

Effects of Physical Exercise on Sensory Perception and Hedonic Response

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Abstract

Sensory perception and hedonic response to foods and beverages depend not only on the characteristics of the food or beverage product, but also on the physiological and psychological state of the person consuming it. Physical exercise provokes physiological changes in human subjects including dehydration through sweat loss and depletion of energy stores, and emotional changes including increased fatigue and vigor; as such it is expected to affect the sensory and hedonic response to foods consumed immediately post-workout. Exercise and proper diet are both well-recognized components of a healthy lifestyle; it is therefore critical to understand how an acute bout of exercise or a chronic training regimen might affect the eating behavior of the exerciser. This review examines published studies – both interventional and observational – on the effect of acute and chronic physical exercise on thirst, hunger, perception and liking of the five basic tastes, and macronutrient choice. This review also touches on macronutrient choice and psychological factors of food choice such as compensatory eating and food restraint. Results suggest that acute exercise of a certain threshold intensity effects consistent perceptual and hedonic changes across the population: immediate hunger suppression, osmoregulatory thirst, increased palatability of salt, increased perception and palatability of sweetness, and decreased perception and palatability of sourness. Effects on bitter and umami appear more limited. However, individual metabolic and psychological variation modulate these effects, and the effects of chronic exercise are complicated by concurrent lifestyle changes and not properly understood through observational studies alone.

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Introduction

Sensory perception and hedonic response are determined not only by the physical and chemical properties of food or beverage products, but also the physiological state and the expectations of the individual consuming (Appleton 2005). Several short-term physiological alterations have been shown to occur during and following exercise:

- dehydration and loss of electrolytes, especially sodium, through perspiration
- depletion of glycogen stores or free fatty acids for energy
- changes to mood, particularly fatigue and vigor

According to Cabanac (1971), a stimulus “can feel pleasant or unpleasant depending upon its usefulness as determined by internal signals.” Logically, the level of metabolic fuels should affect behaviors to rectify deficiencies and restore bodily balance (Hopkins et al 2011). Under this theory of physiological usefulness, physical exercise may then be expected to:

- increase pleasantness of fluids
- increase pleasantness of electrolytes such as sodium (salty taste)
- increase pleasantness of simple carbohydrates such as sucrose and glucose (sweet taste) or fats (fatty / creamy mouthfeel)

These increases in pleasantness may direct the subject to counteract losses from acute exercise.

This literature review will discuss the impact of exercise on thirst and hunger, perception and hedonic response to the basic tastes (salty, sweet, sour, bitter and umami) and macronutrient choice, as well as psychological factors of food choice such as compensatory eating and food restraint. The current understanding will yield implications for both food product development and sensory practice, which will be touched upon in the latter part of this review.

Chapter 1 - Thirst, Hunger and Their Impact on Overall Liking

Westerterp-Platenga et al (1997) noted higher perceived thirst immediately following exercise as well as immediately following sauna. In their study, 10 obese and 10 non-obese men, all healthy but untrained, performed in randomized order four 2-hour sessions of ergometer cycling at 60% maximal workload and four 2-hour sessions of seated reading. Similarly, 10 healthy but untrained non-obese men performed in randomized order four 2-hour sessions of sauna and four 2-hour sessions of reading. Each session was preceded by a breakfast standardized to each subject, and followed by an ad libitum meal, and subjects rated their perceived thirst on a 100mm Visual Analog Scale (VAS) prior to breakfast, after breakfast, prior to the ad lib meal, and after the ad lib meal. Perceived thirst was significantly higher post-cycling versus post-reading as well as post-sauna versus post-reading ($p < 0.001$), with no significant difference pre-reading versus post-reading, suggesting that the increase in thirst was associated with the loss of body water through sweating in exercise or sauna.

During the ad libitum meal, subjects also selected a higher proportion of liquid foods following cycling ($p < 0.001$) and sauna ($p < 0.01$), compared to before either intervention. This finding is consistent with Thompson et al (1988) who noted that, while total calorie and solid-source calorie intake did not change, liquid-source calorie-intake significantly increased in 15 fasted subjects ($p < 0.05$) after exercise at 35-68% maximal oxygen consumption (VO_{2max}). Increased thirst following exercise is then associated with increased voluntary drinking.

While increased fluid intake does not necessarily imply greater enjoyment, Appleton (2005) found that 81 regular exercisers rated the pleasantness of all fluids – a regular sports drink, a weak sports drink, a very weak sports drink, water, a regular fruit drink, a weak fruit drink and a very weak fruit drink – significantly higher on a 100mm VAS scale ($p < 0.01$).

Moreover, subjects exhibiting high fluid loss rated all fluids significantly higher than subjects exhibiting low fluid loss ($p < 0.01$), confirming a link between dehydration through exercise and increased fluid liking.

Though all fluids appear to be more palatable following dehydration through exercise, the sensory and compositional characteristics do seem to matter. Wilk and Bar-Or (1996) exercised 12 boys via four consecutive 20-minute cycling bouts at 50% VO_2max in warm conditions (35°C, 40-45% relative humidity). The boys were allowed rest periods and ad libitum access to one of three beverages: water, water with a grape flavor, or a grape-flavored carbohydrate-electrolyte drink. Perceived thirst on a 100mm VAS scale increased with exercise regardless of the beverage provided, however boys tended to report higher thirst with water only. Total drink intake was also 44.5% higher when the ad lib beverage contained a grape flavor compared to only water. These results suggest that adding a flavor – which the authors assumed to increase the palatability of the beverage – increased voluntary consumption and decreased thirst. However, the difference did not reach significance, implying that greater improvements in palatability may be necessary to affect voluntary intake.

Similarly, in Passe et al (2004), 50 triathletes and runners performed 75 minutes of aerobic exercise at 80-85% of their maximal heart rate (HRmax) and evaluated their overall liking via a 9-point hedonic scale of various beverages at frequent intervals. The authors found that the beverage intake of water, diluted orange juice and homemade carbohydrate-electrolyte beverage was not closely related to their palatability; however a commercial carbohydrate-electrolyte beverage was rated significantly more pleasant and was consumed in significantly greater quantities during exercise. This finding suggests that beverages may need to be extremely pleasant compared to water in order to trigger compulsive rehydration or that the

subject must be allowed more time to consume the beverage in order for taste and flavor to affect fluid intake.

In fact, with extreme dehydration, water replacement may take priority over any taste and nutrient effects. While pleasantness of all beverages increased with exercise in Appleton (2005) and the sweetest beverages remained the best-received, the greatest increase in pleasantness occurred in the beverages with low osmolarity – the water, the very weak sports drink, and the very weak fruit drink. Appleton suggested that, in situations where water replacement is a priority, beverages which do not satisfy this requirement would not be expected to increase in pleasantness. In the high osmolarity beverages, high amounts of solute particles may interfere with rehydration, explaining their non-significant increase in pleasantness. As osmolarity of a fluid can be detected immediately upon tasting via osmoreceptors on the tongue, dehydration via exercise can significantly affect the homeostatic regulation of body water balance and the hedonic response to fluids. Conversely, Ali et al (2011) found no significant difference in overall liking for high osmolarity drinks versus low osmolarity drinks during and following a 60-minute treadmill run at 70% HRmax, despite significant changes in taste perception: overall liking increased similarly across all beverages during and immediately after exercise. The authors suggested in this case that the lack of a significant difference in fact indicated that replenishment of lost fluids dominates over replenishment of the nutrients in the high osmolarity drinks as mediated by taste effects.

The importance of fluid replacement may however be mitigated with acclimatization. As noted above, Wilk and Bar-Or (1996) found flavor to increase voluntary rehydration in boys exercising in the heat. However, in Wong and Sun (2014), 14 children exercised in warm and

humid conditions (30°C, 70%RH) via four 20-minute rounds of treadmill walking at 50% VO_2max . In the latter study, the authors found no significant difference in intake of beverages consistent in taste (sweetness, saltiness, sourness) and varying only in flavor (orange, lemon, grape, none). Regardless of drink flavor, all children consumed sufficient fluid to replace that lost and subsequently measured during the exercise, and perceived thirst on a VAS was not significantly different. Therefore, children were able to balance their water intake to compensate for their fluid losses in exercise despite hot and humid conditions, and liking for a particular flavor did not affect hydration status. However, this exercise was also insufficient to trigger changes in plasma osmolarity, and may therefore have been too light to elicit a compensatory preference for water over flavored beverages of presumably higher osmolarity. Regardless, taken together, the results of these two studies suggest that acclimatization may mitigate the effects of thirst.

Finally, as suggested by the oral detection of osmolarity in Appleton (2005), oral status may play a large role in the rehydration response. Guest et al (2006) simulated exercise conditions by artificially drying the mouths of 22 subjects, then measuring by Labeled Affective Magnitude Scales (LAMS) their perceived mouth wetness as well as the pleasantness of small amounts of water presented at varying temperatures; in a follow-up experiment, the authors measured the salivation rate of 21 subjects under the same conditions. Though Guest et al (2006) noted no significant differences in perceived mouth-wetness for normally hydrated subjects presented with small amounts of water, change in perceived wetness was significantly higher after the mouth-drying protocol ($p < 0.0001$), and particularly large for the coldest water ($p < 0.004$). Colder samples were also rated more pleasant after mouth-drying than after normal hydration, with pleasantness correlated with change in perceived mouth wetness ($p < 0.0009$).

These findings suggest that mouth state alone (without systemic dehydration) can alter fluid hedonics. Furthermore, while mouth-drying significantly increased the salivation rate, Guest et al noted no significant effect of water temperature, suggesting that the increase in perceived mouth wetness was illusory and consistent with the physiological usefulness or reward of cooler water.

Conversely to the increase in thirst during and following exercise, Thompson (1988) found that perceived hunger rated on a 9-point intensity scale decreased significantly after cycling at moderate intensity (68% VO_2max) compared to control, but was restored 50 minutes after exercise ($p < 0.05$). In contrast, hunger was not significantly different from control after cycling at low intensity (35% VO_2max), and in fact steadily rose from the start of the intervention to a test meal 1 hour after the intervention. Exercise was then associated with an immediate suppression of hunger, provided the intensity is sufficient. As subjects did not consume significantly different amounts of food at the test meal, acute exercise can cause a significant energy expenditure without immediate compensation, i.e. a negative energy balance.

Similarly, Lluch et al (1997) exercised 12 dietary-restrained women with 50 minutes of cycling at 70% VO_2max – corresponding to the high intensity condition of Thompson – then presented them with either a low-fat or a high-fat test lunch. The authors measured tastiness, pleasantness and fillingness of the test lunch via a 100mm VAS, as well as motivations to eat (hunger, desire to eat, fullness, thirst) and mental state (contentment, lethargy, tension) on VAS via an Electronic Appetite Rating System. While all subjects were presented with a standardized breakfast for a similar hunger baseline, hunger ratings were significantly lower during exercise and in the 20 minutes separating exercise and the test lunch ($p < 0.1$). In the hours following the test lunch and preceding dinner, hunger rose across all conditions, with a slight trend for higher

hunger following exercise versus rest. In the hours following dinner, hunger again rose across all conditions, with a significantly greater increase with exercise in both the low-fat ($p = 0.01$) and high-fat ($p < 0.001$) conditions. Therefore, exercise was associated with a relatively short anorexia, which Bellisle (1999) identified as lasting on average 1 hour, and no immediate compensation in restrained eaters. Because the increase in hunger and energy intake was not sufficient to completely compensate for the expenditure, there was a net energy balance (high-fat meal) or loss (low-fat meal) following exercise.

As suggested the results of Thompson (1988) and Lluch et al (1997), duration, intensity and type of exercise likely affected the extent of post-workout anorexia. In a crossover design, Martins et al (2014) exercised 12 overweight but healthy males and females with cycling at either 70% or 85-90% HRmax, matched in duration to create an energy expenditure of 250 calories. While neither exercise condition elicited significant differences in subjective hunger on VAS or in energy intake at a subsequent meal, the authors also noted no significant difference in various hormones associated with appetite. Exercise may require a certain threshold of energy expenditure above 250 calories in order to provoke post-exercise anorexia.

Elder and Roberts (2007) further suggested that increases in post-exercise energy intake are associated with lower fatty acid oxidation during exercise and that, conversely, post-workout anorexia would be associated with higher fat oxidation. Long moderate-intensity exercise, as well as fasting, have been shown to cause greater fat oxidation, especially in trained subjects, while higher-intensity exercise conversely causes lower fat oxidation and higher carb oxidation (Horowitz and Klein 2000, Hopkins et al 2011). Therefore post-workout anorexia should be expected particularly after long, moderate-intensity and fasted workouts. However, it bears to mention that metabolically-inflexible individuals – in which the ability to switch between

carbohydrate and fat as an energy source is impaired, and carbohydrates are preferentially oxidized – exercise may not cause the fat oxidation required for post-workout anorexia. As will be further discussed below, long-term chronic exercise interventions have also been associated with lower self-reported energy intake. This finding suggests improved metabolic flexibility over time, leading to preferential fat oxidation during exercise, and regular post-workout anorexia.

Because exercise consists of physical movements which may become uncomfortable on a full stomach, it is within reason that exercise might decrease hunger due to gastro-intestinal discomfort. However, Havermans (2009) noticed no such discomfort in 58 healthy subjects following a 30-minute treadmill run at 80% HRmax. Whether subjects drank 300mL of a flavored beverage prior to the exercise or simply sipped and expectorated, subjective gastro-intestinal discomfort after exercise was not significantly different on a 100mm VAS. However, whether drinking or merely tasting, subjects rated liking of both odor and taste for this same beverage significantly lower ($p < 0.05$) on VAS 15 minutes after exercise. This second result suggested that exercise conditioned a flavor aversion not linked to gastro-intestinal discomfort. The authors then performed a backward regression analysis with all potential gastro-intestinal symptoms: nausea, belching, stomach ache, vomiting, side ache, gastro-intestinal cramps. Results of this analysis further confirmed that none of these potential gastro-intestinal symptoms significantly contributed to the observed negative hedonic shift of the beverage following exercise ($p > 0.21$). In other words, gastro-intestinal discomfort is unlikely to explain the immediate decrease in hunger or change in hedonics.

Rather, while Westerterp-Platenga et al (1997) noted higher thirst following both exercise and sauna, only after exercise did the authors note significantly lower hunger ($p < 0.01$),

significantly lower energy intake ($p < 0.01$) and directionally higher satiety ratings ($p > 0.01$) on 100mm VAS. Because the reduction in hunger and energy intake occurred only with exercise, and not with sauna, the authors suggest their cause to be increased sympathetic nervous system activity. The objective of such nervous system activity would be to overcome the temporary energy deficit caused during exercise, however may also reduce motility of the intestinal tract, leading to anorexia. McNeil et al (2015) also proposed that resistance exercise in particular favors a hormonal milieu which may lead to the immediate suppression of food reward, modulating neural pathways and neuropeptides to modify the liking for food.

In line with this hormone-based theory, various appetite-regulating peptides have been shown to vary with exercise. Though the majority of studies show no significant change in total ghrelin (TG) with exercise, the few studies which have measured the active component of the hormone acylated ghrelin (AG) have shown a significant effect: with 60 minutes of running at 75% VO_2 max for example, Broom et al (2007) noted a suppression of AG and a simultaneous suppression of appetite during and immediately following exercise, despite no change in TG (King et al 2011). Because ghrelin is a ‘hunger hormone’ released by the gastro-intestinal system and which stimulates appetite, it is logical that lower levels would be associated with decreased hunger. Conversely, anorexigenic gut peptides – notably cholecystokinin (CCK), polypeptide YY (PYY), and glucagon-like peptide 1 (GLP-1) – have also been shown to increase with exercise, which would be associated with decreased hunger (King et al 2011).

However, peptides released by the gut would need to travel via the blood and through the blood-brain barrier all the way to the hypothalamus in order to elicit a suppression of hunger; Hopkins et al (2011) therefore suggested that hormones tend to be more important in controlling satiety than affecting the initial consumption decision.

Instead, any decrease in hunger or increase in satiety sufficient to affect post-exercise eating behavior would require swift evaluation of the satiation effect of a particular food.

Bertenshaw et al (2013) observed the satiating effects on 26 participants of preload drinks varying in macronutrient content and textural properties:

- a low-energy drink (LE)
- a high-protein drink with relatively low thickness and creaminess (HP-)
- a thick and creamy high-protein drink (HP+)
- an equally thick and creamy high-carbohydrate drink (HC+)

The subjects evaluated the pre-loads via 100mm VAS confirming that HP+ and HC+ were not significantly different from each other, but both significantly thicker and creamier than HP-, as well as no significant difference in pleasantness across the three energy-containing drinks.

Subjects consumed a standardized breakfast prior to the preload and an ad libitum lunch 30 minutes after the preload, and rated their hunger on a 100mm VAS before and after each meal.

Though hunger decreased significantly after all preloads, this decrease was only sustained for HP+ and HC+, conditions under which subjects also reported the greatest increases in fullness after preload; subsequently, lunch intake was significantly lower for HP+ and HC+ compared to control, but not HP- compared to control. Because hunger was reduced by HP+ but not HP- despite similar macronutrient composition, post-ingestive effects must not be the root of short-term satiety. Rather, the similar effect of HC+ compared to HP+ suggested that the sensory characteristics – i.e. thickness and creaminess which were the only manipulated characteristics – allowed participants to quickly judge satiety. Similarly, Hogenkamp et al (2011) found that the expected satiation of semi-solid food products (yogurts and custards) was explained in majority by the thickness of the products as rated on a VAS ($p < 0.001$), but not by the flavor (lemon vs

meringue)($p = 0.98$) or by means of consumption (straw or spoon)($p = 0.63$). Therefore while gut peptides may play a role in the satiation of foods after exercise, the immediate evaluation of a foods satiation ability is likely mediated by orosensory cues during consumption, and not by macronutrient content during digestion.

Elder and Roberts (2007) noted a trend in the literature for increased food palatability following exercise, which is in line with the trend for increased beverage palatability but seems contradictory to the trend for decreased hunger immediately after exercise. An example of such an increase can be found in a more recent randomized crossover study by Cameron et al (2016). In this study, 10 men underwent a 25% energy deficit for 4 days by either diet alone or exercise alone – a treadmill walk at 50% VO_{2max} . Subjects rated their appetite and the palatability of their favorite food within a set on the first and last day, using VAS. Both mean ad libitum energy intake following the last day ($p = 0.001$) and AUC for palatability of favorite food ($p = 0.005$) significantly varied by condition. Palatability of the favorite food was significantly higher after exercise compared with control ($p = 0.009$), and the authors found a higher reinforcing value of food after exercise.

However, increased food palatability and decreased hunger are not as antithetical as they seem. Elder and Roberts suggested that on one hand, overall levels of hunger are suppressed due to overall more stable levels of circulating metabolic fuels (glucose and fatty acids), increased insulin sensitivity and greater lipolysis capacity in fatty tissues. On the other hand, exercise-induced depletion of carbohydrate stores in liver or muscle causes acute increases in hunger associated with greater enjoyment of food. In other words, exercise is able to simultaneously yield a lower perception of hunger and a greater overall liking of food.

This view is further supported by Hopkins et al (2011), who explained that appetite is regulated by both short-term ‘episodic’ signals and more stable long-term ‘tonic’ signals. In other words, acute exercise causes swift decreases in the relatively limited (400-800mg) liver and muscle stores of glycogen, which increases hunger; but chronic exercise also induces adaptations such as increased insulin sensitivity and increased lipolysis capacity, both of which decrease hunger. King et al (2011) noted another long-term adaptation to chronic exercise in the form of improved gut peptide release, despite no effect on fasting levels, e.g. subjects would be able to reach satiety more quickly after meal initiation following chronic exercise. So though hormones may not entirely explain post-workout anorexia and satiation, over time their potential to decrease time to satiation in post-workout meals and to decrease hunger even further post-workout can play an important role in sensory evaluation of exercise foods.

Chapter 2 - Salty Taste Perception & Preference

Due to the critical role of sodium in human fluid balance, nervous signaling and muscle function, the psychobiology of thirst and sodium appetite in humans is complex. In the case of fluid balance, water can be lost alone (expiration and transpiration) or in conjunction with sodium (salivation, emesis, lactation, sweating, blood loss, urine and defecation). These losses lead to anomalies at arterial and renal baroreceptors (blood pressure), cardiopulmonary receptors (blood volume), and visceral and plasma osmoreceptors (blood osmolarity). In turn, hormones renin and angiotensin increase, and higher integrative areas of the brain trigger changes in motor pattern generators to rectify the loss (Johnson 2007). Sodium also differs from other ingesta in that it is not stored, but takes up its life-sustaining roles unaltered; as such, any loss in bodily sodium can be easily and swiftly resolved by increased salt ingestion, which would be similar to the salt appetite already demonstrated in many animals (Leshem 2009). Is it possible that humans too develop a sodium appetite to counteract losses through sweat in exercise?

In order to determine whether salt perception is affected by exercise, Ali et al (2011) exercised 14 healthy and trained males with a 60-minute treadmill run at 70% HR_{max}. They measured perceived saltiness via 100mm VAS 30 minutes before exercise, at three points during exercise, 30 minutes after exercise, and 60 minutes after exercise. The stimuli presented were:

- a high carbohydrate high electrolyte beverage (HiC-HiE)
- a high carbohydrate low electrolyte beverage (HiC-LoE)
- a low carbohydrate high electrolyte beverage (LoC-HiE)
- and water as control

Carbohydrates in the test beverages consisted of sucrose and maltodextrin, while electrolytes consisted of sodium and potassium. The authors noted a main effect of activity type: ratings for

saltiness were significantly lower during exercise compared to before exercise for all electrolyte-containing beverages ($p = 0.003$), and did not significantly increase from intra-exercise levels following exercise, suggesting a reduced oral sensitivity to sodium during and immediately following exercise.

In contrast, Passe et al (2009) noted no such difference in salt perception following exercise. In this study, 55 trained male and female triathletes and runners completed a 2-hour aerobic circuit at 70-75% HRmax, i.e. similar intensity but longer duration than Ali et al (2011). Over the course of five different sessions, subjects evaluated five ad libitum test drinks varying only in sodium concentration (0 – 60mmol/l). The stimuli formulas were constant in potassium concentration (2.9mmol/l), carbohydrate concentration (6%) and in flavor (lemon-lime). Subjects evaluated perceived taste (sweet + salty + sour + bitter) and flavor intensity on a 100mm VAS. Then subjects rated overall liking and liking for each individual taste (sweet + salty + sour + bitter) on 9-point hedonic scales. This evaluation was performed immediately before, halfway through, and immediately after exercise. Though the authors noted a main effect of sodium level on saltiness ($p = 0.000$) indicating the experimental drinks were perceptibly different from one another, there was no significant effect of exercise status. While subjects in both studies were fasted for 3 hours, Passe et al (2009) presented their subjects with a standardized nutrition shake containing 300mg of sodium prior to exercise. Passe et al (2009) also allowed their subjects ad lib access to the test drinks during exercise. In contrast, Ali et al (2011) mentions no pre-exercise sodium supplementation or ad libitum beverage. It is possible that the increased salt intake in the experimental conditions of Passe et al (2009) confounded the perception of salt at various points. It is also possible that the length of exercise affected salt perception.

Despite no significant difference in salt perception, Passe et al (2009) did find an effect on salt liking. Across the multiple beverages of various salt concentrations, the main effect of exercise status approached statistical significance ($p = 0.065$), and overall liking was similarly subject to significant main effects of sodium level ($p = 0.000$) and exercise status ($p = 0.027$). Though there were no significant differences among pre-exercise, during exercise and immediately post-exercise, overall acceptance and liking of saltiness increased significantly for the highest sodium concentration (60 mmol/l) when consumed in an exercise context versus a sedentary control context. Multiple regression modeling confirmed the perception of saltiness as significantly more important than that of other tastes in predicting overall acceptance, indicating subjects became more accepting of the highest sodium concentration (60 mmol/l) while in an exercise context. But higher salt liking within the context of exercise – i.e. before exercise compared to sedentary control – suggested a role of expectation: subjects may perceive high-salt beverages as more pleasant pre-exercise because they expect from their past training that this type of solution will aid in their performance or recovery.

However, several studies indicated an increased liking for saltiness following exercise in untrained subjects as well. Horio and Kawamura (1998) exercised 58 healthy university students with a 30-minute session on a bicycle ergometer, with target heart rate of 130 (roughly 65% calculated maximal heart rate for undergraduate-aged adults). The authors tested taste perception thresholds via triangle testing with probit methodology, as well as taste liking using a 7-point hedonic scale. In contrast to the abovementioned studies, Horio and Kawamura used pure taste solutions with different levels of sucrose only (sweet), NaCl only (salty), citric acid only (sour), caffeine only (bitter) and MSG only (umami). This methodology allowed the authors to isolate the effect of exercise on the threshold for various tastes without the confounding effect of other

tastes in a complex formulation such as a carbohydrate-electrolyte beverage. The salt perception threshold and overall salty taste liking were not significantly different after versus before exercise ($p > 0.05$). However, salt liking for the lower concentrations (0.019mol/l and 0.038mol/l) were directionally lower following exercise, and salt liking for the higher concentrations (0.152mol/l and 0.304mol/l) were directionally higher. Potentially, the shorter exercise duration explains the lack of statistical significance; longer duration may be necessary to bring on the salt appetite in a statistically significant way (Passe et al 2009). The directional results of this study therefore suggest that untrained subjects may prefer saltier beverages following acute exercise, just as trained subjects did.

Similarly, Wilk and Bar-Or (1996), who exercised boys in warm conditions via consecutive cycling bouts, noted that adding carbohydrates (glucose + sucrose) and salt (NaCl) to flavored water – though eliciting no significant change in perceived saltiness or in flavor profile prior to exercise – increased drink intake compared to water ($p < 0.05$) and flavored water ($p < 0.05$) by the end of the exercise. Though no post-exercise sensory was performed, these results suggested that the beverage supplemented with carbohydrates and salt was significantly preferred over flavored water during and immediately following exercise. While the added flavor explained the increase in intake between plain water and flavored water, either sodium or sugar must explain increased intake between flavored water and carbohydrate-electrolyte flavored water. Based on earlier studies, Wilk and Bar-Or attributed the difference to salt, due to the importance of sodium concentration in extracellular fluid to the rate of rehydration.

So, for the most part, the literature indicated mild or non-significant effects on salt perception, but changes in palatability with exercise. However, studies with longer duration and higher intensity exercise (> 120 minutes) tended to record a greater or more significant effect on

both perception and preference (King et al 2011). And the availability of sodium before and during exercise in the form of regimented supplementation or ad lib electrolyte beverage intake appeared to affect the outcome of the study. Additionally, timing of evaluation may be critical. Takamata et al (1994) observed the sensory and hedonic response after exercise during but also in the hours following exercise: 7 healthy volunteers exercised for a total of 6 hours, consisting of 8 30-minute bouts of cycling at 35°C with rest and glucose solution for the first half of the exercise session, but no water for the remainder of the session. Subjects rested for an hour then rehydrated with ad lib deionized water for the following 23 hours. At regular intervals throughout the exercise session and the rehydration protocol, the authors measured subjective ratings of thirst and palatability to various NaCl solutions using 180mm VAS, perceived salt intensity to these solutions using 120mm VAS, fluid balance (intake of water versus water lost during urination and sweating) and blood plasma characteristics. Immediately after exercise, Takamata et al (1994) noted significantly higher plasma osmolarity and sodium concentration, increased thirst and increased palatability ratings for more hypotonic solutions ($< 0.03\text{mol/l}$ NaCl) for 1 hour. Meanwhile, palatability ratings of hypertonic solutions were increasingly negative with NaCl concentration. Due to the associated changes in plasma characteristics over the rehydration period, Takamata et al (1994) proposed that high plasma sodium initially stimulates osmoregulatory thirst, which increases deionized water intake and renal H₂O reabsorption to reduce elevated body fluid osmolarity.

In the same study, plasma characteristics returned to control levels fairly quickly – within 1 hour of access to ad lib water – then continued to decrease as subjects drank water without sodium. Notably, plasma sodium concentration dropped significantly lower than control after 6 hours of rehydration, and osmolarity dropped significantly lower than control after 23 hours of

rehydration. Over rehydration time, ratings for hypertonic solutions became less negative, reaching positive values after 3 hours of rehydration, and becoming indirectly preferred after 6 hours of rehydration. Takamata et al attribute a second period of thirst starting at 17 hours post-exercise, accompanied with increased sodium preference but not water preference, to regulation of extra-cellular fluids (ECF): decreased ECF and/or plasma volume, with low plasma osmolarity and sodium, may trigger increased salt palatability and renal sodium reabsorption in order to defend against additional salt losses from the body. This physiological and behavioral response is likely related to the increased plasma aldosterone noted by the end of rehydration with water only, a theory supported by Elder et al (2007).

Because the response observed by Takamata et al (1994) was greatly dependent on subjects' fluid balance and plasma osmolarity, sweat loss was expected to predict the change in preference from low-salt to high-salt drinks in the hours following exercise. Importantly though, bodily sodium must be depleted in order to trigger increased ECF thirst. Therefore, while Passe et al (2009) found through regression analysis that sweat loss was not a significant predictor of saltiness liking, their use of sodium-containing beverages ad libitum during the exercise would confound the amount of sodium lost through sweat with the amount consumed through drinking. In contrast, Wald and Leshem (2003), who examined the effect of untasted salt capsules, found significant interactions between salt dose and sweat loss. In their study, eighty student exercisers participated in 4 90-minute sessions of either aerobics or basketball (HR matched). The subjects then swallowed a capsule containing 0, 200, 400 or 600mg NaCl and evaluated an unfamiliar root beer drink for overall palatability, familiarity and flavor intensity on a 100mm VAS. While baseline preference was not significantly different across NaCl dose groups, preference change was greatest for subjects exhibiting high sweat loss, followed by medium and low sweat loss.

Preference with 400mg sodium supplementation was significantly increased for high sweat loss compared to lower sweat loss subjects, while preference with 600mg sodium significantly decreased for low sweat loss subjects. In other words, moderate amounts of salt (400mg) may trigger an increase in drink palatability following high sweat loss because subjects are conditioning to replace water sodium lost through exercise, while high amounts of salt (600mg) may trigger a decrease in drink palatability following low sweat loss because their plasma sodium is not being greatly reduced by exercise. Wald and Leshem (2003) concluded that the interaction of sodium and sweat loss in conditioning a flavor preference supports the theory that state-dependent post-ingestive nutrient intake affects hedonic response, whether associated with improved recovery, rehydration, hormonal levels, or homeostasis.

But does this hedonic conditioning in response to exercise represent a true sodium appetite? Leshem (2009) pointed out several critical differences in human sodium regulation:

- humans typically do not consume sodium in its pure state like certain animals do, but rather consume it within the context of food
- humans do not exhibit sodium selectivity over other salts, but rather respond to saltiness
- response is not necessarily immediate to sodium deficit.

That is not to say that salt palatability is not modulated by bodily sodium levels. To the contrary, Takamata et al (1994) clearly demonstrated a link between plasma sodium concentration and palatability of salt solutions. However this increase in salt palatability is likely to develop without assuming a regulatory role as with sodium appetite. In fact, the increase in salt palatability without increased intake in multiple studies suggested that the purpose of salt preference is not regulatory per se. Rather, it could be linked to sympathetic activation or, more likely, conditioning via post-ingestive restorative role of sodium on hydration and electrolyte

balance. In other words, humans learn to associate the restorative benefit of higher electrolyte beverages with the taste for salt, and so salt palatability is increased in the context of physical exercise.

Additionally, Havermans et al (2009) explored exercise-induced taste and odor aversion learning by subjecting 58 healthy college students to a 30-minute treadmill run at 80% of HRmax as mentioned above, and noted that flavor aversion readily occurred to a conditioning stimulus presented before a single bout of exercise, but that either preference or aversion for a conditioning stimulus presented after exercise would likely require multiple trials to induce backward conditioning. Moreover, the authors expanded that familiarity with the unconditioned stimulus (exercise) had previously been shown to promote flavor preference learning while attenuating flavor aversion learning. It follows that while the subjects unfamiliar with the exercise in this study developed a flavor aversion, athletes who performed the same physical exercise regularly are more likely to develop a backwardly paired preference, such as for salt in an electrolyte beverage that improves recovery.

In conclusion, the development of a salt preference depends on the intensity and length of the exercise, the amount of sweat loss, the availability of fluids with or without sodium during exercise and recovery, and the time at which the sample is evaluated, among other variables. As suggested by Passe et al (2009), a more conclusive understanding of the salt response to exercise could be achieved by combining within a single experiment the effects of: drink sodium level, exercise intensity, sweat loss, blood volume, blood osmolarity, circulating hormone status, voluntary fluid intake and rehydration. Though certainly a complex undertaking, such comprehensive research would greatly benefit the current understanding in sensory science.

Chapter 3 - Sweet Taste Perception & Preference

While sodium can be utilized unaltered shortly after consumption, sweet taste more often signals for carbohydrates, which the body needs to break down, store under a different form (glycogen) and mobilize for energy during physical exercise. However carbohydrate stores in the liver and muscle are limited, so it is foreseeable that depletion through exercise may trigger behavior that favors compensatory ingestion.

In their examination of normal-weight and obese men undergoing multiple 2-hour sessions of seated reading, sauna or cycling at 60% maximal workload, Westerterp-Plantinga et al (1997) noted that perceived sweetness intensity as measured on a 100mm VAS increased significantly after exercise for both a pure 50g/l sucrose solution ($p < 0.01$) as well as for a more complex carbohydrate-electrolyte solution ($p = 0.0001$). Appleton (2008) as well noted a significant increase in perceived sweetness as measured on a 100mm VAS following a 1-hour exercise session of moderate-to-high intensity in 81 regular exercisers ($p < 0.01$). Similarly, Narukawa et al (2009) evaluated the taste threshold of 35 male and female runners before and after completion of a half marathon – likely about 2 to 2.5h of running – via a triangle test followed up with probit analysis. The authors found the sucrose detection threshold to be significantly lower after exercise, along with an increase in the degree of physical fatigue. They suggested this behavior to be consistent with seeking carbohydrates to replenish liver and muscle stores. Ali et al (2011) found no significant difference in sweetness intensity 30 minutes before and 30 minutes after a 60-minute treadmill run at 70% HRmax. However sweetness intensity was significantly higher during and presumably right after exercise across all beverages ($p < 0.001$ compared to before exercise). This increase was particularly marked for the low-carbohydrate high-electrolyte drink, where post-exercise sweetness remained higher than the pre-

exercise sweetness ($p = 0.003$). In contrast, perceived sweetness for the high-carbohydrate high-electrolyte beverage decreased post-exercise, perhaps due to a predominance of saltiness, while the high-carbohydrate low-electrolyte beverage simply returned to baseline. Together, these findings suggest an increased perception of sweetness with exercise, particularly at lower concentrations.

Conversely, Nakagawa et al (1995) contrasted the effects of a mental task (40-minute letter search) and a physical exercise (10-minute bicycle ergometer) on bitter, sour and sweet taste intensity perception in 55 men and women. Though the mental task resulted in lower perception of the three test tastes, and physical exercise significantly increased perceived fatigue and tension, the physical exercise did not elicit a significantly different perception of sweet taste. However, Hopkins et al (2011) suggested that the carbohydrate storage of the human body is limited to 400 – 800g, corresponding to the expenditure of 90 minutes of high intensity exercise. Therefore, it is unlikely that 10 minutes of exercise in this study would be sufficient to elicit any changes in sweet perception, though the implication of lower taste perception with mental stress, presumably through central inhibition, is noteworthy for sports that include both a physical component and a mental one.

But though Narukawa et al (2009) noted a significant increase in sweet perception with a half marathon, Narukawa et al (2010) recorded no significant difference in taste intensity via 100mm VAS following a 12-hour 36km mountain hike. In this case, the 13 subjects would surely have reached the level of carbohydrate expenditure suggested by Hopkins et al (2011), however it is possible that they replenished these stores sufficiently through the unrestricted energy intake allowed during the hike. It is also very likely that the participants were able to distinguish between the low-sucrose (100mmol/l) and the high-sucrose sample (300mmol/l) and that the

VAS methodology with these obviously-different samples allowed them to give constant answers even if their perception had change. In contrast, the triangle method previously employed with multiple concentrations of sucrose would be more sensitive to changes in sweet perception.

So sweetness perception is likely improved following exercise, provided it is long and intense enough. But does this change have any impact on hedonic responses to sweet solutions? In Narukawa et al (2010), though again no significant change in sweetness detection threshold was recorded following the 12-hour 36km mountain hike, the pattern of change in palatability differed between the 100mM and 300mM sucrose solutions. While palatability of the 100mM solution increased steadily until the 25km point, the palatability by 36km decreased back to baseline levels; in contrast, palatability of the 300mM solution increased through the final 36km evaluation. Narukawa et al (2010) suggested that, though the lower sucrose concentration may have been increasingly satisfying initially, it may have become insufficient for the subjects by the time they reached the 36km point, by which point subjective physical fatigue was rated as significantly greater than fatigue at 0km, 16km and 25km. Subjects may preferentially choose higher sweetness foods following extreme physical exertion, in order to more quickly and completely replenish severely diminished glycogen stores.

Horio and Kawamura (1998) also did not note a significant change in sweetness detection threshold after 30 minutes of bicycle ergometer at a target heart rate of 130 (roughly 65% HRmax as mentioned previously), however overall liking as measured on a 7-point hedonic scale increased as well significantly following exercise for both the lowest-concentration (0.029mol/l) and the highest-concentration (0.232mol/l and 0.464mol/l) test solutions ($p < 0.01$). It is possible that the exercise duration was insufficient to trigger a lower sweetness threshold consistent with

an urgent search for carbohydrates, however the deficiency of calories may have been able to stimulate preference and consumption to discourage complete glycogen depletion.

Horio (2004) further examined the effect of a similar exercise session on the sweetness liking of various sweet tastants – sucrose, glucose, stevioside, sorbitol, erythritol and saccharin – again measured on a 7-point hedonic scale, by 44 healthy university students. Although previous studies have linked the increased liking of sweetness from sucrose or glucose to the need to replenish glycogen stores, Horio noted a significant main effect of exercise on liking across solution concentrations for sucrose ($p < 0.01$), glucose ($p < 0.05$), stevioside ($p < 0.01$), sorbitol ($p < 0.01$) and erythritol ($p < 0.05$) but not for saccharin. These results indicated that sweetness liking increased after exercise for a variety of sweet chemicals: saccharides which are expected to replenish glycogen stores, but also glycosides and sugar alcohols which provide little to no metabolic energy. The implication of this finding is that though the increased liking for sweetness may be predicated by the recovery of depleted glycogen, it is entirely mediated by the perception of sweetness on the tongue rather than post-ingestive effects. The finding that saccharin sweetness is not perceived as more pleasant with exercise can be explained by either the initial lower quality (off-notes or a different sweetness onset) compared to the other sweeteners. The synthetic manufacture of saccharin may also have played a role in its lower hedonic acceptance, as all other sweet stimuli presented were naturally occurring. It is possible that the increase in sweetness liking only applies to sweet tastants that humans might have been exposed to during their evolution, or that resembles them enough in structure to trigger the same exact receptors on the tongue.

In free-living conditions however, humans are more likely to select from a variety of complex foods following exercise, rather than sugar solutions. Given that liking for saltiness may

increase with exercise, and the more immediate requirement for sodium for fluid regulation, it is possible that need for sodium would obscure the preference for sweetness in such conditions.

McNeil et al (2015) subjected 16 fit men and women to calorie-matched aerobic (treadmill at 70% VO₂max) and resistance (weight circuit) exercise. The subjects then made hypothetical food choices via the Leeds Food Preference Questionnaire. This methodology consists of both a forced choice exercise during which subjects must select a preferred food within a pair (implicit wanting) as well as a set of 100mm VAS for liking or wanting of each of the foods individually (explicit liking). The stimuli in this study were divided into:

- high fat sweet foods – blueberry muffin, milk chocolate, shortbread, jam doughnut
- low fat sweet foods – jelly candies, candied popcorn, marshmallows, fruit salad
- high fat savory foods – salted peanuts, French fries, salted chips, Swiss cheese
- low fat savory foods – bread roll, spaghetti, Pilau rice, boiled potatoes

Though both types of exercise were associated with a significant bias against high fat foods in relative preference ($p = 0.03$) and explicit liking ($p = 0.04$) as will be discussed later, there was no significant bias for sweet foods versus savory foods in either relative preference ($p = 0.62$), implicit wanting ($p = 0.90$), explicit wanting ($p = 0.20$) or explicit liking ($p = 0.69$). This finding suggested that though sweetness liking may increase with acute exercise, choice from available foods in more realistic situations complicates this relationship.

Finally, while the aforementioned studies examined the effect of an acute bout of exercise, it bears mentioning that chronic exercise may otherwise affect either the perception or the hedonic response to sweetness. Thus Crystal et al (1995) in their comparison of 16 female competitive swimmers (14-17 hours of exercise per week) to 28 female non-athletes (0 – 7 hours of exercise per week), noted that the competitive athletes perceived high-sucrose dairy beverages

as significantly sweeter on 160mm VAS than the non-exercising controls, particularly when fat content was 0% or 3.5% ($p < 0.05$). The competitive athletes, but not the non-exercising controls, also displayed an apparent aversion for higher sucrose beverages, which was particularly pronounced for the higher fat beverages ($p < 0.05$). Therefore chronic exercise may induce greater sensitivity to sweetness and lower liking of high sweetness. However, these results should be taken with a grain of salt considering the more monotonous low-fat low-sugar training diet of the athletes, as well as potential psychological effects related to the dietary restraint of competitive athletes (c.f. Chapter 8 – Compensatory Eating & Psychological Factors of Food Choice).

Chapter 4 - Sour Taste Perception & Preference

Nakagawa et al (1995) noted lower perception of sourness in the form of a citric acid solution, after a short physical task – 10 minutes on a bicycle ergometer set at 60 r.p.m., corresponding to the ascent of a gentle slope at considerable speed, and sufficient to cause light perspiration. Both the intensity ($p < 0.001$) and the total amount of sour taste ($p < 0.01$) decreased significantly on a time-intensity scale after exercise; the duration of the sour aftertaste tended to decrease as well albeit non-significantly. The authors followed up this experiment with an analysis of saliva buffering capacity: 12 males each provided a 1mL saliva sample under resting conditions, then exercised for 15 minutes in slightly more strenuous conditions than the first experiment and provided another saliva sample. Titration with HCl immediately after sample collection showed a significant enhancement of the buffering capacity of saliva following exercise ($p < 0.05$), and the authors attributed the lower sour perception to the higher pH citric acid solution now buffered by saliva.

Horio and Kawamura (1998) too noted a trend after 30 minutes exercise on a bicycle ergometer for higher perception threshold of citric acid through triangle testing and probit analysis, though this difference did not reach significance – the authors do not mention water intake during the exercise condition, however that use of distilled water during the triangle test cleared the mouth of saliva thus limiting its buffering capacity. In terms of palatability however, Horio and Kawamura noted significantly higher liking on a 7-point hedonic scale of 0.0024 mol/l and 0.0096 mol/l citric acid solutions ($p < 0.05$) following exercise. At other concentrations, liking tended to be higher following exercise, however the difference was non-significant; in the case of the highest concentrations, it is possible that the acidity exceeded the buffering capacity of the subjects' saliva. Though sourness has traditionally been viewed as an indicator of

unripeness for certain fruits or vitamin content in others (ascorbic acid in lemons for example), this increase in palatability in light of the work of Nakagawa et al (1995) suggested that because the subjects are not as sensitive to sourness, increased levels are required to obtain the same hedonic response.

This response however does not appear to be constant across all food, or organic acids. Hobo et al (2001) assessed the impact of 30 minutes of cycling (HR = 130bpm) on the hedonic response to citric, malic and tartaric acid solutions. The authors noted no significant difference on a 9-point hedonic scale for the various solutions of citric acid before and after exercise ($p > 0.05$). However, liking for tartaric acid at low concentrations increased significantly immediately after exercise ($p < 0.05$). Liking for malic acid at low concentrations likewise increased significantly immediately after exercise, and remained high after a period of rest ($p < 0.05$). It bears mentioning that hedonic ratings were negative for all pure-acid solutions and that liking for these solutions decreased as concentration increased; however addition of glucose was noted to entirely rectify this dislike in the case of the lower acid concentrations, and mitigate it in the case of the higher acid concentrations. This finding suggested that though exercised subjects may tolerate pure organic acids to various extents after exercise thanks to the improved buffering capacity of saliva, their liking for these acids only increases into the positive in the context of complex systems also contributing sweetness, and this liking is not necessarily uniform across all organic acids.

Chapter 5 - Bitter Taste Perception & Preference

Research in the realm of bitterness perception and hedonic response following exercise is more limited, and the findings more equivocal. Though Westerterp-Platenga et al (1997) found a significantly higher perception of bitterness following 2 hours of cycling at 60% maximal workload ($p < 0.001$), the finding was limited to a solution of 25mg/l quinine sulfate and all other bitter solutions – 0, 12.5, 50 and 75mg/l quinine sulfate – were not significantly different after cycling. Horio and Kawumara (1998) used caffeine instead of quinine, and found no significant difference in perception at any level – 0.0009M, 0.0018M, 0.0036M, 0.0072M and 0.0144M – following 30 minutes of cycling at 50% VO_{2max} . The longer exercise session in Westerterp-Platenga et al (1997) may have induced a greater bitter sensitivity for a specific concentration range, which Horio and Kawumara (1998) may not have been able to pick up with their shorter exercise session. The use of different bitter tastants in the two studies certainly complicates the comparison too. As with Hobo et al (2001) for sour taste, more research on different bitter tastants would need to be performed to conclusively declare an effect of exercise on bitter taste. Given the heterogeneous human response to bitter tastants, the inclusion of multiple bitter tastants at various concentrations would be beneficial as well.

Chapter 6 - Umami Taste Perception & Preference

As with bitterness, umami perception and hedonic response following exercise have not been extensively studied, perhaps owing to its relatively recent recognition as a distinct taste. Horio and Kawamura (1998) evaluated umami threshold using the triangle method with 0.0002M, 0.0004M, 0.0008M, 0.0016M, 0.0032M and 0.0064M solutions of MSG, and noted no significant difference before and after 30 minutes of cycling at 50% VO_2max . Nor was liking on a 7-point hedonic scale significantly affected for any of the MSG concentrations ($p > 0.05$).

However, umami tends to go untasted in pure solutions, so it is possible that its use in more complex systems may create a greater effect. Keast and Breslin (2002) for instance noted that MSG can enhance sweetness and saltiness, but suppress sourness and bitterness, at moderate concentrations; and that it can enhance saltiness but suppress sweetness and bitterness at higher concentrations. Given these interactions, it may be of interest to investigate the effect of exercise on umami perception in a more complex system – with a source of sweetness, with a source of saltiness, and with both.

Chapter 7 - Macronutrient Choice

As noted previously (c.f. Chapter 1 – Thirst, Hunger and Impact on Overall Liking), orosensory cues can solicit the release of hormones and cue satiety during consumption of liquid carbohydrate or protein meals, suggesting a minor effect at best of post-ingestive nutrient absorption on satiation (Bertenshaw et al 2013). However, as humans choose from a variety of complex foods rather than single-taste solutions, could the taste or texture of various macronutrients differentially affect the selection of and the hedonic response to foods after exercise, potentially to replace the type energy expended as suggested by the theory of physiological usefulness?

Westerterp-Platenga et al (1997) noted a shift in macronutrient selection after 2 hours of cycling compared to after rest: exercised subjects selectively chose more carbohydrate-rich foods at the expense of fats and proteins. However, upon closer inspection, the foods available in the ad libitum meal differed in moistness. Items higher in carbohydrates – jam, honey, juices, yoghurt, buttermilk – potentially appealed more to subjects dehydrated by exercise due to their higher water content and ease of ingestion on a dry mouth. Similarly, using the Leeds Food Preference Questionnaire, McNeil et al (2015) noted a post-exercise bias against high fat foods, both sweet and savory. However the explicit liking score was only significantly different in the case of resistance exercise, and hypothetical food choice was not mirrored by decreased energy intake during ad libitum meal as would be expected from preferential low-fat choice. Lluch et al (1998) again noted a significant increase in pleasantness on VAS of low-fat ($p < 0.05$) but not high-fat foods following 50 minutes of cycling at 70% VO_2max , however the sample consisted of dietary-restrained women whose hedonic responses may not be representative of the general population (c.f. Chapter 8 – Compensatory Eating & Psychological Factors of Food Choice) and

absolute scores for tastiness, pleasantness, and fillingness were all still higher for high-fat foods in both conditions. Crystal et al (1998) also observed that competitive swimmers perceived high fat foods as significantly more fatty and low fat foods as significantly less fatty, and rejected the higher fat foods. However the authors suggested that these athletes may have been sub-clinically disordered eaters based on their scores on the Disordered Eating Attitude Scale and that their normal low-fat training diet, rather than regular exercise, may have affected their perception. The authors further suggested that athletes with little bodyfat may have a particular physiological aversion to fat not mirrored by the general population.

In contrast, Elder et al (2007) noted no significant difference in long term macronutrient choice following adoption of chronic exercise. However the authors did caution of the limitations of the food log methodology utilized. Not only are food logs less controllable and verifiable, they also only capture what the subject consciously chose to consume – not the drive or implicit wanting for certain macronutrients. Actual consumption may be confounded by factors such as performance / athletic philosophy (for example consuming high levels of protein in order to build muscle mass) and restraint (for example avoiding fatty foods considered ‘bad’).

Overall, the literature suggested a potential for preferential choice of low-fat foods following exercise in only certain populations (such as dietary-restrained subjects) and, while there are evident differences in the food choices of athletes versus sedentary individuals, there is:

- no consistent evidence of a drive to consume a specific macronutrient
- no evidence of causation - low-fat choice could be a correlation to athletic lifestyle
- no evidence that the macronutrient oxidized is matched by proportion of macronutrient consumed (Bellisle 2009)

Factors other than a physiological preference for one macronutrient may affect food choice.

Chapter 8 - Psychological Factors of Food Choice: Compensatory Eating and Disordered Eating

Aside from physiological differences in taste perception and acceptance, a major factor in the human response to complex food (rather than to pure taste solutions) after exercise is compensatory eating behavior. In Finlayson et al (2009), 24 healthy women – of normal BMI and with no history of eating disorders – cycled for 50 minutes at 50% HRmax, then consumed an ad libitum meal. The authors compared pre- and post-exercise hunger, thirst, fullness, and desire to eat, as well as hedonic responses to the ad libitum meal using VAS. Though the women exhibited no significant difference in energy expenditure:

- some maintained their energy intake at the ad libitum meal constant, whether they had exercised or rested, and were termed non-compensators
- others increased their energy intake at the ad libitum meal significantly after exercise compared to after rest, and were termed compensators

While compensators and non-compensators were not significantly different in terms of BMI, body fat percentage or stated exercise frequency, compensators rated the post-exercise meal as significantly more pleasant. This finding was consistent with Martins et al (2014), in which healthy overweight subjects did not consume significantly more at lunch following exercise, in line with findings in normal-weight subjects: compensatory behavior was no more prevalent in subjects with higher BMI.

In other words, exercise may affect hedonic ratings and compensatory eating for only a subset of the population, which might explain some of the discrepancies in past studies performed without segmentation: researchers may not find a significant effect of exercise on the

hedonic response to food if all subjects are non-compensators for example, and, given the resources required for studies involving close physiological monitoring during exercise and the subsequent smaller sample sizes in some of the aforementioned studies, it is likely that only one group or the other was adequately represented.

Employing the Leeds Food Preference Questionnaire, Finlayson et al (2009) further noted no significant difference in the explicit liking for specific foods between compensators and non-compensators. But, in the implicit wanting task, which is less likely to be affected by cognitive interpretation of subjective feeling, the reaction time of compensators decreased after exercise while that of non-compensators remained the same; in particular, compensators responded slower for low-fat stimuli and faster for high-fat stimuli. Mean frequency of choice per food category further suggested a preference for high-fat sweet foods in compensators, regardless of exercise condition. Acute exercise may therefore selectively modulate neural pathways associated with wanting for food in susceptible individuals. Because selective preference for high-fat sweet foods has also been demonstrated in subjects with artificially-induced hypoglycemia, the authors also posited that compensation may be driven by differences in glucostatic metabolism or status following the lowering of blood glucose via exercise.

More importantly than glucostatic metabolism however, compensatory eating behavior is associated with particular psychological patterns, in particular within traits measured in the Three Factor Eating Questionnaire – a 51-item questionnaire developed by Stunkard and Messick in 1985, evaluating cognitive Restraint of eating, Disinhibition, and Hunger. Hopkins et al (2011) explained that subjects who responded positively to an exercise regimen (i.e. lost weight) exhibited constant Hunger levels before and during the intervention. Consequently, these subjects did not compensate for the energy expenditure with higher energy intake. In contrast,

compensators, whose energy intake increased after exercise, were deemed non-responders to the treatment due to their failure to lose weight as expected. Their higher energy intake was explained by increased Hunger levels during the intervention. King et al (2011) further noted that overeating in compensation for exercise was characterized by higher Hunger and Disinhibition scores on the Three Factor Eating Questionnaire, while undereaters decreased their Disinhibition and Hunger over time, and increase their Restraint.

Finally, other psychological factors come into play with competitive athletic performance, particularly in young women. As mentioned above (c.f. Chapter 7 – Macronutrient Choice), young female athletes in Crystal et al (1995) answered the Disordered Eating Attitude Scale (DEAS). Through 25 questions, this scale measures of relationship with food, concerns about food and weight gain, restrictive and compensatory practices, feelings towards eating, and idea of normal eating. Based on this scale, Crystal et al (1995) categorized the subjects as sub-clinically restrained in their eating behavior. Consequently, their response to a high-fat high-sugar dairy beverage was significantly more negative than that of their non-competitive peers. Similarly, Bellisle (1999) noted that dancers gave low palatability ratings to high-fat high-sugar foods, and that this was more likely indicative of social or psychological factors. Strict dietary discipline that these individuals observe so as to optimize performance may underlie these lowered ratings, rather than in the physiological effects of exercise per se. These low palatability ratings for food stimuli signaling high food energy content (high sweetness and high fattiness) are also comparable to the hedonic responses from women with anorexia nervosa or bulimia. In contrast, women who simply participated in various types of exercise more than 3 hours per

week, without the concern for athletic performance, found these types of foods significantly more palatable than less active peers.

Privitera and Dickinson (2015) too categorized their 102 male and female athletes using the DEAS, in combination with a delay-discounting task for desserts (high fat high sugar), fried food (high fat), fruit (high sugar) and vegetable (control): participants were presented with a photograph of each of the 4 foods individually, and indicated whether they would prefer to consume a specific amount of the food immediately or wait 4 hours and receive the full portion. The authors calculated the “indifference point” as the average of the points at which a participant switched from choosing a larger portion of food later to a smaller portion of that food immediately, with lower values indicating greater self-controlled food choice. Though high-DEAS male athletes displayed significantly more self-controlled behavior than their low-DEAS male counterparts, there was no significant difference between in self-controlled behavior of low-DEAS female athletes and high-DEAS female athletes, not between female athletes and high-DEAS male athletes. These findings suggested that female athletes overall are more susceptible than male athletes to controlled or restricted eating, even when their scores on the DEAS fall within a normal range. In other words, female athletes and disordered male athletes are susceptible to self-controlling behavior that affects their food choices away from fat and sugar. Privitera and Dickinson further posit that athletes in lean sports such as cross-country may be more susceptible than athletes in non-lean sports such as baseball, and similarly athletes in aesthetic sports such as gymnastics may be more susceptible than athletes in non-aesthetic sports such as basketball.

Chapter 9 - Implications for Product Development & Sensory

Testing

At the concept development and formulation stages, developers of sports nutrition products would greatly benefit from understanding the specific taste sensitivities and preferences of exercised subjects, compared to rested subjects. Increased thirst in the preliminary stages of exercise recovery suggested that fluids may be the most appropriate vehicle for immediate post-workout supplementation. For example creatine, which is often taken after resistance exercise to increase lean muscle mass and muscle strength, may be more positively received in a ready-to-mix beverage powder than in a protein crisp bar. Semi-solid foods – such as jams, puddings, purees and gels – also represent an area of opportunity, as they would be easier to consume than solid foods when the mouth is dried by exercise.

Given the immediate anorexia common in exercised subjects, products perceived as lighter and less satiating may be preferred as well. Orosensory cues of thickness and creaminess are critical to the immediate sensation of satiation: thicker, creamier foods may be perceived as too filling, and either rejected after initial taste, or consumed in smaller quantities. Lower viscosity liquids, such as water-based protein isolate drinks, may conversely be perceived as more thirst-quenching and less filling. Ready-to-mix protein powders would also benefit from lower thickness, which could easily be achieved by adjusting the on-label directions to mix with water or juice rather than milk, and by increasing the amount of fluid to be added per serving of powder. And, as sports nutrition bars remain a growing category in the marketplace, development of softer and moister bars that nevertheless deliver the required supplementation may increase immediate post-workout palatability.

In terms of basic tastes in pure solutions, exercised subjects tended to prefer higher sweetness and higher sourness (especially malic and tartaric), as well as higher saltiness depending on recovery stage (after osmoregulatory thirst) and availability of fluids during exercise (ad lib per good practice). For example, grape (with characteristic tartaric acid) may be an appropriate flavor right after a workout. Apple (with characteristic malic acid) may be an appropriate flavor throughout recovery. Lemon (with characteristic citric acid) may only receive a modest increase in palatability after exercise. Per Wald et al (2003), even untasted sodium can increase overall liking of beverages. So a predominantly sweet and sour beverage with relatively high sodium is expected to perform better in exercised subjects than the same beverage with relatively low sodium levels. Wald et al (2003) recommend 200mg to 400mg, which is in line with the amounts per 500mL of commercial electrolyte beverages in the market.

Most importantly, product developers should understand the target demographics and psychographics clearly and in great detail: is it the college female athlete who will reject sweet and high-fat nutrition bars? Or is it the casual exerciser looking to rehydrate and craving some sweetness? Engagement in acute physical activity represents but one variable, along with these target characteristics, that inform the taste sensitivities and preferences of consumers.

Sensory professionals as well should seek to understand when a sports nutrition product to be tested should be consumed (during the workout, immediately after, or hours after?) as both perception and hedonic response seem to vary from the beginning of the workout to the following hours. Rested subjects for example, even if regular consumers of the product category or the specific brand, may not accurately represent the reception of a product intended for immediate post-workout consumption: a product rated just-about-right on sweetness and

sourness right after exercise would likely be perceived as both too sweet and too sour when evaluated in a rested state, and this feedback to the development team would be counter-productive.

Sensory professionals should also discuss the target consumer with the product development team, and aim to recruit from this population for hedonic testing: competitive female college athletes and dietary-restrained individuals may for example penalize a product for being too sweet even after exercise, while the general public may rate it just-about-right. Even difference testing, which tends to be more lenient in the use of non-consumers and internal panelists, should be approached with caution, as the heightened sensitivity to certain tastes (particularly sweet) in the immediate post-workout window could lead to perception of differences in the market that an un-exercised panel may not notice with any statistical significance.

Conclusions

Acute exercise of a certain threshold intensity appears to effect perceptual and hedonic changes across the population: immediate hunger suppression, osmoregulatory thirst (especially when beverage access during exercise is limited), increased palatability of salt, increased perception and palatability of sweetness, decreased perception and palatability of sourness, and limited effects on bitter and umami. The increased liking of beverages and of sweet and salty tastes is in accordance with the theory of physiological usefulness: replacing lost water, glycogen, and electrolytes respectively. However the increased liking of sour tastes seems more likely linked to its decreased perception, with the increased buffering capacity of saliva after exercise. The compensatory liking for high-fat sweet foods meanwhile depends heavily on the primarily psychological factor of compensatory eating. And while high or chronic physical activity itself does not imply anti-compensatory behavior, the high-performance frame of competitive athletes further complicates the equation with dietary restraint, especially in young women, and thereby reduces the hedonic response to otherwise ‘rewarding’ foods of high nutrient value.

Taken together, these findings lead to implications for post-workout food and beverage product development – higher sweetness, higher sodium, higher sourness, lower thickness and creaminess – as well as sensory practice – careful target consumer selection and testing under exercised conditions.

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Appendix A - Exercise Interventions Surveyed

Author(s)	Year	Subjects	Exercise			Key Sensory / Hedonic Measures
			Type	Intensity	Length	
Ali, Duizer, Foster, Grigor, Wei	2011	14 M, trained	treadmill run	70% HRmax	60 minutes	Visual Analog Scale: sweetness, saltiness, thirst-quenching ability, overall liking of 4 beverages varying in carbohydrate and electrolyte content
Appleton	2005	81 M / F, regular exercisers		moderate / high	60 minutes	Visual Analog Scale: sweetness, flavor strength, pleasantness, overall liking of 7 fluids varying in energy, electrolytes, and osmolarity
Cameron, Goldfield, Riou, Finlayson, Blundell, Doucet,	2016	10 M	treadmill walk	50% VO2max	sufficient to induce 25% energy deficit	Visual Analog Scale: appetite, palatability of food self-selected as favorite, nasal chemosensory performance Relative Reinforcing Value of Food
Finlayson, Bryant, Blundell, King	2009	24 F, healthy	cycling	70% HRmax	50 minutes	Visual Analog Scale: desire to eat, thirst, hunger, fullness, hedonics of ad lib meal Leeds Food Preference Questionnaire
Havermans, Salvy, Jansen	2009	58 M / F, healthy, college-age	treadmill run	80% HRmax	30 minutes	Visual Analog Scale: liking of odor and taste of 3 differently-flavored drinks, subjective gastro-intestinal discomfort during exercise
Hobo, Moritaka, Naito, Okonogi, Kimura, Madenokoji, Watanabe, Nagata, Fukuba,	2001	45	cycling	HR = 130	30 minutes	9-point Hedonic Scale: overall liking of citric, tartaric, and malic acid solutions at 3 different levels
Horio	2004	44, healthy college-age	bicycle ergometer	HR = 130	30 minutes	7-point Hedonic Scale: pleasantness of sucrose, glucose, stevioside, sorbitol, erythritol, saccharin solutions at different sweetness-matched levels

Author(s)	Year	Subjects	Exercise			Key Sensory / Hedonic Measures
			Type	Intensity	Length	
Horio, Kawamura	1998	58 M / F	bicycle ergometer	HR = 130	30 minutes	9-point Hedonic Scale: overall liking of pure taste solutions Triangle Test: detection threshold of 5 basic tastes
Lluch, King, Blundell	1998	12 F, dietary-restrained	cycling	70% VO ₂ max	50 minutes	Visual Analog Scale: perceived hunger, desire to eat, fullness, thirst, tastiness and pleasantness of high fat or low fat lunch consumed 20 minutes post-exercise
Martins, Stensvold, Finlayson, Holst, Wisloff, Kulseng, Morgan, King	2014	12 M / F, healthy overweight	cycling	70% HRmax or 85-90% HRmax	sufficient to match energy expenditure	Visual Analog Scale: subjective hunger, fullness, desire to eat Leeds Food Preference Questionnaire
McNeil, Cadieux, Finlayson, Blundell, Doucet	2015	16 M / F, fit	aerobic (treadmill run) or resistance (weight circuit)	70% VO ₂ max	sufficient to match energy expenditure	Visual Analog Scale: appetite Leeds Food Preference Questionnaire
Nakagawa, Mizuma, Inui	1995	55 M / F	bicycle ergometer	to light sweat	10 minutes	Time Intensity: perception of bitter, sour and sweet taste solutions Profile of Mood State
Narukawa, Ue, Morita, Kuga, Isaka, Hayashi	2008	35 M / F, runners	half-marathon			Triangle Test: detection and difference thresholds of sucrose in solution at 6 different concentrations
Narukawa, Ue, Uemura, Morita, Kuga, Isaka, Hayashi	2010	13 M / F	mountain hike		12 hours	Visual Analog Scale: sweetness of sucrose solutions at 2 different concentrations 5-point Hedonic Scale: palatability of sucrose solutions at 2 different concentrations

Author(s)	Year	Subjects	Exercise			Key Sensory / Hedonic Measures
			Type	Intensity	Length	
Passe, Horn, Stofan, Murray	2004	50 M / F, triathletes or runners	aerobic circuit	80-85% HRmax	75 minutes	9-point Hedonic Scale: overall liking, flavor liking of 4 beverages (commercial carbohydrate-electrolyte drink, homemade carbohydrate-electrolyte drink, diluted orange juice and water) 9-point Intensity Scale: sweetness, saltiness, flavor strength Visual Analog Scale: perceived exercise intensity 5-point JAR Scale: sweetness, saltiness, tartness, flavor strength
Passe, Stofan, Rowe, Horswill, Murray	2009	55 M / F, triathletes or runners	aerobic circuit	70-75% HRmax	120 minutes	Visual Analog Scale: sweetness, saltiness, bitterness, sourness, and flavor strength of 5 lemon-lime carbohydrate drinks varying in sodium concentration 9-point Hedonic Scale: sweetness liking, saltiness liking, bitterness liking, sourness liking, overall liking
Takamata, Mack, Gillen, Nadel	1994	7 M / F, healthy	cycling in 35°C		8x30 minutes	Visual Analog Scale: thirst, salt intensity, palatability through rehydration time of
Thompson, Wolfe, Eikelboom	1988	15 M, college-age	fasted cycling	35% VO ₂ max or 68% VO ₂ max	sufficient to match energy expenditure	9-point Hedonic Scale: palatability of sucrose solutions of increasing intensity 9-point Intensity Scale: hunger energy intake 1-hour post-exercise
Wald, Leshem	2003	80 M / F, student exercisers	aerobics or basketball	HR-matched		Visual Analog Scale: tastiness, familiarity, flavor intensity of unfamiliar root beer with untasted salt at varying levels

Author(s)	Year	Subjects	Exercise			Key Sensory / Hedonic Measures
			Type	Intensity	Length	
Westerterp-Plantenga, Verwegen, Ijedema, Wijckmans, Saris	1997	30 M, obese and non-obese	cycling	60% Wmax	120 minutes	Visual Analog Scale: taste intensity at 4 levels of 4 pure taste solutions, hunger, thirst, satiety
Wilk, Bar-Or	1996	12 M, prepubertal exercisers	cycling in 35°C	50% VO2max	4x20 minutes	Visual Analog Scale: sweetness, saltiness, sourness of unflavored water, grape-flavored water, and grape-flavored carbohydrate water prior to exercise Visual Analog Scale: thirst before, during and after exercise 5-point Intensity Scale: stomach fullness before, during and after exercise Voluntary fluid intake during exercise
Wong, Sun	2014	14 M / F, prepubertal	walk in 30°C	50% VO2max	4x20 minutes w/ 25-minute rest	Visual Analog Scale: sweetness, saltiness, sourness of 4 beverages (plain water, grape-flavored water, orange-flavored water, and lemon-flavored water) prior to exercise 5-point Hedonic Scale: overall liking of 4 beverages prior to exercise Voluntary fluid intake during exercise

Appendix B - Observational Studies Surveyed

Author(s)	Year	Subjects	Key Sensory / Hedonic Measures
Crystal, Frye, Kanarek	1995	16 F swimmers, 28 F non-athletes	Visual Analog Scale: fattiness, sweetness, overall liking of 16 dairy stimuli varying in fat and sugar content
Privitera, Dickinson	2015	102 M / F college athletes across 8 different sports	Disordered Eating Attitude Scale Delay-Discounting: forced-choice for delay- discounted foods varying in fat and sugar content (dessert, fried food, fruit, vegetable)