

## The Effects of Initial Self-Control Exertion and Subsequent Glucose Consumption on Search Accuracy by Dogs

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### Psicología Comparada y Cognición Animal

#### Abstract

Previous reports have suggested that canine self-control is sensitive to fatigue and that an initial act of behavioral inhibition (sit-stay 10 min) relative to a control condition (cage 10 min) can deplete self-control, increase risk-taking, and reduce subsequent persistence on a puzzle task. Glucose, but not a calorie-free placebo drink has been shown to replenish this depletion. The current study sought to complement and extend these findings by examining whether initial exertion of self-control would also affect canine working memory as measured by search accuracy on a subsequently administered invisible displacement rotation task. The results evidenced that initial self-control exertion (relative to the control condition) resulted in poorer search accuracy. The consumption of glucose did not have a replenishing effect. If anything, glucose was associated with poorer search accuracy.

#### Key Words:

Self-control; Depletion; Glucose; Working-memory; Object Permanence.

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#### 1. Introduction

It has been observed that when dogs exert self-control (10 min sit-stay) on an initial task they then subsequently take more risks in a dangerous situation (Miller, DeWall, Pattison, Molet, & Zentall, 2012), and also persist less on a puzzle task in comparison to dogs that were not initially required to exert self-control (Miller, Pattison, Rayburn-Reeves, DeWall, & Zentall, 2010). Differences in persistence are eliminated when dogs consume a glucose or fructose drink following the exertion of self-control (Miller et al., 2010; Miller, 2012), but not by the consumption of a palatable sugar free placebo drink. These findings are analogous to those reported in the human literature (Gailliot,

#### Resumen

Evidencias previas han sugerido que el auto-control canino es sensible a la fatiga y que un acto inicial de inhibición conductual (permanecer quieto y sentado 10 min) puede agotar el auto-control, incrementar las conductas de riesgo y reducir la persistencia en un rompecabezas posterior. La administración de glucosa, pero no la de un placebo libre de calorías, ha mostrado revertir esta depleción. El presente estudio pretende complementar y extender estos hallazgos examinando si el esfuerzo inicial de auto-control puede afectar también a la memoria de trabajo en los perros medida como la eficacia de búsqueda en una subsecuente tarea de rotación de desplazamiento invisible. Los resultados muestran que el esfuerzo inicial de auto-control (relativo a la condición control) resultó en una menor eficacia de búsqueda. El consumo de glucosa no tuvo un efecto de reversión del agotamiento. Si tuvo algún efecto, la glucosa estuvo asociada a una menor precisión de búsqueda.

#### Palabras Claves:

Auto-Control, Agotamiento, Memoria de Trabajo, Permanencia de Objeto.

Baumeister, DeWall, Plant, Brewer, & Schmeichel, 2007; Miller, Bourrassau, & Blamplain, 2013) and suggest that self-control in dogs and humans is subject to fatigue, and that an initial act of self-control can impair the ability to evoke again behavioral control, a consequence that results in subsequent performance impairments that can be modulated by the consumption of carbohydrates.

It has been argued by Gailliot et al. (2007) that self-control is subject to fatigue because it relies on a limited energy resource. Initial acts of self-control deplete this resource and consequently impair controlled, but not reflexive responding. For example, controlling attention

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or inhibiting the consumption of a tempting food (but not an unappealing food) has been observed to reduce persistence, problem solving, increase aggression, and impair memory updating in humans (Baumeister, Bratslavsky, Muraven, & Tice, 1998; DeWall, Baumeister, Stillman, & Gailliot, 2007; Schmeichel, 2007). Since glucose can replenish depletion and eliminate these deficits, Gailliot et al. (2007) have suggested that depletion may represent a decrease in systemic and/or cerebral glucose levels, thus implying that the limited energy resource is physiological in nature.

The purpose of the current experiment was to complement and extend the previous research with dogs but, instead of examining the effects of self-control on risk-taking or persistence, we chose to examine working memory using an invisible displacement search task. Research with humans has observed that initial self-control impairs subsequent memory updating (Schmeichel, 2007). Thus, an initial act of self-control was likely to impair subsequent search accuracy by dogs, a possibility that merited investigation for practical reasons. Humans rely on dogs to search for hidden items such as food, drugs, and victims, and little is known about the situational variables that might

affect accuracy.

The version of invisible displacement selected was a rotation task. Here a food object is visibly displaced in one of two identical containers mounted on the ends of a rotating beam that is initially placed parallel to the dog (see Figure 1b). Following visible displacement, rotating the beam of the apparatus 90° to the left or right, so that the beam is perpendicular to the dog and the containers equidistant (see Figure 1a), invisibly displaces the hidden object. It is believed that dogs need to ‘infer’ the new location of the object in order to search accurately (Miller, Gipson, Vaughan, Rayburn-Reeves, & Zentall, 2009). Previous research has observed that dogs can succeed on this task, and control conditions have evidenced that they do so by using a visual memory (Miller et al., 2009). In general, search accuracy by dogs is rather high. Nonetheless, error rate increases when delays are interpolated by drawing a curtain (opaque cloth) between the dog and the apparatus following invisible displacement (Miller, Rayburn-Reeves, & Zentall, 2009). When delays are interpolated between the displacement and the search, large individual differences emerge suggesting that dogs have differing capacities for remembering the location of the hidden object over time.



a.



b.

**Figure 1.** Apparatus and dog in the starting position for the visible displacement test (a). Apparatus and dog in the starting position for the 90° invisible displacement test (b).

Research with humans has observed that the degree to which an initial act of self-control taxes a subsequent act depends on the cognitive load of the task. Performing more difficult tasks produces more depletion, and greater impairments are observed for subsequent tasks that are more demanding (Hagger, Wood, Stiff, & Chatzisarantis, 2010). Accordingly, the invisible displacement task used in the current study

was designed to be as demanding as possible for each dog. This was accomplished by inserting delays of variable duration in between the invisible displacement and the release to search, and by titrating the delay set (e.g., 0, 4, 8, 16 sec) for each dog so that search accuracy was above chance when there was no delay but at chance levels for the longest delay. It was hypothesized that depletion would impair search

accuracy more for trials with longer delays, since these would place the greatest demands on working memory. However, it deserves noting that attention control, like working memory, requires great self-control and is highly susceptible to fatigue in humans (Muraven & Baumeister, 2000). Furthermore, proactive memory interference (where memory for a previous trial interferes with that for the current trial) is known to factor into response accuracy (Brown & Robertson, 2007). Thus, since one could argue that no-delay trials required more attention control than they did memory (Nelson & Wasserman, 1978), and that they were more likely to be affected by interference due to their temporal proximity to the previous trial, it was also possible that cognitive fatigue would induce greater performance decrements for trials with shorter delays.

There is considerable evidence that glucose can replenish cognitive fatigue and enhance working memory in humans and animals (Gailliot et al., 2007; Gold, Vogt, & Hall, 1986; Messier, 2004; Miller et al., 2010). According to research on memory, the effects of glucose are dose-dependent. For example, the consumption of 10 g of glucose does not enhance memory when participants are tested 5 min later, whereas 25 g does (Parsons & Gold, 1992). Similarly, 10-30 mg/kg of glucose does not enhance memory in rats (Kopf & Baratti, 1996) whereas 100 mg/kg or 2 g/kg produces a positive modulation (White, 1991). Accordingly, a dosage of 2 g/kg was adopted in the current study with the expectation that its consumption would replenish cognitive fatigue and facilitate search accuracy more than a placebo. However, it was also possible that glucose could negatively affect performance since its consumption has been reported to negatively affect rat and human memory if subjects are stressed during testing (Gold et al., 1986; Mohanty & Flint, 2001; Parent, Varnhagen, & Gold, 1999). Stress itself is associated with an endogenous release of glucose, and it has been hypothesized that exogenous glucose impairs performance when it augments that which is endogenously released by stress, or when there is just too much systemic glucose.

In order to test the hypothesis that the exertion of self-control by dogs depletes self-control and temporarily impairs working memory, and that glucose consumption modulates these deficits, dogs were required to exert self-control over their movement (i.e., sit still) in a room by themselves for 10 min (self-control condition) or their physical movement was constrained by being placed inside of a cage for the same duration (control condition). Dogs were then administered a glucose (2 g/kg) or calorie-free placebo

drink. After drink consumption, all dogs were tested on the invisible displacement task with variable delays.

## 2. Method

### 2.1. Subjects

Eight dogs were recruited (*Canis familiaris*), 3 males and 5 females, ranging from 12 to 120 months in age ( $M = 46.1$  months), belonging to private owners. All dog owners were given a short questionnaire. Owners confirmed that their dogs matched several selection criteria: they were motivated by the opportunity to interact with the experimenters, by food rewards, and they were current on their vaccinations. Owners also agreed to withhold breakfast from their dogs so that we could test them in a fasted state. Of the dogs that participated in the experiment, 2 were Belgian terriers, 2 were golden retrievers, one was a beagle, one was a boxer and 3 were of mixed breeding. All of the dogs had been trained to sit on command.

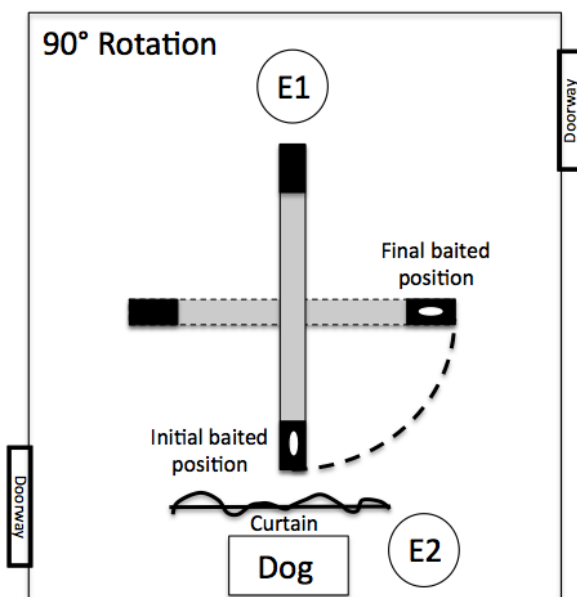
### 2.2. Apparatus

During the self-control manipulation a bath mat was placed on the floor and the dog sat on this mat when required to sit and stay (self-control condition). This mat was placed inside of a dog cage (.9 m x .6 m x .7 m) during the control condition. A mirror was strategically placed on the wall so that the experimenters could observe the dog from outside the room through a small opening in the door.

The apparatus used for visible and invisible displacement testing consisted of a wooden beam (1.83 m long x 14.0 cm wide x 3.8 cm thick) attached to a wooden base by a small post (7.6 cm long) at its center (see Figure 1). The post rested inside a hole that was slightly larger in diameter and 2 cm deeper than the screw itself, so that the beam easily rotated around the post. A 2 m length of transparent fishing line (5.5 kg test, 0.30 mm diameter) was attached to each end of the beam so that the beam could be rotated from a distance. Two identical opaque occluders (container 25.4 cm wide x 30 cm high x 20 cm deep) were attached to the beam, one on each end. A plastic container (20 cm wide x 10 cm high x 14 cm deep) containing approximately 100 g of microwaved Oscar Mayor® hot dogs was placed inside each occluder. This container was covered tightly with a perforated plastic lid that allowed the odor of the hot dogs to escape but prevented access to them. The same hot dogs were cut into 1 g portions and were used to bait the occluders. Each occluder also contained a plastic bowl (15 cm diameter x 7.5 cm high). A third bowl served as the target object for all dogs. An opaque barrier (1.4 m wide and 1.22 m tall)

placed in between the dog and the apparatus during the delay was constructed from a metal frame, on which an opaque cloth was hung with shower hooks as a curtain. A length of transparent fishing line was attached to the shower hooks so that an experimenter could open and close the curtain from a seated position (see Figure 2). This barrier was used previously to effectively block the dog's view of the apparatus (Miller et al., 2009).

All testing took place during the day (between 09:00 and 15:00) inside a white painted room (3.9 m long x 3.8 m wide). Delays were timed with a digital stopwatch.



**Figure 2.** A schematic representing the invisible displacement testing. The curtain was drawn open before the object was placed into an occluder and rotated into the final position. Once the object was invisibly displaced, the curtain was drawn closed for variable delays before being opened again. The dog was then allowed to search for the object.

### 2.3. Procedure

*Self-Control training.* The experimenter worked with each dog individually over a period of 3 weeks to maintain a 10-min sit-stay. Initially, each dog was reinforced while sitting still for short durations (5, 10, 15, 30 sec). Once the dog could successfully remain still for these durations, the durations were doubled (10, 20, 30, 60 sec) and were increased in this way until the dog could reliably stay still for 10 min. If the dog moved from its position at any time during the stay, the experimenter made a buzzing noise and recued the dog. The dog was released from the sit-stay with the word "Okay".

*Visible Displacement testing.* Each dog was first tested with visible displacements to give it experience

searching for hidden food. At the beginning of the testing session the dog was given a treat from each of three bowls. One of these bowls was then placed inside each of the occluders. Then the experimenter cued the dog to sit and stay on a bath mat that was located approximately 2 m away from the center of the apparatus (the exact distance was determined by the size of the dog such that each dog was far enough away from the apparatus that it could not see inside the occluders).

Each dog was initially tested with one session of visible displacements that consisted of 24 trials. At the start of each visible displacement trial, an experimenter (E1) cued the dog to sit and stay on the mat and placed the beam perpendicular to the head to tail axis of the dog so that one occluder was to the right of the dog and the other to the left (see Figure 1a). The experimenter placed a treat inside the target bowl and attracted the dog's attention by saying "Cookie!" or "Treats!" Once the dog was visually attending, the experimenter walked to the left or right occluder (the location was to the left or right equally often and was randomly assigned with the provision that the same occluder was not baited more than twice in a row). Once the experimenter reached the assigned occluder, she placed the bowl inside of it and on top of the perforated container. She then slowly backed away from the occluder, assumed a neutral position equidistant from each occluder, and looked straight ahead at a point on the wall. The experimenter then waited 4 sec while a second experimenter (E2) either closed then opened the curtain barrier (which took approximately 4 sec) or remained motionless. E2 did this from a seated position facing away from the apparatus. The closing and opening of the curtain barrier was included to prepare the dogs for the subsequent delay testing trials.

After the delay, E1 cued the release of the dog with the word "okay!" The dog was then allowed to approach either occluder. Any physical contact with an occluder or visual inspection of its contents was considered a choice. All dogs were rewarded with additional verbal praise for a correct choice. If the dog did not choose correctly, E1 said "Too bad" before removing the bowl from the correct occluder. If the dog stood up or moved forward E1 ended the trial by saying "Too bad" and replaced the dog on the mat before reinitiating the trial. There was an equal number of barrier and no barrier delay trials. After visible displacement testing the dogs were tested with a session of invisible displacements.

*Invisible Displacement testing.* Invisible displacement testing followed visible displacement

testing because it was more cognitive demanding. On invisible displacement test trials (24) the beam was placed in line with the dog so that one occluder was directly in front of the dog (see Figure 1b). Once E1 placed a treat in the target bowl, she attracted the dog's attention, walked towards the dog on the right side of the beam, and placed the bowl inside the occluder. She then collected the nylon line attached to that end of the beam and backed away to collect the nylon line attached to the other end. While standing behind the far occluder, she used the lines to rotate the beam 90° (see Figure 2; the occluder and direction of rotation were randomly assigned). Once the beam was rotated, E1 assumed a neutral position behind the center of the apparatus and then waited 4 sec while E2 closed then opened the curtain barrier or remained motionless. After the delay, E1 cued the release of the dog. An equal number of trials involved barrier and no barrier delays. After this testing session, the dogs were tested with variable delays following the invisible displacement.

*Invisible Displacement tests with delays.* Invisible displacement delay testing was similar to invisible displacement testing except that variable delays were inserted following the 90° rotation. Initially all dogs were tested with short delays (0, 4, 8, 16 sec). The curtain was closed for the duration of the delay. There were 24 trials per session and an equal number of trials (6) at each delay. If a dog performed above chance levels at the longest delay it was tested with longer delays (0, 8, 16, 32 sec). If it continued to search accurately at the longest delay, it was tested with even longer delays (0, 16, 32, 64 sec). Delay testing continued until each dog performed at chance levels at the longest delay. Once the longest set of delays was determined for a particular dog, the dog was tested for four sessions during which self-control and glucose were manipulated before invisible displacement delay testing.

*The Self-Control Manipulation.* Experimental sessions followed an ABBA design for condition such that, for example, on the first and fourth session, the dog was tested in the self-control condition and on the second and third session, it was tested in the control condition. Half of the dogs were tested in this order ( $n = 4$ ), the others were tested using the opposite order. Each dog was required to either exert or not exert self-control. In the self-control condition, E1 cued the dog to sit and stay on the mat in the experimental room. E1 then exited the room while the dog maintained its position with the door slightly ajar. She then watched the dog (without being seen by the dog) via a carefully

placed mirror. If the dog moved from its position, she returned and gave the sit-stay cue again. Both the number of cues and the time at which each cue was given was recorded by E2. The dog remained alone in the room for a total of 10 min. After 10 min, E1 returned to the room and released the dog using the verbal cue "okay" and gave it three small pieces of wiener (1 g each) from each of the three blue bowls used for invisible displacement testing while praising the dog for 30 sec. After 30 sec, the dog was given either the glucose or placebo drink.

The procedure for the control condition was similar to the self-control condition except that E1 placed the dog inside a dog cage and closed the door of the cage before exiting the room for 10 min. To control for the number and duration of human revisits between conditions, E1 returned to the dog and "recued" it to get inside of the cage at the same times it had been previously recued to "stay". The dogs tested with the control condition first ( $n = 4$ ) were recued 3 times during the initial session at minutes 1, 5 and 7. This was similar to the average number of times that dogs were recued in a previous experiment (Miller et al., 2010). After 10 min, the dog was released from the cage, fed from the blue bowls, praised, and given either the glucose or placebo drink.

*Glucose Manipulation.* Following the self-control manipulation, each dog was randomly assigned a glucose drink or a sugar-free placebo. The glucose drink consisted of powdered glucose mixed with water (1 g/2 ml) and BaconSalt® (1 g/8 ml). Dogs were given 2 g of glucose per kilogram of body weight, a dosage that is known to facilitate memory in rats (Messier & White, 1987; White, 1991). The placebo drink consisted of water and BaconSalt® mixed proportionally with Splenda® (.25 g/2 ml).

Following the consumption of the drink, the dogs were allowed to digest the beverage for 2 min. This 2-min duration has been shown to be sufficient for digestion and for the orally administered glucose to be transported into the brain (Betz, Gilboe, Yudilevich, & Drewes, 1973; Ishida et al., 1983). After that, the dogs were tested with 24 delayed invisible displacement trials.

### 3. Results

All dogs searched for the hidden object on every trial. Accuracy scores were calculated as the percentage of trials where dogs searched the correct container.

#### 3.1. Visible displacement tests

On average, dogs searched accurately for the

visibly displaced object (85.9%). A two-tailed correlated t-test used to analyze the difference between search accuracy following barrier (83.3%) and no barrier (88.5%) delay trials found no significant differences,  $t(7) = 1.26, p = .2$ . Thus, search accuracy was similar whether the 4 sec delay involved a barrier being placed in front of the subject dog or the researcher remained motionless for the same duration.

### 3.2. Invisible displacement tests

On average, dogs searched accurately for invisibly displaced objects (86.9%). A two-tailed correlated t-test revealed that search accuracy did not significantly differ between barrier (86.5%) and no barrier (87.5%) delay trials,  $t(7) = .28, p = .8$ .

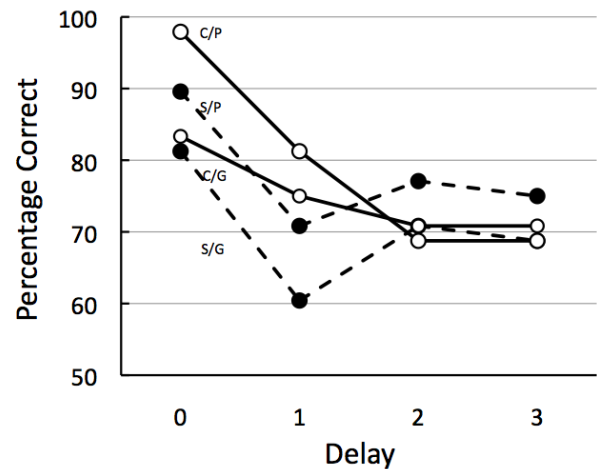
### 3.3. Invisible displacement tests with delays

Of the eight dogs tested, five were tested with short delays (0, 4, 8, 16 sec), two with longer delays (0, 8, 16, 32 sec) and one with even longer delays (0, 16, 32, 128 sec). On average, dogs searched more accurately following no delay (86.9%) than when there was a delay (66.2%, 58.3%, and 58.3%).

A one-way repeated measures analysis of variance (ANOVA) was used to analyze the difference in search accuracy as a function of delay. Search accuracy was significantly poorer following a delay,  $F(3,7) = 25, p < .01$ . Tukey post-hoc comparisons of the four delays indicate that the search accuracy was significantly better following no delay ( $M = 86.98, 95\% \text{ CI } [77.25, 96.71]$ ) than the first delay ( $M = 66.15, 95\% \text{ CI } [58.17, 74.13], p < .01$ ), the second delay ( $M = 58.33, 95\% \text{ CI } [50.45, 66.21], p < .01$ ) and the third delay ( $M = 58.33, 95\% \text{ CI } [49.23, 67.43], p < .01$ ). But no differences were detected between delays 1, 2, and 3,  $p > .05$ .

### 3.4. The effects of self-control and glucose on delayed invisible displacement

A  $2 \times 2 \times 4$  repeated factors analysis of variance (ANOVA) was used to analyze the effects of drink (glucose or placebo), condition (self-control or control) and delay on search accuracy. The delay durations were defined as 0, 1, 2, & 3 for the purpose of analysis despite that the actual durations were not identical for all dogs. There was a main effect of prior self-control,  $F(1,7) = 5.92, p < .05$  where dogs searched less accurately following the exertion of self-control than following the cage experience, and a main effect of delay  $F(1,7) = 6.27, p < .01$ , as search accuracy declined with delays. The effect of drink  $F(1,7) = 4.33, p = .08$  approached significance, and on average, the dogs searched less accurately following the consumption of glucose than the placebo. No significant interactions were observed (see Figure 3).



**Figure 3.** Search accuracy on delayed invisible displacement testing as a function of self-control condition (Self-control vs. Control), drink (Glucose vs. Placebo) and delay.

Performance across trials was not statistically analyzed because dogs were given the same dose of glucose (a time sensitive manipulation) but tested for different durations as a function of their individually titrated delay sets.

Despite that a significant effect of drink was not observed, planned comparisons using two-tailed correlated samples t-tests were made to examine whether initial exertion of self-control generally impaired search accuracy more than the control condition, and whether glucose “replenished” search performance. It was observed that following the exertion of self-control, dogs searched less accurately on average than following the cage experience, but only when they concomitantly consumed the glucose drink,  $t(7) = 2.55, p = .04$ . When dogs drank the placebo drink, search accuracy was not less accurate following the exertion of self-control than the caged experience,  $t(7) = .55, p > .60$ .

## 4. Discussion

The primary hypothesis of the current study was that the exertion of self-control by dogs would negatively affect working memory on a subsequently administered search task. This hypothesis was supported; dogs searched less accurately following the exertion of self-control than following a control condition. These findings are similar to those observed in humans (Schmeichel, 2007) and provide convergent evidence that human and non-human self-control are similarly sensitive to fatigue.

It was also expected that depletion would be associated with poorer performance on trials for which

there was a greater working memory load. In other words, the longer the delay, the greater the effect that depletion was expected to have on search accuracy. This hypothesis was not supported; there was no significant interaction between self-control condition and delay. However, on average, the differences in search accuracy by self-control condition tended to oppose our prediction, as they were greater for no-delay trials. This suggests that attending to the transitory elements of the trial and encoding the displacement were more demanding and thus more vulnerable to depletion than maintaining the memory.

It was also hypothesized that glucose would replenish depletion and enhance search accuracy more than the consumption of a placebo. Here again, the results did not support the hypothesis. Search accuracy by dogs was not significantly improved, and in fact showed signs of impairment following the consumption of the glucose drink.

An absence of, or null effect of glucose was unexpected but not unprecedented. It has been previously reported that performance by animals on some tasks is not affected by the consumption of glucose. For example, glucose consumption does not facilitate learning of a water maze alternation task, (Means & Edmonds, 1998) nor does it facilitate acquisition of a shock-motivated maze (Long, Davis, Garofalo, Spangler, & Ingram, 1992). Similarly, when pigeons are presented a sample (e.g., a green key-light) that is then turned off for a short time (delay), and they are subsequently presented with two comparisons (i.e., red and green key-lights) in a matching to sample task, a glucose injection does not enhance the rate of correctly choosing the matching comparison relative to a placebo injection. Differences in performance only emerge when glucose is administered following a memory impairing injection of scopolamine or when the task is made more difficult by reducing the amount of time the pigeon has to encode the stimulus properties of the sample (Parkes & White, 2000). Research with rats has also found that memory for a sample is unaffected by exogenously administered glucose under normal conditions. However, when memory is impaired by cold temperatures glucose can facilitate matching accuracy (Ahlers, Shurtleff, Schrot, Thomas, & Paul-Emile, 1993).

It is possible that the results obtained in the current experiment arose because the memory task administered to dogs was easy and familiar. Search performance may have required a well-rehearsed sequence of actions controlled by stimuli in the environment and not flexible responding to novel

demands. In humans, glucose does not enhance performance for easy or well-learned behaviors (for a review see Messier, 2004), instead, it tends to only facilitate memory when the cognitive demands are high. Thus, in the current experiment, glucose may not have facilitated memory because responding was not effortful. This explanation adequately accounts for the results obtained, however, the assumption upon which it rests is debatable. After all, in order to perform this task dogs were required to control their physical movement during the baiting and rotation of the apparatus, ignore the distraction of the barrier during the delay, and maintain the memory of the correct hiding location despite proactive interference from previous trials. Dogs in the current experiment found this difficult to do and only chose the correct container 75.6% of the time. Given that there were only two alternatives, this means that dogs were often wrong. They were not unmotivated (they searched on every trial); instead they appeared to be unable to remember the location of the invisibly displaced food. Moreover, use of self-control reduced search accuracy. One would expect that under these conditions additional glucose would facilitate search accuracy. But the effects of glucose were, if anything, negative. On average, the dogs searched less accurately following the consumption of the glucose drink.

Impairments to performance may have resulted from differential motivation to search for hidden food rewards. The consumption of 2 g/kg may have been excessive (as it would have been for humans) and following the consumption of a glucose drink dogs may have been less food motivated. Given the demanding nature of the task, this difference in motivation may have caused performance to decline, and masked positive memory modulation by glucose. Such an effect may not have been observed in previous research (Miller et al., 2010) because a smaller dosage was utilized (approximately 1 g/kg). In retrospect, this smaller dosage may have been more appropriate for the current experiment; however, there was reason to believe that the larger dosage would have greater effects on memory (Messier & White, 1987).

It is also possible that dogs in the current study experienced stress and/or food-motivated arousal during testing and that this resulted in the release of an endogenous supply of glucose. Increased arousal can release epinephrine that subsequently increases glycogenolysis and blood glucose levels (Hall & Gold, 1986; Parent et al., 1999). In a more natural setting such an increase in blood glucose levels would have had some adaptive value, as most animals forage or



hunt for food when they are already hungry and their blood glucose levels are low. Releasing stored glucose may facilitate the requisite cognitive and physical processes involved in food-getting behavior. However, under the conditions of the current experiment, the endogenously released glucose may have facilitated search following the placebo drink but impaired it following the glucose drink. This may have occurred because the combination of endogenous and exogenous glucose increased blood-glucose levels beyond an optimal level.

Research with humans and animals has observed that stress hormones negatively interact with exogenously administered glucose on working memory (Gold et al., 1986; Mohanty & Flint, 2001; Parent et al., 1999). For example, when human participants are presented with emotionally arousing pictures and narratives (that induce the endogenous release of glucose) and they are administered additional glucose (consumed in the form of a glucose drink) memory for the previously presented material is poorer relative to those who are given a placebo (Parent et al., 1999). Similar decrements are also observed when participants are required to remember the spatial location of emotionally arousing pictures. The participants given a placebo drink remember the emotionally arousing material more accurately than those given a glucose drink (Mohanty & Flint, 2001). Likewise, when rats are trained to avoid a high intensity shock (which increases epinephrine and glucose levels), and are administered a glucose injection they learn more slowly than rats that are administered a placebo injection (Gold et al., 1986).

In summary, it was observed that an initial act of self-control impaired performance by dogs on a subsequently administered search task and that the consumption of glucose did not reduce this impairment. The latter evidences that depletion, (i.e., deficits in performance associated with an initial act of self-control), can occur independent of changes in blood glucose. It is worth noting that glucose had, if anything, a negative effect on performance. This is an interesting finding that has only been reported a few other times. Our observation of this tendency is the first in the absence of negative experiences such as shock, or stimuli such as negatively stimulating photos. Future research will explore the mechanism(s) responsible for the results we obtained, and how and when glucose has beneficial effects.

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