



CARBOHYDRATE MOUTH RINSE: PERFORMANCE EFFECTS AND MECHANISMS

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KEY POINTS

- Carbohydrate feeding during moderate intensity endurance exercise is well known to delay fatigue and improve performance.
- The mechanisms responsible are thought to involve maintenance of blood glucose levels and carbohydrate oxidation rates and sparing of liver, and perhaps, muscle glycogen.
- The majority of studies investigating high intensity ($>75\%V_{O_2,max}$) endurance exercise (30-60 min) have also reported a performance benefit with exogenous carbohydrate.
- Traditional metabolic pathways are unlikely to account for the ergogenic effect because endogenous stores of carbohydrate are not limiting and exogenous carbohydrate oxidation is minimal.
- A growing number of studies have now shown that rinsing the mouth with a carbohydrate-containing solution is associated with improved high intensity endurance exercise performance.
- The consistent performance benefits of 2-3% occur without any ingestion of carbohydrate but are similar in magnitude to those reported when carbohydrate is ingested.
- Brain imaging studies have identified areas of the brain activated when carbohydrate is in the mouth, and it is likely that mouth rinsing carbohydrate results in afferent signals capable of modifying motor output.
- The effects appear more profound after an overnight fast, but performance benefits are still present even after ingestion of a meal.
- Further research is warranted to fully understand the separate taste transduction pathways for various carbohydrates, the practical implications for athletes as well as the impact on different sporting events.

INTRODUCTION

Traditionally, carbohydrate has been viewed as a substrate for fuel metabolism during exercise and this has been shown to result in improved endurance capacity (Jeukendrup, 2011). During prolonged exercise, carbohydrate feeding can help to maintain plasma glucose concentration and prevent hypoglycemia; it can maintain high rates of carbohydrate oxidation, spare hepatic glycogen, and in some cases, delay muscle glycogen depletion. However, performance benefits have also been observed during exercise lasting approximately 1 h. During exercise of this duration, hypoglycemia does not develop, blood glucose concentrations do not decrease (and may even increase) and glycogen depletion is not believed to be a performance-limiting factor. So during this type of exercise the performance effects are unlikely to be explained by metabolic factors but are likely to involve the central nervous system (CNS). A landmark study by our group (Carter et al., 2004b) showed that a simple carbohydrate mouth rinse (without ingesting the carbohydrate) resulted in similar performance benefits to ingestion, providing indirect evidence for a “central effect.” It was proposed that carbohydrate is detected by receptors in the oral cavity and that afferent neural signals sent directly to the brain are responsible for observed performance improvements. Since 2004, numerous studies have investigated the effects of carbohydrate mouth rinse with most but not all reporting

a performance enhancement (Tables 1 and 2). This Sports Science Exchange article will examine these studies, potential mechanisms, the influence of the fed state and practical applications for athletes.

CARBOHYDRATE INGESTION AND PERFORMANCE

Although the effects of carbohydrate on prolonged exercise performance ($>2h$) have been established since the 1980s (Jeukendrup, 2011), the observation that carbohydrate feeding can also improve performance during shorter duration exercise of higher intensity is relatively novel. In a study by Jeukendrup and colleagues, cyclists performed a 40 km time trial with or without the ingestion of a carbohydrate-electrolyte solution and were approximately 1 min faster with the carbohydrate feeding: a performance improvement of 2.3% (Jeukendrup et al., 1997). This was a large and unexpected ergogenic effect for which there was no clear metabolic explanation at the time. While endogenous stores of carbohydrate are thought to be sufficient to fuel this type of event, it also takes time before exogenous carbohydrate is absorbed, transported and used by the muscle. As such, it was estimated that the amount of exogenous carbohydrate oxidized during a 40 km time trial was approximately 15 g, equating to roughly 1 kcal/min (Jeukendrup et al., 1997). During the time trial, the cyclists were expending more than 20 kcal/min and most of this would have been from carbohydrate sources.

Table 1. Summary of studies currently in the literature that investigated the effects of a carbohydrate mouth rinse on performance (in chronological order). Glu = glucose, MD = maltodextrin, TTE = time to exhaustion, TT = time trial, NS is not significant.

AUTHORS	n	PERFORMANCE TEST	CHO TYPE	FED/ FASTED	EFFECT (+INDICATES IMPR.)	PERFORMANCE EFFECT (STATISTICAL SIGN.)
Carter et al., 2004b	9	Cycling TT (1h)	MD	4h	+2.9%	Improved
Whitham et al., 2007	7	1h running	MD	4h	-0.3%	NS
Rollo et al., 2008	10	30 min running	Glu+MD mix	+10h	+2.0%	Improved
Chambers et al., 2009	8	1h cycling	Glucose MD	+10h +10h	+1.9% +3.1%	Improved Improved
Beelen et al., 2009	14	1h cycling	MD	2h	+0.5%	NS
Rollo et al., 2010a	10	1h cycling	GLU+MD mix	13h	+2.0%	Improved
Pottier et al., 2010	12	1h cycling	Sucrose	3h	+3.7%	Improved
Rollo et al., 2011	10	1h cycling	GLU+MD mix	3h	+0.7%	NS
Fares et al., 2011	13	TTE 60%Wmax	MD MD	+10h 3h	+11.6% +3.5%	Improved Improved
Lane et al., 2013	12	Cycling TT (1h)	MD	10h 2h	+3.4% +1.8%	Improved Improved
Gam et al., 2013	10	Cycling TT (1h)	MD No Rinse	4h 4h	+5.3% +2.5%	Improved Improved
Sinclair et al., 2013	11	Cycling TT (30 min)	MD 10s Rinse MD 5s Rinse	4h 4h	+6.3% +4.7%	Improved NS

Consequently, the exogenous carbohydrate contribution was thought to be too small to provide additional fuel and result in the relatively large beneficial effect that was observed.

This observation did not occur in isolation, and in fact, confirmed some earlier work. One of the earliest studies to show an effect of carbohydrate during exercise of 1 h duration was an investigation by Neuffer et al. (1987). Subjects cycled for 45 min at 77% $\dot{V}O_{2max}$, followed by 15 min in which they had to complete as much work as possible. It was found that performance was improved by 10% when 45 g carbohydrate was ingested immediately before exercise compared to placebo. Anantaraman and colleagues (1995) studied the effects of carbohydrate ingestion before and at regular intervals during a 60 min cycle in which subjects had to perform as much work as possible. In this study, performance was improved by almost 11% in the carbohydrate trial compared with placebo. Further studies were performed in hot conditions. Below et al. (1995) exercised trained cyclists in 31°C (and 54% humidity) for 50 min followed by a time trial which lasted approximately 10 min. They observed a 6% improvement in time trial performance when carbohydrate was ingested throughout exercise. In a later study by our group (Carter et al., 2003), subjects exercised to exhaustion at 73% $\dot{V}O_{2max}$ in 35°C (and 30% humidity). Time to exhaustion increased by 14% in the carbohydrate trial compared with placebo.

There are, however, also some studies that did not observe performance effects with carbohydrate feeding in these conditions (Desbrow et al., 2004; McConell et al., 2000; Nikolopoulos et al., 2004). There are several possible explanations for the differences among the studies that did and did not find a positive effect on performance. The majority of the studies that did not find an effect actually observed a positive effect on performance but this did not reach statistical significance. It could, therefore, be that the non-significant findings are a result of the lack of statistical power. Furthermore, the studies that showed a difference generally had a longer duration of preceding starvation prior to the performance trial, a possibility that is discussed in more detail later. Finally, exercise duration may also be important: no studies less than 30 minutes have reported a beneficial effect of carbohydrate ingestion (Jeukendrup et al., 2008; Palmer et al., 1998). It is unclear why duration may be important, although it may involve the greater sensations of fatigue and discomfort associated at the higher exercise intensity overriding the beneficial effects of the carbohydrate. In summary though, the majority of studies observe a performance improvement when carbohydrate is ingested during high intensity exercise lasting approximately 1 hour. It is unlikely that the cause of this improvement is related to energy delivery to the working muscle.

CARBOHYDRATE MOUTH RINSE AND PERFORMANCE HIGH INTENSITY ENDURANCE EXERCISE

In order to study the potential role of carbohydrate as a fuel during high intensity endurance exercise, cyclists were asked to perform a 40 km time trial (Carter et al., 2004a). On one occasion they were infused with a glucose solution (1 g/min) and on another occasion they were infused with saline. It was observed that when glucose was infused blood glucose concentrations were twice as high and glucose disappearance was doubled. However, although glucose was taken up (presumably into the muscle) and oxidized (Jeukendrup et al., 1999), there was no effect on performance (Carter et al., 2004a). This provides evidence for the thought that the effects of carbohydrate during this type of exercise are not metabolic and thus there must be an alternative explanation for the ergogenic effect.

In a follow-up study, cyclists were asked to repeat the 40 km time trial but only rinse their mouth with a carbohydrate solution without swallowing it (Carter et al., 2004b). The carbohydrate used in this study was a non-sweet tasteless maltodextrin solution. The rinsing protocol was standardized; subjects rinsed their mouth for 5 seconds with the drink and then expectorated the drink out into a bowl. The results were remarkable; performance was improved with the carbohydrate mouth rinse compared with placebo and the magnitude of the effect was the same as we had seen in the early study with carbohydrate ingestion (Jeukendrup et al., 1997). It was unlikely that much, if any, carbohydrate had been absorbed from the mouth rinse, yet performance was improved by about 3% (Carter et al., 2004b), very similar to the 2.3% improvement observed with carbohydrate feeding (Jeukendrup et al., 1997).

After this initial study by Carter et al. (2004b), several other studies reproduced these findings. Rollo et al. (2008) reported that mouth rinsing with a 6% carbohydrate solution increased total distance covered during a self-selected 30 min run in comparison with a color- and taste-matched placebo. This was the first running study that showed an effect and the first study in which exercise was as short as 30 min. However, it is important to note that this study was not a performance study. Instead participants were asked to run at speeds that equated to a rating of perceived exertion of 15. In addition to recording self-selected speeds and total distance covered, the authors assessed the runners' subjective feelings. The total distance covered was greater during the carbohydrate trial than during the placebo trial. The authors also observed that faster speeds selected during the first 5 min of exercise corresponded with enhanced feelings of pleasure when mouth rinsing with the carbohydrate solution. In a follow-up study, Rollo and colleagues (2010a) studied the effect of a carbohydrate-electrolyte mouth rinse during a 60 min self-paced run. The treadmill was modified so that the runners could change velocity without the need for manual input or visual feedback from the runner (i.e., the treadmill velocity increased or decreased as the runner moved to the front or the back of the treadmill belt respectively). Runners covered 211 m more distance during the carbohydrate trial (14298 ± 685 m) compared to the placebo trial (14086 ± 732 m), a significant improvement of 1.5%.

In another study, the influence of ingestion and mouth rinse with a carbohydrate solution on performance during a high intensity time trial (~1 h) was investigated in trained subjects (Pottier et al., 2010). Subjects rinsed around the mouth or ingested a 6% carbohydrate solution or placebo before and throughout a time trial. In the mouth rinse conditions, time to complete the test was shorter with the carbohydrate mouth rinse (61.7 ± 5.1 min) than with placebo (64.1 ± 6.5 min). Interestingly, the investigators did not see a difference between placebo (62.5 ± 6.9 min) and carbohydrate (63.2 ± 6.9 min) when drinks were consumed (Pottier et al., 2010), which is in contrast to a number of other studies that observed performance improvements with carbohydrate ingestion during exercise of similar duration (Anantaraman et al., 1995; Below et al., 1995; Carter et al., 2003; Jeukendrup et al., 1997; Neuffer et al., 1987). Further evidence for a performance-enhancing effect of an oral carbohydrate mouth rinse came from another study at the University of Birmingham in the United Kingdom. Chambers et al. (2009) showed a 1.9% (glucose) and a 3.1% (maltodextrin) improvement in cycling time trial performance with a carbohydrate mouth rinse compared with non-nutritive sweetened placebos. Finally, two recent studies have both demonstrated performance-enhancing effects in cycle exercise lasting ~1 h with carbohydrate mouth rinsing (Gam et al., 2013; Sinclair et al., 2013).

Although all these studies confirmed the initial findings by Carter et al. (2004b; Table 2), there have also been several studies that did not find this effect (Beelen et al., 2009; Whitham and McKinney, 2007). There may be several reasons for these discordant findings, including a lack of statistical power. The study by Whitham and McKinney (2007), for example, had only seven subjects and used a performance measurement that may have been less reliable and/or sensitive. Runners had to adjust treadmill speed manually as opposed to the modified treadmill used by Rollo et al. (2010a) wherein runners could change velocity without the need for manual input or visual feedback. Another explanation was offered by Beelen et al. (2009) who provided their subjects with a meal two hours before the performance trial, in line with current recommendations (Burke et al., 2011). It was suggested that when fed, the effects of a mouth rinse are diminished and this possibility will be discussed in greater detail in a later section.

OTHER TYPES OF EXERCISE

Most studies have investigated the effects of a carbohydrate mouth rinse on endurance exercise performance in events between 30 and 60 min. Potential effects during supramaximal exercise, intermittent exercise, resistance exercise or very prolonged exercise have not been extensively studied. However, four recent papers have attempted to help fill this knowledge gap (Table 2). Chong and colleagues (2011) studied the impact of carbohydrate mouth rinse during a 30 s sprint on a cycle ergometer and concluded that the use of a 5 s mouth rinse with an isoenergetic amount of either maltodextrin

Table 2. Summary of studies currently in the literature that investigated the effects of a carbohydrate mouth rinse on other types of performance. Where PO = power output, M/S = muscle, Glu = glucose, MD = maltodextrin, NS is not significant, LIST = Loughborough Intermittent Shuttle Test, RST = repeated sprint test.

AUTHORS	n	PERFORMANCE TEST	CHO TYPE	FED/OVERNIGHT	EFFECT (+INDICATES IMPR.)	PERFORMANCE EFFECT (STATISTICAL SIGN.)
Chong et al 2011	14	30 Sprint PO	Glu MD	10h	+0.18%	NS
				10h	+0.65%	NS
Painelli et al 2011	12	M/S strength	Dextrose	8h	-0.3%	NS
Beaven et al 2013	12	5x6 sprint PO	Glu	2h	+39.1 W -39.6 W	Improved- Sprint 1 Declined-Sprint 5
Dorling and Earnest 2013	8	List RST	MD	"Fasted"	+0.5%	NS

or glucose is not beneficial for maximal sprint performance. In the same year, Painelli et al. (2011) came to a similar conclusion for maximum strength or strength endurance performance (Table 2). More recently, Beaven and colleagues (2013) investigated the effect on multiple 5 s cycle sprints with a 6% glucose mouth rinse and reported an improvement in peak and mean power output in the first of the five sprints. However, the improvement in sprint performance was short lived, with peak and mean power output in the final sprint significantly lowered in the glucose rinse condition compared to placebo. Interestingly, this drop-off in performance was prevented and an additive effect reported when the carbohydrate solution was combined with caffeine (Beaven et al., 2013). Finally in running exercise, mouth rinsing carbohydrate has recently been reported to have no effect on maximal, repeated or average sprint performance (Dorling and Earnest, 2013). In this study, eight men routinely rinsed a 6.4% maltodextrin beverage while completing repeated sprint tests throughout the Loughborough Intermittent Shuttle Run Test (LIST), designed to mimic the physiological demands of soccer. Nevertheless, in relation to multiple sprint sports, no studies have investigated potential effects of mouth rinsing carbohydrate on cognitive functioning, decision-making or reaction time, all of which would impact performance. Furthermore, no studies to date have investigated carbohydrate mouth rinse during very prolonged endurance performance or exercise in the heat. It is important to note that this is most likely a consequence of a viable rationale to justify these studies in which the ingestion of fluid and carbohydrate offer obvious advantages to exercise of these durations or environmental conditions.

THE ROLE OF THE CENTRAL NERVOUS SYSTEM

It has been suggested that the alterations in power output commonly observed during a self-paced exercise task is under the influence of a "Central Governor" that controls the recruitment of motor units during exercise to ensure that homeostasis is maintained (Kayser, 2003; Noakes, 2000). The "Central Governor" is postulated to alter power output using afferent signals from peripheral physiological systems and receptors that detect changes in the external and internal environment (Lambert et al., 2005). It is therefore plausible

that during exercise the positive central responses to an oral carbohydrate stimulus could counteract the negative physical, metabolic and thermal afferent signals arising from muscles, joints and core temperature receptors that are sent to the brain and consciously or unconsciously contribute to central fatigue and an inhibition of motor drive to the exercising muscles (St Clair Gibson et al., 2001). For example, the dopaminergic system of the ventral striatum has been implicated in arousal, motivation and the control of motor behavior (Berridge and Robinson, 1998) and increased activity of this pathway during exercise has been postulated to attenuate the development of central fatigue (Davis et al., 2000). This would suggest that the beneficial effects of carbohydrate feeding during exercise are not confined to its conventional metabolic advantage and may serve not as an energy substrate but as a positive afferent signal capable of modifying motor output.

Chambers et al. (2009) used functional magnetic resonance imaging (fMRI) to investigate the responses of the human brain to a carbohydrate and placebo mouth rinse. The study revealed that tasting both a sweet (glucose) and non-sweet (maltodextrin) carbohydrate solution activated areas of the brain, such as the anterior cingulate cortex and ventral striatum, which were unresponsive to artificial sweetener (saccharin). Other neuroimaging investigations have also reported that an oral carbohydrate solution activates additional brain regions compared with an artificial sweetener (Frank et al., 2008; Haase et al., 2009), suggesting there may be taste transduction pathways that respond to carbohydrate independently of those for sweetness. This is in line with the observation that endurance exercise capacity was enhanced compared with the control condition with both a sweet and a non-sweet carbohydrate (Carter et al., 2005).

MECHANISMS AND BRAIN REGIONS INVOLVED

The receptors involved in signal transduction after a mouth rinse have not yet been identified. It is known that whenever food or drink is placed in the mouth, taste receptor cells (TRCs) are stimulated, providing the first analysis of potentially ingestible food (Chandrashekar et al., 2006; Small et al., 2007). TRCs exist

in groups of 50-100 in taste buds, which are distributed throughout the oral cavity, including the tongue, soft palate and epiglottis (Scott and Plata-Salaman, 1999). Electrical activity initiated by a taste cue is transmitted to gustatory neurons that innervate the taste buds (Simon et al., 2006). This information converges on the nucleus of the solitary tract in the medulla, and is subsequently relayed via the ventral posterior medial nucleus of the thalamus to the primary taste cortex, located in the anterior insula and adjoining frontal operculum and the putative secondary taste cortex in the orbitofrontal cortex (Small et al., 2007). The primary taste cortex and orbitofrontal cortex have projections to regions of the brain, such as the dorsolateral prefrontal cortex, anterior cingulate cortex and ventral striatum, which are thought to provide the link between gustatory pathways and the appropriate emotional, cognitive and behavioral response (Kringelbach, 2004; Rolls, 2007). The fact that many of these higher brain regions have been reported to be activated by oral carbohydrates and not non-nutritive sweeteners (Chambers et al., 2009; Frank et al., 2008; Haase et al., 2009) may provide a mechanistic explanation for the positive effects of a carbohydrate mouth rinse on exercise performance. It is not known however, what exactly is detected because most human taste receptors respond to sweetness, not carbohydrate content.

Experimental data from rodent studies supports the existence of mammalian taste transduction pathways that respond to carbohydrate independently of those for sweetness. The mammalian sweet taste receptor combines two G-protein-coupled receptors, T1R2 and T1R3, which form a heterodimer that responds to both natural sugars and artificial sweeteners (Nelson et al., 2001). It has, however, been suggested that homodimers of T1R2 and T1R3 might also exist and function as sugar detectors. Further research is warranted to fully understand the separate taste transduction pathways for various carbohydrates and sweeteners and how these differ between mammalian species, particularly in humans.

THE EFFECT OF THE PRE-EXERCISE FASTING PERIOD

One of the reasons cited to explain the discrepancy between studies reporting a positive or no effect of rinsing carbohydrate on high intensity endurance exercise is the influence, or lack thereof, of the pre-exercise meal. The majority of reports of a beneficial effect have involved subjects commencing exercise following an overnight fast (Chambers et al., 2009; Rollo et al., 2010a) or in a post-absorptive state (≥ 4 h; Carter et al., 2004b). Conversely, it appears that investigations that fail to report an ergogenic action from a carbohydrate mouth rinse tend to be the studies in which subjects received a carbohydrate-rich meal 2-3 h prior to exercise (Beelen et al., 2009). Similar findings (i.e., no effect) have also been reported when carbohydrate has been ingested during high intensity running and cycling exercise following the consumption of a meal rich in carbohydrate in the hours before (Desbrow et al., 2004; Rollo and Williams, 2010b). As such, it is likely that the difference in the pre-exercise fasting period influences the central neural response to an oral carbohydrate stimulus. An fMRI study compared the cortical responses to oral sucrose following a) an overnight fast (12 h) and b)

after ingestion of a 700 kcal liquid meal (Haase et al., 2009). There was significantly greater activity within a number of brain regions, including the ventral striatum, amygdala and hypothalamus, following a prolonged fast compared with in a post-prandial state. The central responses to oral carbohydrate, which are capable of modifying motor output, may therefore be dependent on the pre-exercise nutritional state of the body.

However, several observations exist to suggest that the fed status of the athlete may not be the definitive regulator of whether rinsing with carbohydrate is beneficial or not. First of all, Whitham and McKinney (2007) showed no positive effects of rinsing carbohydrate in the overnight fasted state, while Pottier et al. (2010) did demonstrate performance enhancement with rinsing carbohydrate despite a meal two hours beforehand. Secondly, two recent studies have been conducted to directly address the effect of fed state on exercise performance and capacity with rinsing carbohydrate. The first of these reported significant performance effects on time to fatigue at 60% W_{max} in both the fed (3.5% improvement) and fasted (11.6% improvement) state with a maltodextrin-containing rinse solution versus placebo (Fares and Kayser, 2011). These results were quickly supported by a later study investigating both fed and fasted athletes carrying out a one hour cycle time trial with maltodextrin or placebo rinsing (Lane et al., 2013). Performance benefits were reported regardless of fed state, although the magnitude of improvement was greater in the fasted state (3.3% fasted vs. 1.8% fed), which is aligned with the previous brain imaging observations (Haase et al., 2009), while the best performance was reported in the fed athletes rinsing with carbohydrate.

PRACTICAL IMPLICATIONS

- Routinely rinsing a carbohydrate-containing solution around the oral cavity for between 5-10 s has been shown to improve high intensity endurance performance lasting 30-70 min.
- The magnitude of the performance benefit is similar to that of carbohydrate ingestion, although athletes who are prone to gastro-intestinal (GI) distress during high intensity exercise may want to consider rinsing because of the reduced risk of GI discomfort.
- Although unknown, it is unlikely that rinsing carbohydrate will continue to have a beneficial effect as the exercise duration approaches and exceeds 2 h and fatigue occurs due to carbohydrate store depletion. However, a potential application during very prolonged events, when athletes struggle with GI-discomfort and where absorption may become impaired, would be to revert to rinsing carbohydrate to provide some advantage.
- Rinsing and expectorating carbohydrate may be a useful nutritional strategy for individuals undertaking exercise for weight management purposes. Such a strategy would likely result in a lower perception of effort and/or higher exercise intensities without the intake of additional calories.

- Recent research has suggested that the act of rinsing during high intensity exercise may be detrimental due to disruptions to breathing and/or concentration (Gam et al., 2013). Although this negative influence is corrected and performance further improved, by the addition of carbohydrate, athletes should take care to practice this technique during training.
- For optimum performance, the collective findings of the research suggest that athletes should consume a high-carbohydrate meal 2-3 hours before exercise and ingest or rinse small volumes of a carbohydrate-containing solution periodically throughout high intensity endurance exercise.

SUMMARY

Carbohydrate during exercise has been demonstrated to improve exercise performance even when the exercise is of high intensity ($>75\%VO_2\text{max}$) and relatively short duration (~1h). It has become clear that the underlying mechanisms for the ergogenic effect during this type of activity are not metabolic but may reside in the central nervous system. Carbohydrate mouth rinses have been shown to result in similar performance improvements, which suggest that the beneficial effects of carbohydrate feeding during exercise are not confined to its conventional metabolic advantage. Carbohydrate may also serve as a positive afferent signal capable of modifying motor output. These effects appear to be specific to carbohydrate and independent of taste or sweetness. Further research is needed to fully understand the separate taste transduction pathways for various carbohydrates and sweeteners as well as the practical implications in different sports and different aspects of performance.

REFERENCES

- Anantaraman, R., A.A. Carmines, G.A. Gaesser, and A. Weltman (1995). Effects of carbohydrate supplementation on performance during 1 h of high intensity exercise. *Int. J. Sports Med.* 16:461-465.
- Beelen, M., J. Berghuis, B. Bonaparte, S.B. Ballak, A.E. Jeukendrup, and L.J. van Loon (2009). Carbohydrate mouth rinsing in the fed state: Lack of enhancement of time-trial performance. *Int. J. Sport Nutr. Exerc. Metab.* 19:400-409.
- Beaven, C.M., P. Maulder, A. Pooley, L. Kilduff, and C. Cook (2013). Effects of caffeine and carbohydrate mouth rinses on repeated sprint performance. *Appl. Physiol. Nutr. Metab.* 38: 633–637.
- Below, P.R., R. Mora-Rodriguez, J. Gonzales Alonso, and E.F. Coyle (1995). Fluid and carbohydrate ingestion independently improve performance during 1 h of intense exercise. *Med. Sci. Sports Exerc.* 27:200-210.
- Berridge, K.C., and T.E. Robinson (1998). What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Res. Rev.* 28:309-369.
- Burke, L.M., J.A. Hawley, S.H. Wong, and A.E. Jeukendrup (2011). Carbohydrates for training and competition. *J. Sports Sci.* 29: S17-27.
- Carter, J., A.E. Jeukendrup, and D.A. Jones (2005). The effect of sweetness on the efficacy of carbohydrate supplementation during exercise in the heat. *Can. J. Appl. Physiol.* 30:379-391.
- Carter, J., A.E. Jeukendrup, T. Mundel, and D.A. Jones (2003). Carbohydrate supplementation improves moderate and high-intensity exercise in the heat. *Pflugers Arch.* 446:211-219.
- Carter, J.M., A.E. Jeukendrup, C.H. Mann, and D.A. Jones (2004a). The effect of glucose infusion on glucose kinetics during a 1-h time trial. *Med. Sci. Sports Exerc.* 36:1543-1550.
- Carter, J.M., A.E. Jeukendrup, and D.A. Jones (2004b). The effect of carbohydrate mouth rinse on 1-h cycle time trial performance. *Med. Sci. Sports Exerc.* 36:2107-2111.
- Chambers, E.S., M.W. Bridge, and D.A. Jones (2009). Carbohydrate sensing in the human mouth: Effects on exercise performance and brain activity. *J. Physiol.* 587:1779-1794.
- Chandrashekar, J., M.A. Hoon, N.J.P. Ryba, C.S. Zuker (2006). The receptors and cells for mammalian taste. *Nature* 444:288-294.
- Chong, E., K.J. Guelfi, P.A. Fournier (2011). Effect of a carbohydrate mouth rinse on maximal sprint performance in competitive male cyclists. *J. Sci. Med. Sport* 14:162-167.
- Davis, J.M., N.L. Alderson, and R.S. Welsh (2000). Serotonin and central nervous system fatigue: Nutritional considerations. *Am. J. Clin. Nutr.* 72:573S-578S.
- Desbrow, B., S. Anderson, J. Barrett, E. Rao, and M. Hargreaves (2004). Carbohydrate-electrolyte feedings and 1 h time trial cycling performance. *Int. J. Sport Nutr. Exerc. Metab.* 14:541-549.
- Dorling, J.L. and C.P. Earnest (2013). Effect of carbohydrate mouth rinsing on multiple sprint performance. *J. Int.Soc. Sports Nutr.* 10: Epub Ahead of Print.
- Fares, E.J., and B. Kayser (2011). Carbohydrate mouth rinse effects on exercise capacity in pre- and postprandial states. *J. Nutr. Metab.* 2011:385962.
- Frank, G.K., T.A. Oberndorfer, A.N. Simmons, M.P. Paulus, J.L. Fudge, T.T. Yang, and W.H. Kaye (2008). Sucrose activates human taste pathways differently from artificial sweetener. *Neuroimage* 39:1559-1569.
- Gam, S., K.J. Guelfi, and P.A. Fournier (2013). Opposition of carbohydrate in a mouth-rinse solution to the detrimental effect of mouth rinsing during cycling time trials. *Int. J. Sport Nutr. Exerc. Metab.* 23: 48-56.
- Haase, L., B. Cerf-Ducastel, and C. Murphy (2009). Cortical activation in response to pure taste stimuli during the physiological states of hunger and satiety. *Neuroimage* 44:1008-1021.
- Jeukendrup, A., F. Brouns, A.J. Wagenmakers, and W.H. Saris (1997). Carbohydrate-electrolyte feedings improve 1 h time trial cycling performance. *Int. J. Sports Med.* 18:125-129.
- Jeukendrup, A.E., S. Hopkins, L.F. Aragon-Vargas, and C. Hulston (2008). No effect of carbohydrate feeding on 16 km cycling time trial performance. *Eur. J. Appl. Physiol.* 104:831-837.
- Jeukendrup, A.E., A. Raben, A. Gijzen, J.H. Stegen, F. Brouns, W.H. Saris, and A.J. Wagenmakers (1999). Glucose kinetics during prolonged exercise in highly trained human subjects: Effect of glucose ingestion. *J. Physiol.* 515:579-589.
- Jeukendrup, A.E. (2011). Nutrition for endurance sports: Marathon, triathlon, and road cycling. *J.Sports Sci.* 29(S1): S91–S99.
- Kayser, B. (2003). Exercise starts and ends in the brain. *Eur. J. Appl. Physiol.* 90:411-419.
- Kringelbach, M.L. (2004). Food for thought: Hedonic experience beyond homeostasis in the human brain. *Neuroscience* 126:807-819.
- Lambert, E.V., A. St Clair Gibson, and T.D. Noakes (2005). Complex systems model of fatigue: Integrative homeostatic control of peripheral physiological systems during exercise in humans. *Br. J. Sports Med.* 39:52-62.
- Lane, S.C., S.R. Bird, L.M. Burke, and J.A. Hawley (2013). Effect of a carbohydrate mouth rinse on simulated cycling time trial performance commenced in a fed or fasted state. *Appl. Physiol. Nutr. Metab.* 38:134-13.
- McConnell, G.K., B.J. Canny, M.C. Daddo, M.J. Nance, and R.J. Snow (2000). Effect of carbohydrate ingestion on glucose kinetics and muscle metabolism during intense endurance exercise. *J. Appl. Physiol.* 89:1690-1698..
- Nelson, G., M.A. Hoon, J. Chandrashekar, Y. Zhang, N.J. Ryba, and C.S. Zuker (2001). Mammalian sweet taste receptors. *Cell* 106:381-390.
- Neufer, P.D., D.L. Costill, M.G. Flynn, J.P. Kirwan, J.B. Mitchell, and J. Houmard (1987). Improvements in exercise performance: Effects of carbohydrate feedings and diet. *J. Appl. Physiol.* 62:983-988.
- Nikolopoulos, V., M.J. Arkinstall, and J.A. Hawley (2004). Reduced neuromuscular activity with carbohydrate ingestion during constant load cycling. *Int. J. Sport Nutr. Exerc. Metab.* 14:161-170.
- Noakes, T.D. (2000). Physiological models to understand exercise fatigue and the adaptations that predict or enhance athletic performance. *Scand. J. Med. Sci. Sports* 10:123-145.
- Painelli, V.S., H. Roschel, B. Gualano, S. Del-Favero, F.B. Benatti, C. Ugrinowitsch, V. Tricoli, and A.H. Lancha Jr. (2011). The effect of carbohydrate mouth rinse on maximal strength and strength endurance. *Eur. J. Appl. Physiol.* 111: 2381-2386.
- Palmer, G.S., M.C. Clancy, J.A. Hawley, I.M. Rodger, L.M. Burke, and T.D. Noakes (1998). Carbohydrate ingestion immediately before exercise does not improve 20km time trial performance in well trained cyclists. *Int. J. Sports Med.* 19:415-418.
- Pottier, A., J. Bouckaert, W. Gillis, T. Roels, and W. Derave (2010). Mouth rinse but not ingestion of a carbohydrate solution improves 1-h cycle time trial performance. *Scand. J. Med. Sci. Sports* 20: 105-111.
- Rollo, I., M. Cole, R. Miller, and C. Williams (2010a). Influence of mouth rinsing a carbohydrate solution on 1-h running performance. *Med. Sci. Sports Exerc.* 42:798-804.
- Rollo, I. and C. Williams (2010b). Influence of ingesting a carbohydrate-electrolyte solution before and during a 1-hour run in fed endurance-trained runners. *J Sports Sci.* 28: 593-601.
- Rollo, I., C. Williams, N. Gant, and M. Nute (2008). The influence of carbohydrate mouth rinse on self-selected speeds during a 30-min treadmill run. *Int. J. Sport Nutr. Exerc. Metab.* 18:585-600.

- Rollo, I., C. Williams, and Neville, M (2011). Influence of ingesting versus mouth rinsing a carbohydrate solution during a 1-h run. *Med. Sci. Sports Exerc.* 43: 468-475.
- Rolls, E.T. (2007). Sensory processing in the brain related to the control of food intake. *Proc. Nutr. Soc.* 66:96-112.
- Scott, T.R., and C.R. Plata-Salaman (1999). Taste in the monkey cortex. *Physiol. Behav.* 67:489-511.
- Simon, S.A., I.E. de Araujo, R. Gutierrez, and M.A.L. Nicoletis (2006). The neural mechanisms of gustation: A distributed processing code. *Nature Reviews Neuroscience* 7:890-901.
- Sinclair, J., L. Bottoms, C. Flynn, E. Bradley, E. Alexander, S. McCullagh, T. Finn, and H. Thomas Hurst (2013). The effect of different durations of carbohydrate mouth rinse on cycling performance. *Eur J. Sport Sci.* Epub Ahead of Print.
- Small, D.M., G. Bender, M.G. Veldhuizen, K. Rudenga, D. Nachtigal, and J. Felsted (2007). The role of the human orbitofrontal cortex in taste and flavor processing. *Ann. N. Y. Acad. Sci.* 1121:136-151.
- St Clair Gibson, A., M.L. Lambert, and T.D. Noakes (2001). Neural control of force output during maximal and submaximal exercise. *Sports Med.* 31:637-650.
- Whitham, M., and J. McKinney (2007). Effect of a carbohydrate mouthwash on running time-trial performance. *J. Sports Sci.* 25:1385-1392.