For the month of May, we are highlighting Chapter 9 of Reilly and Schactman’s “Conditioned Taste Aversion: Behavioral and Neural Processes.” This chapter, by Boakes and Nakajima, is entitled “Conditioned Taste Aversions Based on Running and Swimming.”

The authors begin the chapter with a brief description of the wide range of unconditioned stimuli that may produce conditioned taste aversions. One such stimulus is physical activity, e.g., wheel running or swimming. Through traditional Pavlovian conditioning, these behaviors can produce avoidance of novel flavors in ways similar to more traditional aversive stimuli such as lithium chloride or radiation.

Studies on activity-induced taste aversions have primarily utilized running in an activity wheel as the unconditioned stimulus. The authors describe a conditioning procedure in which animals are exposed to a novel taste and then introduced into an activity wheel. Following this procedure, the animal decreases intake of the activity-associated taste. This effect can be seen under a wide range of parametric conditions, including different rat strains, deprivation levels or states, taste substances, age, session durations, and assessment procedures. Although certain parameters may be varied, the studies all employ a Pavlovian conditioning procedure in which the novel taste serves as the conditioned stimulus (CS) and running in the wheel serves as the unconditioned stimulus (US).

After introducing the phenomenon of activity-induced taste aversions, the authors then go on to describe how the properties of running-induced aversions are similar to those of more conventional unconditioned stimuli in the taste aversion preparation. As with other stimuli, running-based conditioning produces aversions that are positively correlated with the duration of time spent in the wheel. Weak aversions can be formed with as little as 5 min, while 30 min sessions produce stronger aversions. Running-based taste aversions also parallel those produced by other traditional aversive stimuli in that altering the CS-US interval can produce graded aversions. Specifically, placing the animal in the wheel immediately following taste presentation produces the strongest subsequent aversion, while placing the animal in the wheel up to 60 min later produces a weaker, although still significant, one. In addition to being dependent on the CS-US interval, the strength of the aversion also depends on a positive contingency between the conditioned and unconditioned stimuli. If during conditioning an animal is exposed to the wheel on days where such exposure is not preceded by the novel taste, it will develop a weaker aversion than an animal who has only received contingent CS-US presentations. The authors describe how a host of other manipulations known to affect aversion conditioning with more traditional aversive stimuli similarly impact aversions induced by wheel running, e.g., CS preexposure, US preexposure and overshadowing.

One interesting phenomenon that the authors explore in this chapter is the potential relationship between running-based taste aversions and activity-induced self starvation. Paradoxically, animals that are given unrestricted access to an activity wheel and restricted (1-2 hours per day) access to food will decrease their food consumption to the point of starvation. This effect has been interpreted to be due to several factors. The first is that animals, even those not on restricted access to food, temporarily
decrease their food intake following a wheel-running session. The second is that, as the rat loses weight, it increases its activity level in the wheel. Therefore, as a rat loses weight, it increases its activity, leading to additional weight loss in a cycle that can lead to self-starvation. The authors pose a third possibility that is directly related to the issue of activity-induced aversions. That is, the running sessions cause an aversion to food which in turn reduces food intake and leads to higher levels of activity and further weight loss. Although a possible factor, the authors note that given that the food is generally familiar aversions would not likely be acquired (due to latent inhibition). As such, activity-induced self-starvation is likely mediated by different mechanisms than activity-induced taste aversions.

Although the focus in the chapter is on the ability of wheel running to induce aversions, the authors note another interesting feature of wheel-running, i.e., its concurrent rewarding properties. If an animal is introduced into a circular alley its activity levels will decrease. In contrast, when the animal is introduced into an activity wheel, it will begin to run more and more. Further, rats will perform an operant response to gain access to a running wheel. Thus, just like a number of drugs of abuse, wheel running appears to produce both aversive and rewarding effects. Interestingly, it appears that these effects are temporally constrained. For example, using the conditioned place preference design, if an animal is exposed to a novel chamber after running it will develop a preference for the chamber, but a place aversion will be produced if the animal is exposed to the chamber before the activity session. Similarly, in the taste aversion design, exposure to the taste before the running session produces an aversion while exposure after the activity session will produce a preference for the flavor. The bivalent (aversive/reward) nature of wheel running may be viewed in two ways: the rewarding and aversive effects may be related or independent. One potential explanation for the view that the factors are related is Solomon and Corbit’s opponent-process model. In this explanation, the aversive effects are primary (a-process) and may be weakened over time, while the appetitive effects are secondary (b-process) and are strengthened through repeated exposures. In contrast, it may be the case that the aversive and appetitive effects are independent. One bases for this position is the opiate hypothesis. This position proposes that endorphins released by running may be responsible for the appetitive effects, and that the aversions may be mediated by some other, unrelated mechanism. Although the nature of the rewarding and aversive effects of wheel running remains unknown, it is clear that activity can produce both.

When looking just at the aversive aspects of wheel running, the authors outline several different mechanisms that may be involved in it ability to induce taste aversions. One potential mechanism is activation of the mesolimbic dopamine system, which has been shown to play a role in both the rewarding and aversive effects of drugs like morphine and amphetamine. Physical factors such as gastrointestinal discomfort, motion sickness or general stress may also have a role in the development of aversions. In relation to general stress, the authors describe cross tolerance work in which preexposure to one aversive stimulus tends to reduce the aversive effects of a second stimulus. In this context, LiCl preexposure weakens aversions induced by wheel running, suggesting that some general effect, possibly stress may be mediating both effects. However, exposure to wheel running prior to aversion conditioning with LiCl is without effect.
One additional explanation for the basis of running-induced taste aversions is energy expenditure. Although the majority of studies examining activity-induced taste aversions have used an activity wheel preparation, the position that energy expenditure mediates such aversions has led to studies with other modalities. One such preparation is the use of forced swimming to condition taste aversions in which exposing an animal to a novel taste prior to 5-30 min of forced swimming will produce a decrease in taste consumption. Although less work has examined this specific unconditioned stimulus, several factors that affect swimming-based aversions parallel those that affect running based aversions, e.g., longer swimming sessions produce greater aversions and preexposure to swimming attenuates subsequent taste aversions. The mechanisms underlying swimming-based taste aversions also seem to be similar to those regulating running-based aversions, e.g., activation of the mesolimbic system or gastrointestinal distress, although the two strongest possibilities seem to be general stress and energy expenditure.

Under certain parameters, activity-based conditioning can produce aversions that are similar in strength to those produced by more traditional stimuli such as lithium chloride. However, there do appear to be differences between running and swimming in their sensitivity to the US-preexposure effect and also to their ability to attenuate aversions conditioned to other stimuli (i.e., cross-familiarization).

The authors conclude the chapter with a brief translational approach to the topic of activity-based taste aversions. Although taste aversions in humans are generally associated with nausea, the potential to develop an aversion to foods consumed prior to exercise may influence a person’s later food choices. With the current rates of obesity and a societal push to increase exercise levels, it is important to understand how these factors may impact food choice. Although little work has been done with humans, animal studies can continue to give us insights into this effect. One area that warrants additional research is the relationship between the rewarding and aversive aspects of activity. Overall, while the authors did an excellent job of summarizing the current work in the area of activity-based taste aversions, they also show us that this may be an under-studied phenomenon. Additional work utilizing animals other than rats and a greater focus on the physiological mechanisms will help to provide a greater understanding of how physical activity may produce taste aversions and the consequences of such conditioning.