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Glucose-specific signaling effects on delay discounting in intertemporal choice

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HIGHLIGHTS

- Glucose ingestion reduces delay discounting, making future options more attractive.
- Different doses of glucose affect delay discounting in a non-linear manner.
- The effects are phagic (appetite related) instead of dipsian (thirst related).
- Only glucose, not all forms of sugar, signals energy budget and affects delay discounting.

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ABSTRACT

We propose that decisions related to resource management (e.g., intertemporal choice between a smaller-and-sooner reward and a larger-and-later reward) are sensitive to and regulated by fluctuating blood glucose levels. Circulating glucose affects intertemporal choice by means of signaling body energy condition instead of serving as a replenishing resource for effortful cognitive processing. We intend to dissociate calorie-supplying functions from glucose-unique anticipatory effects on behavioral resource management, measured by delay discounting in making intertemporal choices. Regarding the anticipatory functions of the glucose–insulin system in regulating the degree of delay discounting, we tested three predictions: First, we predict that the signaling effects of circulating glucose on delay discounting do not need to be dose-dependent as long as glucose fluctuation indicates a directional trend in body energy budget. Second, such effects of glucose fluctuation on delay discounting are phagic (appetite related) instead of dipsian (thirst related). Third, this glucose–insulin signaling system requires glucose as the specific input, thus is insensitive to other forms of sugar that are not insulin regulated. In Study 1, fasting participants were randomly assigned to one of five groups: water consumption, zero-consumption, and three glucose consumption (18 g, 36 g, and 72 g cane sugar/250 ml water) groups. The participants competed two sets of intertemporal choice questions with varying delay discounting rates before and after a beverage intervention. The results showed that the rate of delay discounting was negatively correlated to blood glucose levels. The effects of circulating glucose on delay discounting closely followed the changes in blood glucose levels showing a plateau on both dose-response curves (i.e., the sugar dose-blood glucose level curve and the sugar does-delay discounting curve). Secondly, the effects of circulating glucose on delay discounting were significant only in the glucose ingestion group, but not in the zero consumption and the water consumption groups, suggesting that the behavioral effects were in fact related to hunger-reduction instead of thirst-reduction. Study 2 revealed that glucose ingestion, but not water or another form of sugar (xylitol matched to glucose either for sweetness or for calories), reduced delay discounting, making future options more attractive. This result suggests that signaling of body energy budget is indeed glucose-unique. Our results suggest a forecasting mechanism of the glucose-insulin system for both metabolic and behavioral regulations of resource acquisition and allocation.

1. Introduction

1.1. Delay discounting in interfemoral choice

In this study, we examine the role of fluctuating blood glucose in regulating decision making related to resource management, particularly, delay discounting in making intertemporal choices between a smaller-and-sooner reward and a larger-and-later reward.

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When people are offered the choice between rewards available at different points in time, the relative values of the options are discounted according to their expected delays until delivery [2] . This choice phenomenon of delay discounting is also referred to as time discounting or future discounting. Present goods are preferred over future goods, both because delayed benefits may get lost altogether and because earlier reproduction generally yields a higher fitness value by leaving more time for future reproduction [47]. Deferral of gratification will occur only if it produces an increase in anticipated utility that more than compensates for the decrease in immediate consumption utility.

Since Paul Samuelson [37] proposed his discounted-utility model, it was accepted instantly, not only as a valid normative standard for public policies (e.g., in cost-benefit analyses), but as a descriptively accurate representation of actual behavior, despite of Samuelson's own reservations about the descriptive validity of the model. Within economics, finance, and psychology, a large literature has examined delay discounting functions. Two general types of discounting function over time, i.e., exponential discounting and hyperbolic discounting, have been proposed and tested.

Although classic models on delay discounting in economics and finance often assume an exponential function, humans and other animals typically behave as though they discount near futures at higher rates than more distant futures, such that experimentally assessed discount rates approximate a hyperbolic, rather than exponential, function of delay [23,25].

In general, intertemporal choices are related to resource management, ranging from choices of how much food to eat at a meal to financial planning and policy making, and are regulated by both behavioral and bodily mechanisms ([2,3,8]; Frederick et al., 2002; [46]).

1.2. Blood glucose as an anticipatory signal of bodily energy budget

Considerable evidence from both human and animal studies has accumulated indicating that circulating blood glucose as a metabolic and mental resource can facilitate cognitive functioning (for reviews, see [13,36,40]). However, most of these studies have focused on memory, attention, and verbal performance. Less is known about the effects of blood glucose levels on decision making. Similarly, the studies on the relationship between glucose and self-control typically measure self-control in the tasks of attention, response inhibition, or motor control. Most of these studies adopted a protocol of ego-depletion, where individuals are expected to show less self-controlled behavior on a consecutive task after having completed an initial self-control task. A popular account of ego deletion assumes that self-control consumes mental resource, and glucose ingestion can replenish depleted mental resources and help restore self-control [5,12,15,17,28,45]. More recently, this account has been challenged under empirical scrutiny. A growing body of literature indicates that the ego-depletion relieving effects of glucose have been overestimated and may be of negligible size (e.g., [11, 27,39,44]). It needs to be noted that unlike the ego-depletion paradigm, the present research examined the effects of blood glucose fluctuation on decision making without an "ego-depletion" procedure.

The studies of glucose effects on decision making yield mixed results, and there is no strong consensus on how to interpret these effects. For instance, changes in blood glucose levels have been found to regulate intertemporal choice [46], political attitudes toward welfare policies [1], and sensitivity to food and mating cues [35]. However, other researchers have failed to replicate the effects of glucose levels on delay discounting [26].[1] A recent meta-analysis [34] was conducted using the existing scholarly literature to determine what effects glucose has on decision-making tasks. Controlling for artifacts and construct validity, this most up-to-date meta-analysis estimated the size of the effect of glucose on decision making, in terms of willingness to pay, willingness to work, delay (future) discounting, and decision style. For the purpose of the present discussion, we focus on the 10 identified studies of glucose effects on delay discounting. The results of the meta-analysis revealed a significant, negative main effect of blood glucose levels ($r = -0.21$), indicating that glucose ingestion reduces delay discounting. The analysis also revealed a moderating effect of the type of reward (food vs. non-food), showing that the effect of *blood glucose on delay discounting is stronger for food rewards* ($r = -0.24$) *than non-food/monetary rewards* ($r = -0.17$).

Given these confirmed effects of blood glucose on delay discounting, the aforementioned meta-analysis also evaluated alternative theories of glucose effects. Overall, their results do not support a domain-general theory viewing glucose as a resource for all kinds of cognitive tasks. Instead, the results were more consistent with a signaling view of glucose as "an input that guides adaptive behavior" ([34], *p.* 559).

Based on the current understanding of glucose effects on decision making, we propose a glucose-specific signaling hypothesis to further explore the boundary conditions of glucose effects on decision making and test new predictions regarding glucose-specific effects on delay discounting. Since it is well-known that fluctuations in blood glucose levels indicate body energy conditions [7,31], its behavioral effects are most likely to affect decision behaviors that are also related to resource (metabolic or monetary) management. From this perspective of domain-specific signaling, blood glucose and money are both forms of resources as well as honest signals. Money informs richness and resource availability while blood glucose indicates body energy budget. Blood glucose is functionally similar to money in that money is a currency of gains and losses of external resource while blood glucose is a currency of bodily resource fluctuation. Thus, it is not the current blood glucose level but the increase or decrease in blood glucose levels following glucose ingestion or glucose restriction that results in behavioral changes in resource management. Foraging theories suggest that adaptive values of energy-budget-regulation rely on its anticipatory instead of reactive functions [42,46]. In the context of making intertemporal choices, anticipatory signaling via blood glucose fluctuations should not only affect internal metabolic functions but also behaviors related to external resource acquisition and allocation. When the body energy budget is negative, as indicated by low blood glucose levels, smaller-and-sooner rewards should be preferred over larger-and-later ones to avoid survival threatening consequences. In contrast, when body energy budget is positive, as indicated by high blood glucose levels, larger-and-later rewards should be favored over smaller-and-sooner ones because reserving resources for future use increases the chance of reproductive success. In other words, fluctuations in blood glucose levels regulate the extent of delay discounting for future rewards.

The signaling functions of glucose above and beyond its nutritious functions are also indicated in the studies showing that the taste of glucose without ingestion is motivating (e.g., [16]) and performance enhancing (e.g., [10]). Physiological studies also suggest that the sweet taste of glucose is innately attractive and highly motivating for many species, and is thought to function for detection of readily available carbohydrates [4] and serves as a unique conditioned stimulus that regulates appetitive behavior [6].

The thrust of the singling view is that glucose serves as an anticipatory and preemptive signal beyond its calorie-supplying function. Calorie-providing glucose is a natural candidate for signaling body energy budget and regulating behavioral resource acquisition and allocation accordingly. Fluctuating blood glucose levels indicate upcoming gains and losses in resource management and thus allow behavioral as well as physiological changes that are adapted to anticipated bodily conditions. Recent studies with bumblebees (e.g., [33]) showed that a drop of sugar drink that had no energy boosting effects speeded up foraging decision

[1] The Lange and Eggert study [26], despite the authors' claims to the contrary, suffers nontrivial methodological problems of its own. Experiment 1 of the study intended to "replicate counteracting effect of sugar consumption on ego depletion" (p. 57). However, a selective attention task with 528 trials was used to induce "ego depletion" without any outcome measures of its effects. Instead, delay discounting was measured before and after a sugar or diet drink, following the protocol of Wang and Dvorak [46] which originally did not include any "ego depletion" component before the beverage intervention. In addition, the participants (predominantly females) were required to refrain from eating for only 1.5 h prior to the start of the experiment, which was unlikely to establish a stable blood glucose baseline.