The Role of Glucose on Executive Control Vigor: Evidence in Support of Comparative Research

Holly C. Miller
Université de Valenciennes et du Hainaut-Cambrésis, France

The central executive is theorized to be an overarching cognitive system responsible for coordinating processes that enable self-control (i.e., inhibiting habitual responses), persistence at mental and physical tasks, emotional regulation and working memory (Gailliot, 2008; Miller & Cohen, 2001). There is evidence that the executive system relies on glucose as its energy resource (Gailliot et al., 2007) and that when humans invoke the central executive they expend large quantities of glucose. When glucose levels are low, humans perform more poorly on other tasks that rely on the central executive (Gailliot et al., 2007). Similar results have been obtained with non-human animals. When dogs are required to exert self-control on an initial task they persist for a shorter duration at a subsequent unrewarding task and are more impulsive than if they were not required to exert self-control (Miller, DeWall, Pattison, Molet, & Zentall, in press; Miller, Pattison, Rayburn-Reeves, DeWall, & Zentall, 2010). Given the similarities between human and non-human animals, further research on executive control processing and glucose depletion with non-human animals is encouraged. Such research may lead to interventions that sustain and replenish executive control.

Humans are capable of responding to the immediate environment in both a reflexive and controlled way. Reflexive behaviors are elicited by stimuli in the environment that are strongly associated with particular behavioral responses. These responses can be predisposed (acquired through evolution), or they can be learned when responses to sensory stimuli are reinforced over time. In most situations, automatic behavior enables us to effectively react and interact with our environment. For example, one could argue that automatic processes largely control our driving behavior. Most people can drive a common route while concentrating on unrelated thoughts, listening to the radio, or talking to a friend. However, when an unexpected event is encountered (e.g., the road is closed due to a traffic accident), reflexive behavior may be insufficient for optimal navigation and a more controlled, intentional response may be required to arrive at the goal location (Miller & Cohen, 2001; Norman & Shallice, 2000).

In order for humans to control their response to a novel situation they may invoke an overarching cognitive system (the central executive) responsible for coordinating thoughts and action into purposeful behavior (Miller & Wallis, 2009). The central executive enables self-control (i.e., inhibiting habitual responses), persistence at mental and physical tasks, emotional regulation and working memory (Baddeley, 2003; Gailliot, 2008; Miller & Cohen, 2001). In other words, it allows humans to adaptively respond to situations that require the coordination of sensory inputs, thoughts, and actions, in order to create internal representations of goals and the means to achieve them, and when behavior must be guided by internal states or intentions (Barkley, 2001; Cohen, Bayer, Jaudas, & Golwitzer, 2008).

The central executive is critical for humans to organize and execute daily tasks (Glosser & Goodglass, 1990). Furthermore, good executive functioning is

associated with a variety of positive outcomes such as healthier interpersonal relationships, better academic performance, greater mental health, and less criminal and unlawful behavior (Finkel & Campbell, 2001; Gottfredson & Hirschi, 1990; Tangney, Baumeister, & Boone, 2004). These positive outcomes are desirable, and humans are motivated to coordinate their behavior to obtain them. The paradox is that despite their motivation, and the ability to perform all of the requisite behaviors, humans often fail to consistently behave in goal directed ways. For example, a person who is overweight may decide to start a diet. This person initially maintains healthful eating habits by inhibiting the innate desire for foods that are high in sugar and he is rewarded by weight loss. However, this person (like 80% of those who initiate a diet) is unlikely to persist with the diet over time, and is more likely to stop regulating his eating behavior and to regain the weight (Wing & Hill, 2001). From a logical perspective, this failure seems counterintuitive. There is a desirable goal, the person is motivated to achieve this goal, and initial efforts are rewarded (i.e., by weight loss). According to reinforcement theory, the act of dieting should be strengthened. And yet, these elements appear to be insufficient for maintaining the goal-oriented behavior. This outcome suggests that it is particularly difficult to consistently engage in a behavior if that behavior conflicts with an innate response (e.g., eat sweet foods).

One explanation for this paradox is that intentional and goal directed behavior requires control by executive processes and the ability to invoke them is limited (Baumeister, Bratslavsky, Muraven, & Tice, 1998; Baumeister & Heatherton, 2004; Muraven & Baumeister, 2000). A person cannot consistently engage the central executive because it draws energy from a limited resource. Initial efforts at executive control temporarily deplete this resource, and when this resource is depleted further attempts at executive control are likely to fail. Furthermore, all functions coordinated by the central executive draw upon the same resource which means that seemingly unrelated behaviors can affect one another by depleting the amount of energy available (Gailliot et al., 2007). For example, research has found that if students invoke the central executive to refrain from eating tempting food (i.e., inhibit a pre-potent response), they persist less on a subsequent unsolvable puzzle task, compared to those who did not invoke the central executive because they did not have to refrain from eating tempting food (Baumeister et al., 1998; Segerstrom & Nes, 2007). The student's ability to persist when frustrated and discouraged by a series of failures is diminished because there is insufficient energy to support the central executive processes necessary to inhibit the easier and more appealing response (i.e., quitting) (Muraven, Tice, & Baumeister, 1998). Similarly, research has found that when students engage their central executive to suppress their laughter and positive emotions while watching a humorous video (in comparison to when they do not) they respond less accurately on a subsequently administered difficult, but solvable, anagram task (Baumeister et al., 1998).

The initial exertion of the central executive has also been found to impair the ability to inhibit aggressive responses (Denson, von Hippel, Kemp, & Teo, 2010; DeWall, Baumeister, Stillman, & Gailliot, 2007). Aggressive behavior can be predatory, defensive, or offensive in nature and it is often an adaptive response to stimuli in the environment. However, for most social animals it is important to

be able to override aggressive impulses and refrain from aggressive action. For example, it may be adaptive for wolves to aggressively compete over a food resource but at some point the costs (i.e., loss of energy and risk of injury) outweigh the benefits. It is adaptive for the weaker animal in this situation to submit to the stronger animal (because he has more to lose) and inhibit further aggression. The conflict is then resolved and so the dominant animal inhibits further aggression (Mech, 1999).

Humans are also social animals that utilize aggression to resolve disputes. However, in our cooperative culture, overt aggression is considered socially inappropriate. Thus, humans often invoke executive processes to suppress emotionally driven aggressive responses (DeWall et al., 2007). They are most successful at their efforts when they have the energy to engage their central executive and are less successful when they have depleted the limited energy resource upon which the central executive relies (DeWall et al., 2007; Gottfredson & Hirschi, 1990). Research shows that when students initially deplete this limited resource by inhibiting their consumption of a donut (but not a radish) they are less able to control their aggressive behavior when they are subsequently provoked (i.e., they are negatively evaluated on a previously written essay). Depleted students retaliate by adding more hot sauce to food intended for the essay evaluator. Similarly, when students are initially required to control their attention (inhibit reading words displayed to them), and are subsequently given a negative essay evaluation, they are more likely to administer aversive noises to the essay evaluator. This research suggests that humans are less able to control their aggressive behaviors when depleted. These behavioral changes likely reflect an inability to suppress emotional responses. Indeed, following self-control exertion, students are more likely to report the desire to inflict physical harm on someone who provokes them (DeWall et al., 2007).

More recent research suggests that glucose is the limited energy resource upon which the central executive relies (Gailliot et al., 2007). Glucose is the primary source of energy for brain functioning (Benton, Parker, & Donohoe, 1996; Scholey, Harper, & Kennedy, 2001) and in comparison to the rest of the body the brain uses a disproportionate amount of glucose to engage cognitive processes (Gailliot, 2008). However, not all cognitive processes require a large amount of glucose nor are they all susceptible to normal fluctuations in blood glucose levels. Research suggests that the central executive is unique in that it requires large quantities of glucose to function optimally, is capable of depleting blood glucose levels, and is sensitive to normal fluctuations in blood glucose levels (Fairclough & Houston, 2004; Gailliot et al., 2007). For instance, participants with higher blood glucose levels are able to control their attention and override a strong habitual response to read aloud the name of a word to say the color in which the word is printed (Stroop task) more accurately than those with lower blood glucose levels. Furthermore, when blood glucose levels are measured directly, it has been observed that performance of the Stroop task is associated with significant decreases in blood glucose levels over time (Fairclough & Houston, 2004), and when initial performance of the Stroop task lowers glucose levels, it causes poorer performance on subsequent tasks (i.e., tasks requiring effortful persistence) that also require the central executive (Gailliot et al., 2007). When participants

complete a control task, where inhibition is not required because the name of the word and color in which it is printed are the same, similar decrements in blood glucose levels and performance are not observed. A corresponding pattern of results has been observed when the initial task requires participants to control their attention (or not) while watching a video. Here again, those who invoke executive control experience a significant decrease in blood glucose levels over time whereas those who do not are not similarly affected (Gailliot et al., 2007).

Participants with higher glucose levels (in comparison to those with lower glucose levels) are also able to recall a 20-word target list (California Verbal Learning Test) presented by a male voice more accurately when told to ignore 20 distracter words presented by a female voice. However, glucose levels do not affect memory when there are no distracter words (Sünram-Lea, Foster, Durlach, & Perez, 2002). Similarly, Foster, Lidder, and Sünram (1998) found that lower blood glucose levels resulted in poorer performance of a task that required coordinating sensory input (a list of words) into working memory while also performing hand movements (fist, chop, slap) that changed every fifth word. When the participants were not required to perform the hand movements, lower glucose levels were not associated with poorer memory.

There is also evidence that higher blood glucose levels facilitate performance on demanding but not easy working memory and cognitive tasks. This discrepancy suggests that when there is more information to be coordinated then there is a greater demand for executive processing and glucose. More specifically, participants who are required to perform the serial sevens task, (that requires them to subtract 7 from 100, then subtract 7 from the result and so on), are faster and more accurate when glucose levels are high than when they are low (Kennedy & Scholey, 2000). Similar effects are not observed when participants are required to perform the easier serial threes task. This suggests that the serial sevens task requires the coordination of more information and presumably requires more energy to perform than the serial threes task. Similarly, higher glucose levels facilitate a fluency task in which participants generate as many words as possible that start with three letters that do not occur often in the English language (Donohue & Benton, 1999) but higher glucose levels do not affect the generation of words that start with three common letters. Glucose also improves performance on difficult versions of Porteus mazes (where participants are required to accurately trace lines through drawn mazes) but not easier ones (Donohue & Benton, 1999). These results imply that executive processing has unique energy requirements. All cognition and memory may require energy, but when executive processes are required to coordinate information, performance appears to be more sensitive to and capable of depleting blood glucose levels.

The presumed glucose depletion that results from executive processing and the deficits associated with low glucose levels can be reversed when participants consume a glucose drink (Gailliot et al., 2007). Similar effects are not found when participants consume a calorie-free drink and this suggests that glucose (and not merely the consumption of a sweet beverage) is mediating the improvements in executive functioning. More specifically, when participants control their attention on an initial task and they are subsequently administered a glucose drink, they respond more accurately on the Stroop task than those given a placebo drink

(Gailliot et al., 2007). Similarly, memory is negatively affected following self-control exertion (Schmeichel, 2007) and consuming a glucose drink can improve memory performance compared to consuming a calorie-free drink (Sünram-Lea, Foster, Durlach, & Perez, 2001).

There are other factors that affect glucose levels and that in turn affect executive control processes. Blake, Varnhagen, and Parent (2001) found that when participants view and read emotionally arousing material their blood glucose levels increase (+ 6%). Moreover, these emotionally arousing pictures and narratives are remembered more accurately by fasted participants (presumed to be low in blood glucose) than neutral pictures and narratives. The mechanism responsible for the memory facilitation of arousing stimuli and experiences may be increased blood glucose levels (Blake et al., 2001; Parent, Varnhagen, & Gold, 1999). This suggests that emotional arousal can elicit the release of endogenous glucose reserves by serving as a physiological trigger for the release of stress hormones such as epinephrine (adrenaline). A variety of stressful events such as physical threat, excitement, noise, etc. are capable of inducing the release of epinephrine (Wortsman, 2002) and one of the major physiological consequences of increased circulating epinephrine is the conversion of glycogen (a reserve of glucose energy) into glucose (glycogenolysis). This conversion allows for more energy to be available for the needs of the sympathetic nervous system (i.e., fight or flight), and also for memory processes. Research suggests that the increase in circulating blood glucose caused by epinephrine facilitates memory. Even in the absence of a stressful event, the exogenous administration of epinephrine can enhance working memory and the recall of visual material (Cahill & Alkire, 2003).

There is additional evidence that the levels of circulating blood glucose affect executive functioning. In studies that have examined the affects of different diets on executive processing it has been found that the rate of glucose absorption from different carbohydrates can differentially affect executive processes. Carbohydrates of all types initially facilitate cognition, but those that are digested more slowly and result in a small rise of glucose for an extended time provide optimal energy for executive processes over time whereas carbohydrates that are digested more quickly and lead to a larger rise of blood glucose for a shorter time are not as effective (Benton, Maconie, & Williams, 2007; Benton et al., 2003; Jenkins et al., 1981). When humans are tested on working memory tests hours after the consumption of slowly digested carbohydrates they respond with greater accuracy than when they are tested hours after the consumption of quickly digested carbohydrates. Though these effects are observed for several hours following meal consumption, the greatest differences in performance are observed after two or three hours (Benton et al., 2003). Similar findings have been observed when children are given breakfasts that differ on the glycemic index (a parameter that reflects the rate and extent of the postprandial rise and fall in blood glucose). Children are able to persist longer on a frustrating task, are more capable of controlling attention and working independently, and can remember more when they consumed a breakfast that was low on the glycemic index and was digested more slowly (leading to a slower rise and fall of blood glucose) than when they consumed one that was higher on the glycemic index and that was digested more quickly (Benton et al., 2007).

The research presented thus far has focused on how glucose affects executive processing in humans. However, some have argued that non-human animals also invoke executive processes (Lee, Rushworth, Walton, Watanabe, & Sakagami, 2007; Miller & Cohen, 2001; Miller & Wallis, 2009; Watanabe & Sakagami, 2007). It is not clear, though, which behaviors performed by an animal would require executive control. The definition of executive functioning is broad and the assumptions it makes are difficult to qualify and quantify. In humans, behavior qualifies as requiring executive control when it requires an intention to perform. We identify behaviors that require intention and goal direction from personal report. For example, we can identify in ourselves the ability to exert self-control, maintain information in working memory, and organize a sequence of action as requiring cognitive control. We can also examine humans who have the ability to report their thoughts but have lost the ability to organize their behavior in goal directed ways. However, a similar approach to understanding executive functioning in nonhuman animals cannot be made. Animals cannot report on their goal intention or conscious awareness. Behavioral measures are the only means of examining their covert processes. Thus, we may observe behavior in animals that is analogous to that observed in humans (i.e., the ability to inhibit behavior, persist on frustrating tasks, and respond accurately on conditional discriminations that require working memory (Abram & Chen, 1976; Honig, 1978; Sanabria, Sitomer, & Killeen, 2006) but these behaviors may not require executive processing. However, these behaviors do appear to be reliant on similar neural mechanisms (Miller & Wallis, 2009), and they are similarly dependant on glucose as a limited energy resource (Gailliot, 2008). Consequently, for the purposes of this paper, the terms executive processing and executive control will be applied to animal behaviors that are analogous to those that are presumed to rely on purposeful responding in humans.

Working memory is believed to require executive control by humans and has been extensively studied in animals. Research with rats has found that working memory is sensitive to glucose levels (Gold, 1995; White, 1991). In rats, working memory requires large quantities of glucose to function optimally and acts that require working memory decrease glucose levels in brain extra-cellular fluid (ECF) surrounding the hippocampus. Furthermore, the greater the number of choices and amount of information required to be stored in working memory, the larger the decrease of glucose in hippocampal ECF. Research has found that when rats are tested for spontaneous alternation on a four-arm maze, a large decrease (32%) in ECF glucose is observed while a smaller decrease (11.6%) is observed when rats are tested with a simpler three-arm maze. This decrease in ECF glucose is a reliable phenomenon (McNay, Canal, Sherwin, & Gold, 2006; McNay & Gold, 2002). Moreover, it is location and structure specific and concurrent depletion of glucose is not observed in the neighboring striatum, which suggests that glucose is compartmentalized within the brain (McNay, McCarty, & Gold, 2001). A glucose injection is able to attenuate the depletion of glucose in hippocampal ECF and this suggests that increasing systematic blood glucose levels is sufficient for the brain to specifically recruit glucose for depleted structures (McNay, Fries, & Gold, 2000).

There is additional evidence for a relationship between cognitive demand and depletion of glucose in hippocampal ECF. McNay and Gold (1999) have observed that older rats (in comparison to younger ones) demonstrate age related memory deficits on a four-arm maze. These deficits by older rats are associated with a greater decrease of glucose in hippocampal ECF following maze learning. Together, these results suggest that older rats find it more difficult and demanding to remember spatial information and that this effort can be measured by metabolic costs.

Glucose injections have been found to facilitate working memory in rats when given both pre- and post-training. When glucose is administered before training, it raises the supply of glucose to the brain to a level sufficient to meet the demands of memory processes (McNay, Fries, & Gold, 2000) and facilitates the acquisition of many appetitive and aversive tasks as well as the navigation of mazes (Flint & Riccio, 1997; Hughes, 2003; Messier, 1997). When glucose is administered after training, it facilitates memory processes that take place after learning a new task. As a consequence, rats administered glucose remember more about their experience on appetitive and aversive tasks and perform more accurately on subsequent testing (Flint & Riccio, 1997, 1999; Gold, 1986, 1995; Hughes & Neeson, 2003; White, 1991). For example, when rats are placed into a starting compartment and allowed to move into a dark compartment where they are shocked they subsequently show an increased latency to re-enter the dark compartment. This increased latency is believed to reflect memory for the previous aversive event and a post-training injection of glucose increases this latency and thus is believed to enhance memory (Gold, 1995). However, it should be noted that glucose does not always enhance performance, and some researchers have failed to observe positive effects (for a review see Messier, 2004). It is hypothesized that glucose tolerance may affect whether exogenous glucose enhances memory. It is also hypothesized that the nature of the task determines whether or not glucose will facilitate performance. Research with rats has found that glucose injections facilitate working memory most reliably when the ability to coordinate attention and information is difficult. For example, a glucose injection facilitates learning a water maze alternation task when rats have also been injected with scopolamine (an anticholinergic drug that impairs the ability to maintain working memory) but not when rats have been injected with a placebo (Means & Edmonds, 1998). Similarly, when the ambient temperature is decreased and memory is impaired, rats respond more accurately on a delayed matching to sample task following a glucose (but not a placebo) injection (Ahlers, Shurtleff, Schrot, Thomas, & Paul-Emile, 1993). These differences are not observed when rats are tested on the same task under normal conditions (i.e., the ambient temperature is 70˚). These results suggest that when coordinating information in working memory is more difficult, and the demands for executive processing are higher, increased glucose levels facilitate performance. However, when the task is easier and there are no memory impairing circumstances, additional glucose does not affect behavior because, presumably, there is sufficient energy for optimal performance.

Other factors that affect glucose levels also affect working memory in rats. For example, when rats are trained to avoid high intensity foot shock, epinephrine levels are increased. Higher epinephrine levels increase blood glucose levels and

result in faster acquisition of the avoidance task. When rats are trained to avoid a low intensity foot shock that does not result in increased epinephrine and glucose levels, they do not acquire the avoidance task as quickly (Hall & Gold, 1986; McCarty & Gold, 1981). Furthermore, epinephrine injections have been found to increase glucose levels and facilitate memory in rats (Gold & van Buskirk, 1975, Hall & Gold, 1986).

Research using diet manipulations in animals has also found that the consumption of more slowly digested carbohydrates (relative to the consumption of more quickly digested carbohydrates) improves learning performance when subjects are tested hours after initial consumption despite the fact that both diets are equated for energy content. More specifically, rats are able to learn to press one of two levers (when one lever is active and the other is not) more quickly when tested three hours after the consumption of a slowly digested than quickly digested diet (Benton et al., 2003). Similarly, research with shelter dogs suggests that dogs become less impulsive and reactive after being fed a diet with a low glycemic index (consisting of 35.8% carbohydrates, 44.6% protein, 6.9% fat & other) for 8 weeks in comparison to dogs fed a diet with a higher glycemic index (59.3% carbohydrates, 31.4% protein, 4.8% fat and other) for a similar duration. It deserves noting that the quantity of protein and fat in a meal has a substantial affect on the rate at which glucose is digested and released into the blood. This means that a diet with fewer carbohydrates that are digested more slowly may paradoxically improve performance relative to a diet with more carbohydrates in general. In the context of this study, dogs that consumed the low glycemic index diet crossed a demarcated line in the room less often (i.e., they were calmer) and made fewer escape attempts in the presence of a stranger than dogs that consumed the high glycemic index diet. These results suggest that dogs had greater emotional control when the rate of carbohydrate digestion was slower, despite the fact that the overall quantity of carbohydrate energy was reduced (Hennesy et al., 2002).

The research with humans and nonhumans suggests that executive control relies on glucose as a limited energy resource. When executive control processes are invoked they deplete blood glucose levels. This depletion can be replenished by the administration of glucose (Gailliot et al., 2007). Furthermore, in humans, initial executive control processing affects the subsequent performance of a variety of tasks that require executive processing (Baumeister et al., 1998; Gailliot et al., 2007). This phenomenon is not unique to humans and similar domain general findings have been recently reported with dogs. Dogs that are initially required to inhibit their behavior and control their body movements (i.e., sit-stay) while alone in a room for 10 min persist for less time on a subsequent unsolvable puzzle task compared to dogs that are not required to initially inhibit their behavior (Miller et al., 2010). More specifically, despite being hungry, depleted dogs work to release a wiener trapped inside a tug-a-jug™ mental stimulation toy for a shorter duration than non depleted dogs. These deficits, which result from the initial inhibition of behavior, are eliminated when dogs consume a glucose (but not a calorie-free placebo) drink following behavioral inhibition (Miller et al., 2010).

Research with dogs suggests that initial behavioral inhibition also increases impulsivity, risk-taking, and aggression. When dogs are required to sit-still for 10-min in a room alone they are subsequently more likely to approach and

spend greater time in close proximity with an aggressive caged conspecific than after a control condition (Miller, DeWall, Pattison, Molet, & Zentall, in press). This occurs even though approaching a confined aggressive dog is associated with greater risk of attack and that staying further away from an aggressor defending its territory reduces the motivation for attack (Lindsay, 2001; Sacks, Sattin, & Bonzo, 1989). These results suggest that initial behavioral inhibition by dogs, like that by humans, can subsequently result in behavior that increases risk of an aggressive encounter.

Initial behavioral inhibition appears to have negative affects on canine memory that are sensitive to glucose levels. When dogs consume a breakfast meal 30 min before completing a 10-min sit-stay they subsequently search more accurately for a visibly displaced object hidden in one of 6 containers than they do in a control condition (Miller, Bender, & Zentall, in review). A similar facilitation is not observed 90 min after the consumption of breakfast, which suggests that search accuracy is enhanced while glucose levels are relatively high, and that it declines as a function of time and glucose depletion.

Given the extensive similarities observed between humans and non-human animals on tasks that require intentional responding (by humans) future comparative research on the topic of executive control vigor is warranted. This research could be conducted with a variety of species though recent research suggests that dogs may be particularly suitable (Miller et al., 2010). Dogs descend from a complex social species (wolf), they co-evolved with humans, and they have faced selective pressure from humans for the ability to inhibit behavior. Furthermore, dogs can be tested using self-control paradigms similar to those used in research with humans. Dogs are also easily accessible (like human subjects), do not require housing in a laboratory, and have diets that are easily manipulated. The latter is of significant importance because diet manipulations cannot be easily made with human subjects. Humans do not reliably adhere to dietary regulations, and those who do have altered perceptions and expectations (Head, 2007).

The potential value of additional comparative research on executive control vigor may be a greater understanding of the inherent biological mechanisms. This fundamental research may eventually result in a greater ability to replenish and sustain executive control in humans and non-human animals. This has great practical import. For humans that have the desire to behave in goal directed ways, the ability to sustain and/or replenish depleted executive control may enable goal directed behavior. With greater executive control, motivated individuals would find it easier to quit smoking, maintain healthy diets, succeed in school, and improve interpersonal relationships. Similarly, greater executive control by dogs may improve the human-animal bond and prevent unnecessary relinquishment. Improved executive control has the potential to facilitate the ability of a variety of species to overcome the obstacles inherent to an industrialized world.

References

Abram, A., & Chen, J. (1976). Ontogeny of persistence: Immediate and long-term persistence in rats varying in training age between 17 and 65 days. *Journal of Comparative and Physiological Psychology, 90,* 808-820.

Ahlers, S. T., Shurtleff, D., Schrot, J., Thomas, J. R., & Paul-Emile, F. (1993). Glucose attenuates cold-induced impairment of delayed matching-to-sample performance in rats. *Psychobiology, 21,* 87-92.

Baddeley, A. (2003). Working memory: Looking back and looking forward. *Nature Reviews Neuroscience, 4,* 829-839.

Barkley, R. A. (2001). Executive function and self-regulation: An evolutionary neuropsychological perspective. *Neuropsychology Review, 11,* 1-29.

Baumeister, R. F., Bratslavsky, E., Muraven, M., & Tice, D. M. (1998). Ego depletion: Is the active self a limited resource? *Journal of Personality and Social Psychology, 74,* 1252-1265.

Baumeister, R. F., & Heatherton, T. (2004). Self-regulation failure: An overview. In R. M. Kowalski & M. R. Leary (Eds.), *The interface of social and clinical psychology: Key readings* (pp. 51-69). New York: Psychology Press.

Benton, D., Maconie, A., & Williams, C. (2007). The influence of the glycaemic load of breakfast on the behaviour of children in school. *Physiological Behaviour, 92,* 717-724.

Benton, D., Parker, P. Y., & Donohoe, R. T. (1996). The supply of glucose to the brain and cognitive functioning. *Journal of Biosocial Science, 28,* 463-479.

Benton, D., Ruffin, M., Lassel, T., Nabb, S., Messaoudi, M., Vinoy, S., et al. (2003). The delivery rate of dietary carbohydrates affects cognitive performance in both rats and humans. *Psychopharmacology, 166,* 86-90.

Blake, T., Varnhagen, C., & Parent, M. B. (2001). Emotionally-arousing pictures increase blood glucose levels and enhance recall. *Neurobiology of Learning and Memory, 75,* 262-273.

Cahill, L., & Alkire, M. T. (2003). Epinephrine enhancement of human memory consolidation: Interaction with arousal at encoding. *Neurobiology of Learning and Memory, 79,* 194-198.

Cohen, A. L., Bayer, U. C., Jaudas, A., & Gollwitzer, P. M. (2008). Self-regulatory strategy and executive control: Implementation intentions modulate task switching and Simon task performance. *Psychological Research, 72,* 12-26.

Denson, T. F., von Hippel, W., Kemp, R. I., & Teo, L. S. (2010). Glucose consumption decreases impulsive aggression in response to provocation in aggressive individuals. *Journal of Experimental Social Psychology, 46,* 1023-1028.

DeWall, C. N., Baumeister, R. F., Stillman, T. F., & Gailliot, M. T. (2007). Violence restrained: Effects of self-regulatory capacity and its depletion on aggressive behavior. *Journal of Experimental Social Psychology, 43,* 62-76.

Donohue, R. T., & Benton, D. (1999). Cognitive functioning is susceptible to the level of blood glucose. *Psychopharmacology, 145,* 378–385.

Fairclough, S. H., & Houston, K. (2004). A metabolic measure of mental effort. *Biological Psychology, 66,* 177-190.

Finkel, E. J., & Campbell, W. K. (2001). Self-control and accommodation in close relationships: An interdependence analysis. *Journal of Personality and Social Psychology, 81,* 263-277.

Flint, R. W., & Riccio, D. C. (1997). Pre-test administration of glucose attenuates infantile amnesia for passive avoidance in rats. *Developmental Psychobiology, 31,* 207-216.

Flint, R. W., & Riccio, D. C. (1999). Post-training glucose administration attenuates forgetting of passive-avoidance conditioning in 18-day-old rats. *Neurobiology of Learning and Memory, 72,* 62-67.

Foster, J. K., Lidder, P. G., & Sünram, S. I. (1998). Glucose facilitation of memory performance in normal young participants: Fractionation of enhancement effects? *Psychopharmacology, 137,* 259-270.

Gailliot, M. T. (2008). Unlocking the energy dynamics of executive functioning: Linking executive functioning to brain glycogen. *Perspectives on Psychological Science, 3(4),* 245-263.

Gailliot, M. T., Baumeister, R. F., DeWall, C. N., Plant, E. A., Brewer, L. E., & Schmeichel, B. J. (2007). Self-control relies on glucose as a limited energy source: Willpower is more than a metaphor. *Journal of Personality and Social Psychology, 92*, 325-336.

Glosser, G., & Goodglass, H. (1990). Disorders in executive control functions among aphasic and other brain-damaged patients. *Journal of Clinical and Experimental Neuropsychology, 12,* 485-501.

Gold, P. E. (1986). Glucose modulation of memory storage processing. *Behavioral and Neural Biology, 46,* 342-349.

Gold, P. E. (1995). Role of glucose in regulating the brain and cognition. *American Journal of Clinical Nutrition, 61*, 987-995.

Gold, P. E., & van Buskirk, R. B. (1975). Facilitation of time-dependent memory processes with posttrial epinephrine injections. *Behavioral Biology, 13,* 145-153.

Gold, P. E., Vogt, J., & Hall, J. L. (1986). Glucose effects on memory: Behavioral and pharmacological characteristics. *Behavioral Neural Biology, 24,* 168-184.

Gottfredson, M. R., & Hirschi, T. (1990). *A general theory of crime.* Stanford, CA: Stanford University Press.

Hall, J. L., & Gold, P. E. (1986). The effects of training, epinephrine, and glucose injections on plasma glucose levels in rats. *Behavioral and Neural Biology, 46,* 156-176.

Head, E. (2007). Combining an antioxidant-fortified diet with behavioral enrichment leads to cognitive improvement and reduced brain pathology in aging canines: Strategies for healthy aging. *Annals of the New York Academy of Sciences, 11114,* 398-406.

Hennesy, M. B., Voith, V. L., Young, T. L., Hawke, J. L., Centrone, J., McDowell, A. L., et al. (2002). Exploring human interaction and diet effects on the behavior of dogs in a public animal shelter. *Journal of Applied Animal Welfare Science, 5,* 253-273.

Honig, W. K. (1978). Studies of working memory in the pigeon. In S. H. Hulse, H. Fowler, & W. K. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 211-248). Hillsdale, NJ: Lawrence Erlbaum Associates.

Hughes, R. N. (2003). Effects of glucose on responsiveness to change in young adult and middle-aged rats. *Physiological Behavior, 78,* 529-534.

Hughes, R. N., & Neeson, L.T. (2003). Prevention of memory loss for a brightness change in adult and middle-aged rats by postacquisition treatment with glucose. *Pharmacology Biochemistry and Behavior, 76,* 119–123.

Jenkins, D. J., Wolever, T. M., Taylor, R. H., Barker, H., Fielden, H., & Baldwin, J. M. (1981). Glycemic index of foods: A physiological basis for carbohydrate exchange. *American Journal of Clinical Nutrition, 34,* 362-366.

Kennedy, D. O., & Scholey, A. B. (2000). Glucose administration, heart rate and cognitive performance: Effects of increasing mental effort. *Psychopharmacology, 149,* 63-71.

Lee, D., Rushworth, F. S., Walton, M. E., Watanabe, M., & Sakagami, M. (2007). Functional specialization of the primate frontal cortex during decision making. *The Journal of Neuroscience, 27*, 8170-8173.

Lindsay, S. R. (2001). *Handbook of applied dog behavior and training, Vol. 2: Etiology and assessment of behavior problems.* Ames, IA: Iowa State University Press.

Means, L. W., & Edmonds, S. M. (1998). Glucose minimally attenuates scopolamine — but not morphine-induced deficits on a water maze alternation task. *Journal of Neural Transmission, 105,* 1171-1185.

Mech, L. D. (1999). Alpha status, dominance, and division of labor in wolf packs. *Canadian Journal of Zoology, 77,* 1196-1203.

Messier, C. (1997). Object recognition in mice: Improvement of memory by glucose. *Neurobiol Learn Mem, 67,* 172-175.

Messier, C. (2004). Glucose improvement of memory: A review. *European Journal of Pharmacology*, *490*, 33-57.

McCarty, R., & Gold, P. E. (1981). Plasma catecholamines: Effects of footshock level and hormonal modulators of memory storage. *Hormones and Behavior, 15,* 168–182.

McNay, E. C., Canal, C. E., Sherwin, R. S., & Gold, P. E. (2006). Modulation of memory with septal injections of morphine and glucose: Effects on extracellular glucose levels in the hippocampus. *Physiology & Behavior, 87*, 298-303.

McNay, E. C., Fries, T. M., & Gold, P. E. (2000). Decreases in rat extracellular hippocampal glucose concentration associated with cognitive demand during a spatial task. *Proceedings of the National Academy of Sciences, 97,* 2881-2885.

McNay, E. C., & Gold, P. E. (1999). Extracellular glucose concentrations in the rat hippocampus measured by zero-net-flux: Effects of microdialysis flow rate, strain and age. *Journal of Neurochemistry, 72,* 785-790.

McNay, E. C., & Gold, P. E. (2002). Food for thought: Fluctuations in brain extracellular glucose provide insight into the mechanisms of memory modulation. *Behavioral Cognitive Neuroscience Reviews, 1,* 264-280.

McNay, E. C., McCarty, R. C., & Gold, P. E. (2001). Fluctuations in brain glucose concentration during behavioral testing: Dissociations between brain areas and between brain and blood. *Neurobiology of Learning and Memory, 75,* 325-337.

Miller, H. C., Bender, C., & Zentall, T. R. (in review). The breakfast effect: Dogs remember more when they are less hungry. *Journal of Comparative Psychology*.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24,* 167-202.

Miller, H. C., DeWall, C. N., Pattison, K., Molet, M., & Zentall, T. R. (in press). Too dog tired to avoid danger: Self-control depletion in canines increases behavioral approach toward an aggressive threat. *Psychonomic Bulletin & Review*.

Miller, H. C., Pattison, K. P., DeWall, C. N., Rayburn-Reeves, R., & Zentall, T. R. (2010). Self-control without a self? Common self control processes in humans and dogs. *Psychological Science, 21,* 534-538.

Miller, E. K., & Wallis, J. D. (2009). Executive function and higher-order cognition: Definitions and neural substrates. In *Encyclopedia of Neuroscience* (Vol. 4, pp. 99-104). Oxford, UK: Academic Press.

Muraven, M., & Baumeister, R. F. (2000). Self-regulation and depletion of limited resources: Does self-control resemble a muscle? *Psychological Bulletin, 126,* 247-259.

Muraven, M., Tice, D. M., & Baumeister, R. F. (1998). Self-control as limited resource: Regulatory depletion patterns. *Journal of Personality and Social Psychology, 74,* 774-789.

Norman, D. A., & Shallice, T. (2000). Attention to action: Willed and automatic control of behavior. In M.S. Gazzaniga (Ed.), *Cognitive neuroscience: A reader* (pp. 376-390). Malden, MA: Wiley Blackwell.

Parent, M. B., Varnhagen, C. & Gold, P. E. (1999). A memory-enhancing emotional narrative elevates blood glucose levels in human subjects. *Psychobiology, 2,* 386-396.

Sacks, J. J., Sattin, R. W., & Bonzo, S. E. (1989). Dog bite-related fatalities from 1979 through 1988. *Journal of the American Medical Association, 262,* 1489-1492

Sanabria, F., Sitomer, M. T., & Killeen, P. R. (2006). Negative automaintenance omission training is effective. *Journal of the Experimental Analysis of Behavior, 86,* 1-10.

Schmeichel, B. (2007). Attention control, memory updating, and emotion regulation temporarily reduce the capacity for executive control. *Journal of Experimental Psychology, 136*, 241-255.

Scholey, A., Harper, S., & Kennedy, D. O. (2001). Cognitive demand and blood glucose. *Physiology & Behavior, 73*, 585-592.

Segerstrom, S. C., & Nes, L. (2007). Heart rate variability reflects self-regulatory strength, effort, and fatigue. *Psychological Science, 18,* 275-281.

Sünram-Lea, S. L., Foster, J. K., Durlach, P., & Perez, C. (2001). Glucose facilitation of cognitive performance in healthy young adults: Examination of the influence of fast-duration, time of day and pre-consumption plasma glucose levels. *Psychopharmacology, 157*, 46-54.

Sünram-Lea, S. I., Foster, J. K., Durlach, P., & Perez, C. (2002). The effect of retrograde and anterograde glucose administration on memory performance in healthy young adults. *Behavioural Brain Research*, *134,* 505-516.

Tangney, J. P., Baumeister, R. F., & Boone, A. L. (2004). High self-control predicts good adjustment, less pathology, better grades, and interpersonal success. *Journal of Personality, 72,* 271-322.

Watanabe, M., & Sakagami, M. (2007). Integration of cognitive and motivational context information in the primate prefrontal cortex. *Cerebral Cortex, 17,* 101-109.

White, N. M. (1991). Peripheral and central memory-enhancing actions of glucose. In R. C. A. Frederickson, J. L. McGauugh, & D. L. Felten (Eds.), *Peripheral signaling of the brain* (pp. 421-441). Toronto, Canada: Hogrefe & Huber.

Wing, R. R., & Hill, J. O. (2001). Successful weight loss maintenance. *Annual Review of Nutrition, 21,* 323-341.

Wortsman, J. (2002). Role of epinephrine in acute stress. *Endocrinology & Metabolism Clinics of North America, 31,* 79-106.