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Self-regulatory depletion in dogs: Insulin release is not necessary for the replenishment of persistence

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ABSTRACT

It has been hypothesized that self-control is constrained by a limited energy resource that can be depleted through exertion. Once depleted, this resource can be replenished by the consumption or even the taste of glucose. For example, the need to inhibit reduces subsequent persistence at problem solving by humans and dogs, an effect that is not observed when a glucose drink (but not a placebo) is administered following initial inhibition. The mechanism for replenishment by glucose is currently unknown. Energy transfer is not necessary, although insulin secretion may be involved. This possibility was investigated in the current study by having dogs exert self-control (sit–stay) and subsequently giving them (1) glucose that causes the release of insulin, (2) fructose that does not result in the release of insulin nor does it affect glucose levels (but it is a carbohydrate), or (3) a calorie-free drink. Persistence measures indicated that both glucose and fructose replenished canine persistence, whereas the calorie-free drink did not. These results indicate that insulin release is probably not necessary for the replenishment that is presumed to be responsible for the increase in persistence. This article is part of a Special Issue entitled: Canine Behavior.

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1. Introduction

Relative to other animals, humans have remarkable self-control. Some psychologists argue that this difference exists because humans have a sense of “self”, and the ability to compare their current self with that of a standard or idealized self (Baumeister and Heatherton, 1996). Some have proposed that the desire to behave in consonance with one’s standard or ideal self is what sustains self-control (Carver and Scheier, 1998; Baumeister et al., 1998). According to self-discrepancy theory, young children and animals may not be able to override their impulsive responding because they have not yet developed a self-concept (Higgins, 1987; Carver and Scheier, 2002). This perspective on human behavior reflects a belief in dualism, and although popular, it fails to account for common inhibitory processes and the neurophysiological mechanisms that maintain them. For example, Gailliot et al. (2007) have observed that human self-control is reliant on blood glucose, which is a limited physiological energy resource that can be depleted

through use. Requiring participants to exert self-control (by having them control their attention while watching a video) depletes their blood glucose levels and once depleted, participants persist less in solving word puzzles and make more errors on the Stroop task. But, if participants consume a replenishing glucose drink (but not a calorie-free placebo), these performance decrements are not observed (Gailliot et al., 2007). Analogous research has reported a similar phenomenon in dogs (Miller et al., 2010). Dogs that are required to control their physical movement and sit still for 10 min (in comparison to dogs placed in a cage for the same duration) show reduced persistence on an unsolvable puzzle task. Furthermore, a glucose (but not a sweet calorie-free) drink eliminates this effect.

According to Gailliot et al. (2007) the consumption of glucose replenishes persistence by raising blood glucose levels and providing direct energy for brain processes. Yet, a recent series of experiments by Molden et al. (2012) have challenged this metabolic hypothesis by investigating whether self-control exertion by humans reliably depletes systemic glucose levels and whether increases in blood glucose levels are necessary to observe the replenishment of persistence. Their results suggest that there are no self-regulatory induced decreases in blood glucose levels for participants who are food restricted for 4 h and tested in the evening with a perceptual vigilance task. Furthermore, Molden et al. (2012) observed that fasted participants, who rinsed their mouths

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with a sugar solution for 5 s after completing a depleting task, were replenished (as measured by increased persistence on a handgrip task and performance of the Stroop task) more than participants who rinsed with a noncaloric aspartame solution. Thus, the taste of glucose was sufficient for replenishing persistence even in the absence of increases in blood glucose levels. Subsequent research by Sanders et al. (2012) replicated these results. In addition, Hagger and Chatzisarantis (2013) observed that the taste of glucose also replenished human participants and increased persistence on an unsolvable anagram task more than the taste of an aspartame placebo.

The observation that the taste of glucose is sufficient for replenishing persistence argues that energy transfer is not necessary. Thus, it has been suggested that the oral detection of glucose by taste receptors replenishes by stimulating areas of the brain that affect motivation. The taste of glucose activates the anterior cingulate cortex (ACC) and the ventral striatum (Chambers et al., 2009), which are two regions of the brain involved in the representation of food rewards (Rolls, 2007), and are likewise involved in the motivation and regulation of goal-oriented behavior (Holroyd and Yeung, 2012; Harsay et al., 2011). Glucose also elicits the release of dopamine in the medial prefrontal cortex (Touzani et al., 2010). Accordingly, it is proposed that it is the dopaminergic activation of these regions by glucose that replenishes persistence (Chambers et al., 2009; Molden et al., 2012). This account is plausible; however, researchers have not yet eliminated alternative and perhaps complementary metabolic mechanisms.

Insulin release may be a metabolic mechanism that contributes to replenishment of persistence by glucose. The act of rinsing one's mouth with glucose has been shown to elicit a cephalic phase insulin response in humans (Goldfine et al., 1969; Yamazaki and Sakaguchi, 1986) in contrast to aspartame (Smeets et al., 2005; Bruce et al., 1987). Given that insulin is critical for neural processes (Mielke and Wang, 2011), and the administration of insulin to human and nonhuman animals improves cognitive abilities (Hajali et al., 2009; Schiöth et al., 2012), glucose induced release of insulin may contribute to replenishment. It is worth noting that cephalic phase insulin responses are elicited when taste receptors activate afferent fibers of the vagus nerve (Teff, 2011). The vagus nerve regulates autonomic functions such as heart rate and gastric function (for a review see Ruffoli et al., 2011) and it is of particular interest as it is also implicated in self-control (Thayer et al., 2009), and the depletion of persistence (Segerstrom and Nes, 2007).

The purpose of the current study was to examine whether insulin is a necessary contributor to the replenishment of persistence by glucose. To accomplish this objective, we investigated whether fructose, like glucose, would eliminate the deficits caused by initial exertion of self-control. Fructose does not directly provide energy for cellular processes, nor is it actively transported across the blood brain barrier like glucose (Simpson et al., 2007). In addition, it has little effect on blood glucose levels as it is digested primarily in the liver (Tappy and Le, 2010). The liver metabolizes fructose much like a lipid, and the energy is either converted to glucose or lactate (a process that takes hours, not minutes) or it is converted into glycogen (for a review see Sun and Empie, 2012). The stored glycogen then can be converted to glucose if necessary through glycogenolysis (Tappy and Le, 2010). Humans and dogs share this metabolic process (Shiota et al., 1998). Furthermore, the consumption of fructose does not increase insulin synthesis or secretion like glucose does, because insulin is unnecessary for metabolizing fructose by humans (Tappy et al., 1986; Tappy and Le, 2010) and nonhuman animals (Curry, 1989).

If insulin secretion contributes to self-control replenishment, then depleted subjects should be more replenished following the consumption of glucose than fructose or a calorie-free placebo.



Fig. 1. The Tug-A-Jug toy (available in three sizes from Premier Pet Products, Midlothian, VA) that was used to measure persistence.

However, if other mechanisms are involved which rely on the detection of carbohydrates, both fructose and glucose should be capable of replenishing persistence, but not a sweet calorie-free placebo.

This research was conducted with dogs using a conventional two-task paradigm (Baumeister et al., 1998). Self-control was manipulated by initially requiring dogs to sit still alone in a room for 10-min (stay) or caging them for the same duration (cage). Dogs were then presented with an unsolvable puzzle toy and their persistence was assessed.

2. Methods

2.1. Subjects

Dogs were selected as subjects for this study as it has been previously observed that requiring the exertion of behavioral inhibition by dogs depletes subsequent persistence, a deficit that can be eliminated by the consumption of glucose (Miller et al., 2010). Moreover, since dogs do not recognize themselves in mirrors and do not have a sense of “self” which some have theorized to be integral in human self-control (see self-discrepancy theory: Higgins, 1987), the results obtained would have general implications for the mechanism responsible for the depletion and replenishment of persistence.

We recruited 12 dogs (*Canis familiaris*; six males and six females), all privately owned by students and faculty of the Department of Psychology at the University of Kentucky. The dogs had been previously trained on command to sit and stay for at least 3 min using positive reinforcement. Owners deposited their dogs at the Canine Comparative Cognition Laboratory for further training and testing by researchers familiar to them. Three dogs were dropped from the experiment: one (female) died from an accidental injury, one (male) was dropped due to medical problems, and one (male) was dropped for behavioral reasons, leaving data from 9 dogs for analysis. The participating dogs' ages ranged from 24 to 96 months ($M = 52$ months); all had been spayed or neutered. Of the dogs that participated in the experiment there were 4 Golden Retrievers, a Soft-Coated Wheaten Terrier, a Cavalier King Charles Spaniel, a Boxer, and 2 dogs of mixed breeding.

2.2. Materials and training

Dogs were given a Tug-A-Jug toy (available in three sizes from Premier Pet Products, Midlothian, VA). This toy consists of a clear cylinder with a hole at the end through which treats can be obtained when the cylinder is appropriately manipulated (see Fig. 1). When dogs received this toy for training sessions it was half-filled with

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