indirect mechanisms (132), which may vary nonlinearly with the degree of obesity (115).

A key concept driving food-related decisions is the extent to which pleasurable stimuli are rewarding, or the psychobiological trait of “sensitivity to reward.” Increased sensitivity to reward induces differential motivational drive that may promote excessive eating. Indeed, sensitivity to reward predicted emotional overeating (133), preference for foods high in fat and sugar, and BMI (134). A behavioral approach to estimate the subjective value of specific items uses paradigms that quantify food demand. In these paradigms, subjective value is estimated based on willingness to pay – the maximum price decision-makers are willing to pay to acquire an item (135), or willingness to work – the effort that participants are willing to exert to acquire an item, for example by repeatedly pressing a button (136). Several studies demonstrated higher willingness to work for food rewards in individuals with obesity compared to controls (136–138), but this pattern may reverse when physical effort is required (139). Interestingly, excessive eating is cost-dependent in some animal models such that obesity develops in low-effort environments but not in high-effort ones (140,141). This result suggests that rather than affecting the value of food, dopamine affected the rats’ motivation or sensitivity to effort (142).

In addition to testing the role of decision traits in food-related choices, animal models allow testing the reverse causal relation, the effect of specific dietary regimes on decision-making. In particular, the effects of the Western diet, a diet high in fat and sugar, were studied in relation to changes in feeding patterns and decision characteristics. When exposed to Western diets, rats developed binge-like feeding behavior (143) and demonstrated impairment in learning and cognitive functions (144,145). Moreover, rats that were chronically exposed to such diets experienced alteration in striatal areas that promote goal-directed behavior, leading to reduced sensitivity to outcome values (146). These alterations could relate to increased inflammatory markers in the hippocampus, a critical region involved in memory (147). These findings suggest a bi-directional relationship between impaired learning and obesity, whereby obesogenic diet is not only the outcome of impaired learning but also its cause. Together, these factors point to a potentially vicious cycle by which impaired learning is caused by obesity and then behaviorally aggravates it (148).

An additional perspective on food-related learning is the dysregulated food consumption associated with eating disorders. A few small-sample studies suggest that this dysregulation may be associated with alterations in the reinforcing value of food. For example, women with bulimia (n=10) worked more than controls (n=10) for food reward in a “binge” condition, but this pattern was reversed in a

condition that allowed participants to “drink comfortably” (149). More research, however, is needed to establish this connection between food-related learning and eating disorders.

From isolated features to holistic decision profiles

A mechanistic understanding of obesity is critical for devising behavioral and pharmacological interventions. Behavioral economics and reinforcement learning paradigms identify individual preferences that, interacting with the environment, can contribute to the development and maintenance of obesity. Neuroeconomic approaches validate these traits by identifying a neural basis for general traits and individual differences in behavior. A central concept in neuroeconomics is that of value: from an economic perspective, an obesogenic choice could result from altered subjective valuation. Emerging literature points to several features of value-based decision-making which may be linked to obesity, including increased preferences for immediate rewards, increased risk tolerance, and altered reward learning.

A bulk of the literature focuses on intertemporal choice. These studies suggest that individuals with obesity are, on average, more present-oriented compared to healthy-weight controls. While findings are quite consistent in the food domain, in the monetary domain results are mixed, with about half of the studies reporting no correlation between temporal discounting and obesity. This is one example for the potential role that neural measures can play in shaping our understanding of the mechanisms of obesity. While there is ample evidence for overlapping representations of value across domains (150), there are also unique neural substrates for food valuation (6,90). Valuation alterations in obesity may thus be unique to the food domain in some cases, but more general in others.

There is also some evidence for increased risk tolerance in obesity, although findings here are also mixed. To our knowledge, ambiguity - a type of uncertainty with unknown probabilities that is of particular interest for eating behavior - has not been studied in obesity using behavioral economics tools. Finally, reward learning seems to play a role in obesity. Obesity is associated with greater reliance on habit-like, model-free decisions in contrast to goal-oriented, model-based ones. It is also associated with less efficient utilization of new evidence for guiding future decisions, in both humans and animals. Similar to delay discounting, the domain specificity of the learning effects is not clear, with reports of both food-specific effects (103,104) and domain-general effects (102). Longitudinal studies are needed to explore the bi-directional causal relationship between obesity and learning in humans.

The strength of the neuroeconomics approach is the ability to tease apart specific computations that underlie the decision process. Studying the neural basis of obesogenic decision-making allows for the

development of biologically-sound behavioral models and thus a better understanding of the behavior leading to obesity. Obesity, however, is a multidimensional phenomenon of which individual decision-making is just one facet. There are bound to be substantial individual differences in the path to obesity, with subgroups of individuals exhibiting decision variations. We propose that the next stage in applying the neuroeconomics approach to obesity is to examine the various processes described here within individuals in order to construct individual behavioral profiles. Such examination is also important because the various decision characteristics are not independent. For example, individual uncertainty attitudes may be confounded with discount rates (151), or influence reinforcement learning (152).

These individual profiles are valuable because they may point to differences in the underlying mechanisms of obesity and guide individually tailored interventions. For example, behavioral nudges that make future consequences more salient are suitable interventions for domain-general steep discount rate (153–155) whereas food-specific learning impairments could be treated by easy-to-follow dietary guidelines and external reinforcement to successful compliance. Individual differences may also relate to population differences. In particular, existing literature already hints at sex differences in food-as-reward processing. Identifying age- and sex-dependent decision characteristics could reveal their true effect magnitudes and prevalence and serve as the basis for more effective targeting of interventions. Tracking these profiles in longitudinal studies is important for revealing the underlying causal structure of the association between different decision characteristics and weight status; for example, whether impaired learning is the source or the outcome of dietary decisions.

Many of the studies make some implicit assumptions. First, the prevalent comparison between healthy and unhealthy weights in the literature is useful, but implicitly assumes a linear relationship between weight status and the expected expression of a studied decision characteristic. However, different weight statuses, for example, overweight and obese, may be associated with different characteristics that define separate decision profiles. The non-linear relationship between obesity severity and dopaminergic tone offers neurobiological evidence that obesity is not necessarily “more of the same” behavior under overweight status (115). Second, most studies use BMI as an indication for obesity, but there is still debate on how accurately BMI defines obesity (156,157). Future studies should be aware of this heterogeneity and strive to better understand sources of obesity while being diligent in publishing “null findings”, e.g. those that do not identify discounting effects in population with obesity (158).

How could these understandings be used to help decision-makers make better decisions? Restructuring menus to make healthier choices more attractive and salient, and picking healthier defaults (159); distancing calorically dense products from checkout counters to discourage impulse

purchases (160); matching lower willingness to pay (demand) with cheaper supply of healthy foods; all these are examples of potential interventions that leverage the understanding of human decision-making to structure environments that promote healthier food choices. The behavioral economics and neuroeconomics approaches integrate environmental factors and individual dispositions by considering the potential gains and losses underlying choice. Applying these approaches to the study of the neural mechanisms underlying obesity-inducing behaviors provides a pivotal perspective on the understanding of the complex phenomenon of obesity and the design of effective interventions.

Acknowledgments

The work was supported by NSF grant BCS-1829439 and NIH grant R01MH118215 to IL.

We thank Megha Chawla, Or Duek, Ruonan Jia, and Ruby Larisch for very helpful comments on the manuscript.

Disclosure

The authors have nothing to disclose.

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Figure legends

Figure 1. A schematic model of value-based decision-making

Value representations in the medial prefrontal cortex integrate external information about potential rewards (delay, uncertainty) with internal representations of these rewards (learning, memory) and homeostatic demands. dlPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; Hipp, hippocampus; Hyp, hypothalamus; OFC, orbitofrontal cortex; PPC, posterior parietal cortex; vlPFC, ventrolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex; VS, ventral striatum; VTA, ventral tegmental area

Figure 2. Decision-making in the monetary and food domains. A. Temporal preferences depend on how subjective value diminishes over time. In the monetary domain, a preference for a small immediate monetary reward or a greater future reward is determined by an individual's discounting rate. Similarly, discounting of future health outcomes affects choices between outcomes with low immediate satisfaction (apple), but better future outcome (good health), and high immediate satisfaction (pizza), but worse future outcome. B. Decision-making under uncertainty is often assessed by testing choices between alternatives that vary in outcome and in the likelihood for obtaining that outcome. In the monetary domain, a "safe" alternative (right) is associated with a certain outcome (more generally, with reduced outcome variability), whereas a "risky" alternative provides a chance for a greater reward but also a chance for a smaller one. Analogously, in the food domain, a safe alternative (an apple) may provide lower satisfaction while a riskier, but more rewarding, option (pizza) may incur health costs with some probability. C. Rewards and punishments imply a gain or loss of money in the monetary domain. In decisions regarding food choice, some food items (pizza) may be more rewarding than others (apple). Food choices may also incur punishments in the form of deteriorated health status. In a process of learning, gains and losses are integrated into values that guide decisions.

