

The highlight for February, 2008 is by Michael Domjan, from the University of Texas at Austin. In my Introduction to Jim Smith in January, I noted that there are few individuals in the field with as extensive and extended history in food aversion learning. Dr. Domjan is another of these few. His work in taste aversion learning dates back to the early 1970's when he and Nancy Wilson examined the role of ingestion in the acquisition of aversions and in the selective associations initially reported by Garcia and his colleagues. As Dr. Domjan describes in his highlight, his focus on aversion learning has been in examining its apparent adaptive nature and how it impacted general process learning theory. Such issues led him and his collaborators to study a host of phenomenon (e.g., CS and US preexposure effects, proximal and distal preexposure, learned safety, effects of lithium-conditioned stimuli, backward conditioning, aversions in preweanling rats, neophobia), many of which pointed to aversion learning as an adaptive specialization. His creative work with ingestion as a possible gating mechanism illustrated how ingestion itself imbued olfactory and tactile cues with the ability to suppress consumption after they had been paired with toxicosis. Dr. Domjan's strong empirical work has been matched by his comprehensive understanding of and his thought-provoking reviews on aversion learning. In 1977, he edited (along with Bud Barker and Mike Best) the first collection of papers from leading researchers in aversion learning (Learning Mechanisms in Food Selection) that not only brought the field together but also introduced it to a wide audience. As early as 1983, he (along with Jeff Galef) published an interesting and challenging review on the issue of biological constraints in operant and classical conditioning in which the question of taste aversion conditioning and its implications for general process learning theory was broached. His insights into aversion learning have been broad and important. As he notes in his highlight, his interest in the implications of adaptive behavior for general process learning theory has not abated as he has two new reviews on this topic. Over the past 20 years, Dr. Domjan's research interests have focused on sexual conditioning in quail (as opposed to aversion learning), but as he points out his findings with sexual conditioning parallel those that he initially reported with taste aversion learning in rats. These parallels highlight the issue of adaptive specializations in learning and the necessity of understanding the ecology of the animal in discussing specific learning preparations as well as general models of learning.

From Taste Aversion Learning to Sexual Conditioning and Back:
Reflections on 40 Years in the Lab

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Conditioned taste aversion (CTA) has attracted the attention of scientists from many disciplines and perspectives, including animal behavior, psychopharmacology, neurobiology, behavioral neuroscience, and learning theory. My interest in CTA was motivated by my interest in learning.

The Pre-CTA Years

I was introduced to learning theory (or should I say “non-theory”?) in the mid 1960’s by Skinnerians at the Behavior Science Institute, directed by Neil D. Kent. I first attended the Behavioral Science Institute in 1963 at Grinnell College and then joined the staff when the Institute was moved to Western Michigan University. Summers at the Behavior Science Institute were marvelous for both the intellectual stimulation and the camaraderie. Visiting instructors included Nathan Azrin, Ogden Lindzey, Murray Sidman, Joe Brady, Fred Keller, Ron Hutchinson, Jack Michael, and Bill Hopkins. The science was exciting, and the enthusiasm of the faculty was infectious. But, they said nothing about conditioned taste aversions or much about Pavlovian conditioning.

For Skinnerians in the mid 1960’s, Pavlovian conditioning was “the other” type of learning that modified only reflexive and smooth muscle responses. Much of their excitement in those days stemmed from developing new applications of operant conditioning – applications that would significantly improve the lives of patients in psychiatric hospitals and mental retardation facilities, inmates in correctional facilities, and students at all levels from pre-school to college.

Skinnerians in the 1960’s were out to change the world. It was an exciting time and a lofty goal, and I was eager to sign on. I was particularly captivated by the emphasis on data collection and the insistence that even in complex applied settings, data has to drive decisions. Sidman’s *Tactics of Scientific Research* became my bible. I read the book several times and was glad to see a recent announcement that it is still in print. When I got the opportunity to design my first research project, I picked a topic that was central to the development of Skinnerian principles, namely his “superstition” experiment (Skinner, 1948). Skinner claimed that contiguity between a response and a reinforcer was all you needed to produce increases in the rate of that behavior. A causal relation between response and reinforcer was superfluous.

I read Herrnstein’s treatment of Skinnerian superstitious behavior in the seminal *Handbook of Operant Behavior*, edited by Honig (1966), and was struck by the fact that all of the relevant data were obtained in studies with positive (food) reinforcers. To

correct the imbalance, I used the Herrnstein approach to conduct a series of studies of superstitious behavior based on aversive stimulation – what I referred to as superstitious escape behavior (Domjan, 1969; Domjan & Rowell, 1969ab). The studies showed, among other things, that rats could discriminate procedures in which their responses turned off shock versus procedures in which shock was turned off independent of their behavior. This type of contingency detection was also demonstrated in the learned helplessness experiments that were being conducted at the University of Pennsylvania at the same time (e.g., Maier, Seligman & Solomon, 1969). I wish I had been aware of that line of work, but I missed it with my focus on the Skinnerian literature.

In addition to the laboratory work, I also got involved in applied projects, during what were the formative years for the now vibrant field of applied behavioral analysis. Under the supervision of Louise Kent, I worked for about 8 months as a Program Development officer at the Fort Custer State Home for the mentally retarded. Although I enjoyed my activities there, laboratory work was more compelling, and on the advice of Ron Hutchinson, I entered the Ph.D. program in Biopsychology at McMaster University in the fall of 1969. Hutchinson recommended that program because it did not involve many required courses and permitted students to concentrate on their research. I had great respect for Hutchinson as a scientist. If McMaster was good enough for Hutchinson, it was good enough for me.

McMaster and My First Encounter with CTA

McMaster had a distinguished faculty in learning. Leo Kamin did all of his seminal work on conditioned suppression and the blocking effect at McMaster (Kamin 1965, 1969) and moved to Princeton just before I arrived. Others on the faculty included Herb Jenkins and Abe Black. The vacancy left by Kamin's departure was filled by Shep Siegel, who got his Ph.D. at Yale with Allan Wagner a few years earlier. Another new faculty member was Jeff Galef, who just got his Ph.D. at the University of Pennsylvania with Paul Rozin. I have continued to cross paths with Siegel and Galef ever since, most recently in Austin, where each of them gave invited presentations at the 2007 meeting of the Pavlovian Society, during my term as President of that organization.

McMaster was an exciting place, at the cross-road of many of the key developments in learning theory in the 1970's. Herb Jenkins had just published his seminal paper on autoshaping, and the Rescorla-Wagner model was first presented there at a conference on Pavlovian conditioning (Black & Prokasy, 1969). Several years after that, Shep Siegel started work on what was to become his conditioning model of drug tolerance. My work in his lab included latent inhibition, backward and conditioned inhibition and rabbit jaw movement conditioning.

Shep was not working on problems in taste aversion learning when I joined the lab, but there was a lot of discussion of Garcia's CTA research in classes, seminars and hallways. The blocking and relative validity effects that inspired the Rescorla-Wagner model served as one line of attack on traditional contiguity theories of associative learning. Garcia's long-delay learning and cue-consequence specificity served as a major second

line of attack. However, those pursuing the Rescorla-Wagner reformulation of learning theory never joined forces with investigators interested in CTA. They were just as skeptical of CTA as was everyone else in those days.

Jeff Galef began his landmark studies on the social transmission of food preferences soon after his arrival at McMaster and had a major role in stimulating discussions of the Garcia effect. His dissertation advisor, Paul Rozin, completed a beautiful series of experiments at Harvard that led to a re-interpretation of the Curt Richter cafeteria studies, which showed that rats fed a nutritionally deficient diet tend to select foods that help alleviate their dietary deficiency. Rozin demonstrated that this medicinal food choice is not driven by a specific hunger for the missing nutrients but by an aversion acquired to the nutritionally deficient food. Rozin's data were clear, but the acquired aversion interpretation needed firmer legs in learning theory. After all, illness caused by nutritional deficiency is slow to develop, and if an aversion is learned to the deficient food, why are aversions not learned to other cues that may also be present as the deficiency develops? Garcia's long-delay learning and selective association effects provided the missing legs for Rozin's story.

Rozin needed the Garcia phenomena to complete his reinterpretation of the specific hunger results, and he subsequently used long-delay learning and selective associations to formulate a more comprehensive approach to adaptive specializations in learning (Rozin & Kalat, 1971). Garcia also greatly benefited from Rozin's attentions. By highlighting the Garcia phenomena at the University of Pennsylvania, Rozin brought the phenomena to the attention of not only future investigators like Jeff Galef, but also of colleagues like Marty Seligman, who quickly jumped on the "constraints on learning" bandwagon with his concept of preparedness (Seligman, 1970; Seligman & Hager, 1972). Seligman has been a masterful popularizer throughout his career and helped make Garcia a household name.

Galef carried Rozin's fascination with CTA to McMaster, where it faced close critical scrutiny by the learning faculty. Attention focused on two main issues. First, were long-delay learning and selective associations artifacts of poor experimental design? Second, if the effects were genuine, did they require abandonment of general process learning theory or just modifications of it? As I became steeped in these arguments, it became clear to me that what we needed were more data – not more argument.

The Role of Ingestion in CTA

The first question I tried to answer about CTA was what made it unique – what was different from CTA that made it different from other forms of Pavlovian conditioning? The most obvious difference to me was that in CTA the subject was in control of contact with the conditioned stimulus (CS). Rats had to drink a flavored solution to become exposed to it prior to receiving the illness-inducing agent (the source of the unconditioned stimulus or US). In all other Pavlovian paradigms, both the CS and the US are presented independently of the subject's behavior. In fact, this response-independence of the CS and US is often emphasized as a distinguishing, if not defining, feature that sets

Pavlovian conditioning apart from operant and instrumental conditioning. Perhaps violation of the response-independence rule produced some of the unique features of CTA.

If ingesting the CS was responsible for some of the unique features of CTA, then these features might be lost if the CS was presented without ingestion. But, how could we present taste without ingestion? I discussed these issues with another graduate student, Nancy Wilson, who had followed Jeff Galef to McMaster from the University of Pennsylvania, where she got her bachelor's degree. Nancy was in Ed Stricker's lab, and Abe Black's lab was down the hall – not that these distinctions made much difference. The animal laboratories at McMaster were housed in old Army barracks at the time. The place was crowded, and students from various laboratories invariably ran into each other during the course of their daily activities.

Among other things, Abe Black's lab was concerned with interactions between autonomic and instrumental behavior. To study this question, one of his students' techniques involved injecting rats with curare, which paralyzed the skeletal musculature without affecting sensory processing. The preparation was a bit tricky because curare also paralyzed the musculature required for breathing and the rats had to be maintained on a ventilator. The ventilator pump provided air through a nose cone that left the mouth of the rats unobstructed. Therefore, one could rinse the tongue with various taste solutions while the animal was prevented from licking and swallowing by the curare. Nancy and I adopted the curare procedure to study CTA in the absence of ingestion and found that rats conditioned while paralyzed with curare learned weaker aversions to saccharin than rats injected with lithium after ingesting saccharin in the normal fashion (Domjan & Wilson, 1972a, Experiment 1).

Our curare experiment was promising in isolating the role of ingestion in taste aversion learning, but one could argue that various unusual aspects of the curare preparation caused the reduced CTA. Therefore, we sought to develop a less invasive procedure for presenting taste without ingestion.

I was trying to condition jaw movement responses in rabbits in Shep Siegel's lab at the time. That line of work did not go very well, and Shep and I never published any jaw movement studies, but the procedures we used to elicit jaw movement in the rabbits suggested an alternative to curare for the taste aversion experiments. The rabbits were fitted with an oral cannula that allowed us to squirt a small amount of water into the mouth using an infusion pump. Nancy and I adopted the cannula preparation and tried infusing taste solutions into the oral cavity of rats. We discovered that if the fluid was infused into the oral cavity at a slow rate (3 ml/min) while the rats were thirsty, the infusion would elicit licking and swallowing responses. Less licking and swallowing occurred if the infusion rate was increased, and no licking and swallowing occurred if the rats were not water deprived while getting the oral infusion at a high rate (46 ml/min). Under those conditions, the rat would simply open its mouth and let the fluid rush over the tongue and out of the mouth.

We repeated the taste aversion experiment using the oral infusion technique and again found that in the absence of ingestion, CTA was significantly weaker than if the rats received the taste solution under conditions that permitted ingestion (Domjan & Wilson, 1972a, Experiment 2). This was an all-or-none effect. If any of the infused fluid was ingested, the attenuation of CTA did not occur. Furthermore, it was an effect related to long-delay learning, since the lithium injection was administered 25 min after the CS exposure.

Other Applications of the Oral Infusion Technique

Nancy Wilson and I subsequently used the oral infusion technique in a replication of the Garcia-Koelling (1966) cue consequence specificity experiment. Garcia and Koelling were also concerned with the fact that tastes are usually encountered contingent on licking whereas audiovisual cues in most laboratory studies are presented independently of behavior. Their solution to this contrast was what has come to be known as the “bright-noisy water” technique. To make the audiovisual presentations comparable to lick-contingent taste stimulation, they presented audiovisual cues contingent on rats licking a drinking tube containing water. Nancy and I repeated the Garcia-Koelling experiment with a saccharin solution and a buzzer as the conditioned stimuli, but this time both types of CSs were presented in a response independent fashion. To meet some of the criticisms that were leveled against the Garcia-Koelling study, we repeated the experiment twice, once with the taste and buzzer presented as a compound before lithium poisoning or shock and the second time with independent groups that received only one of the CSs (Domjan & Wilson, 1972b).

After these initial experiments, I used the oral infusion technique extensively in a wide range of CTA studies. The technique was especially useful, if not essential, in studying manipulations that ordinarily would have induced different levels of drinking during a conditioning trial. While still at McMaster, I used the technique to study water deprivation and stimulus exposure parameters in the CS preexposure or latent inhibition effect (Domjan, 1972). Subsequently, I used the technique in studies of the attenuation of flavor neophobia (Domjan, 1976), the blocking effect in CTA (Gillan & Domjan, 1977), the proximal preexposure effect (Domjan & Gemberling, 1980) and studies of CTA in pre-weanling rats (Gemberling & Domjan, 1982; Gemberling, Domjan & Amsel, 1980; Gregg, Kittrell, Domjan & Amsel, 1978).

Ingestion as a “Gating” Mechanism

I also continued to pursue my interest in the role of ingestion in CTA. After the initial taste-aversion experiments, I examined the role of ingestion in odor aversion learning. Odor aversion learning is interesting because odors can emanate from both food and nonfood sources. Garcia and his colleagues have argued that taste serves to “gate” odors into the ingestive system and makes possible illness-induced conditioning of odors (Rusiniak, Hankins, Garcia & Brett, 1979). I found that drinking water during an odor conditioning trial facilitates the expression of an odor aversion without a distinctive taste (Domjan, 1973). This effect did not reflect an acquired aversion to water but seemed to

reflect the conditioning of a configural cue that involved ingestion-related sensations. Thus, I have come to regard ingestion-related sensations as the “gating” mechanism that makes odors and other cues relevant to feeding.

Another category of stimuli that is “ambiguous” in the same sense as olfactory cues is tactile stimuli. Animals encounter tactile cues during the course of locomotor behavior. However, species that hold their food while ingesting it also encounter tactile cues related to ingestion. In a series of experiments with rats and monkeys, I demonstrated illness-induced aversions to tactile cues with delays as long as 30 min (Domjan & Hanlon, 1982; Domjan, Miller & Gemberling, 1982). The experiments involved a discrimination between two foods that were identical in taste but differed in tactile cues. The role of visual cues was eliminated by conducting the experiments in the dark.

Long-delay odor and tactile aversion learning is remarkable because subjects are likely to encounter other odors and tactile cues during the delay interval, and these intervening stimuli could present concurrent interference for the target aversion. I think ingestion related cues play a major role in limiting such interference. Since the odor and tactile cues encountered during the delay interval are not related to ingestion, they are not “gated” into the ingestive system and are not effective CSs for subsequent food-induced illness. As Domjan and Hanlon (1982) noted, “perhaps the ingestive context serves to direct tactile information to a special ingestion-related memory mechanism in which information is segregated from other tactile stimulation and stored long enough for association with delayed toxicosis (p. 300). A similar process may be involved in learning aversions to temperature cues (Nachman, 1970).

Sexual Conditioning and Adaptive Specializations in Learning

After spending about 15 years studying taste aversion conditioning (working on various problems that I will not mention here), I changed the focus of my research to how learning occurs in the sexual behavior system. Although this involved a different species (to the coturnix quail) and behavior systems, I remained very much interested in adaptive specializations in learning and the fundamental challenges that CTA presented to learning theory. Sexual conditioning was a fairly unexplored area at the time. My hope was that at the broad theoretical level my work in sexual conditioning would help us better understand specialized learning effects. However, when I started the work with quail I had no way to predict that any of the phenomena that I might encounter would hark back to some of my CTA experiences. As it has turned out, my research has come full circle. Some of the most interesting things that my collaborators and I have found in sexual conditioning have a striking resemblance to some of the special features of CTA.

My early studies of sexual conditioning followed the standard format of pairing an arbitrary cue with copulatory reinforcement that served as the US (Domjan et al., 1986). The work went well, and I had no trouble attracting students and grant funds. One of the people who was attracted to the work was Falih Köksal, who joined my lab in 1992, on sabbatical from a faculty position at Bogaziçi University in Istanbul, Turkey. We had been doing various experiments testing the responses of male quail to taxidermically

prepared females and taxidermic models of various female body parts. This line of work had identified the head and partial neck feathers of a female as “sign stimuli” for male social affiliative behavior (Domjan & Nash, 1988). However, these head and neck cues were not unconditioned stimuli. Rather, their effectiveness required prior sexual experience in which the female head+neck cues were paired with copulatory reinforcement. Copulation in quail begins with the male grabbing the back of the female’s head and then mounting on her back and making cloacal contact. Thus, the natural sequences of events that ensue during copulation can serve to pair head+neck cues with sexual reinforcement. One can also condition such cues by preparing a taxidermic model of a female’s head and neck and using this as a CS paired with copulation with a live female.

Even though the head+neck cues are not fully effective unconditioned stimuli, it seemed to Falih Köksal that they were highly relevant to the sexual behavior system since they were a part of what a male naturally encountered as it copulated with a female. He reasoned that if female head+neck cues were highly relevant to sex, then the conditioning of these cues should be very difficult to block using the Kamin blocking design. In contrast, an arbitrary cue should be readily susceptible to the Kamin blocking effect. This prediction reminded me of the early claim that CTA could not be disrupted by the Kamin blocking procedure, also because taste was highly relevant to the US employed (Kalat & Rozin, 1972). That claim has turned out to be incorrect (e.g., Gillan & Domjan, 1977). Nevertheless, I thought that Falih’s prediction was well worth testing. I am glad we went forward because the results turned out great and opened up an important new line of research for the lab. As Falih predicted, the conditioning of female head+neck cues could not be blocked by the presence of a previously-conditioned audiovisual cue. However, the conditioning of a comparable CS object that did not include naturalistic quail cues was readily blocked (Köksal, Domjan & Weisman, 1994).

Falih and I were pleased to find that conditioning of a sexually relevant CS was resistant to the blocking effect but I did not fully appreciate the significance of the results until we obtained a series of related findings. Brian Cusato and Mark Krause joined the lab and conducted a series of comparisons of sexual conditioning with a naturalistic CS (that included female head+neck cues) versus an arbitrary CS of similar size and shape without female cues. The results of these experiments showed that conditioning occurs much faster with a naturalistic CS (reminiscent of the emphasis on one trial learning in CTA). Furthermore, the conditioning is much more robust in a variety of respects. A broader range of conditioned responses (including consummatory sexual responses) develop as a result of conditioning with a naturalistic CS than with an arbitrary cue. A naturalistic CS is also resistant to habituation, supports better second-order conditioning and shows very little extinction (see Domjan, Cusato & Krause, 2004, for a review).

Perhaps the most striking finding was obtained by Chana Akins, a former student of mine who had taken a faculty position at the University of Kentucky. She found that as you increase the CS–US interval from 1 min to 20 min, conditioned responding drops out if the CS is an arbitrary cue. However, sexual conditioning (in relation to an unpaired control) remains robust with a CS–US interval if the CS is a naturalistic cue (Akins,

2000). This latter finding is reminiscent of long-delay food aversion learning and has encouraged me to develop a unified framework for thinking about CTA, sexual conditioning, and other examples of what might be called ecological learning (Domjan, 2006, 2008).

CTA and Sexual Conditioning as Ecological Learning Paradigms

My experiences with CTA and sexual conditioning have convinced me that to understand Pavlovian conditioning we have to consider how such learning occurs in nature. Textbooks describe Pavlovian conditioning as the pairing of an arbitrary or “neutral” stimulus (the CS) with an unconditioned or biologically powerful event (the US). However, if a stimulus is truly arbitrary or neutral, it will not happen often enough (if ever) in conjunction with a US to enable the development of association. For Pavlovian conditioning to occur in nature, the CS has to have an inherent or pre-existing relation to the US. For example, the CS might be some feature of the US that is evident at a distance or before the subject comes in intimate contact with the US. Such a pre-existing relation is necessary for the CS to be reliably paired with the US outside the laboratory and to produce the important anticipatory conditioned responses that make Pavlovian conditioning an adaptive process. (Domjan, 2006, 2008).

CTA was not an ecological learning phenomenon when it was first examined by John Garcia and Jim Smith. Their early experiments involved rats drinking saccharin before being exposed to ionizing radiation. Neither saccharin nor x-irradiation is a natural event that rats are likely to encounter outside the laboratory. However, Garcia moved to a more ecological interpretation of CTA as he learned more about it, and that approach was certainly central to how others, like Paul Rozin, thought about the phenomenon.

I think CTA is a beautiful example of ecological learning. CTA no doubt evolved as a process to reduce the ingestion of poisonous foods. A poisonous food is a multifaceted stimulus object. Some of its features (e.g., odor) are evident at a distance, whereas others (texture and taste) are encountered only with more intimate contact. The most intimate contact is to swallow something, which then activates the aversion-inducing features of the poisonous food. CTA outside the laboratory does not require the interventions of an experimenter because pairings of the CS and US are natural contingencies of the environment. The CS and US “belong” with each other, to use Thorndike’s term, or are “relevant” to each other, because they are features of the same object, and the CS–US interval is determined by how the subject interacts with the object.

Sexual behavior also involves interacting with a complex multifaceted object—in this case a potential sexual partner. Numerous features of the partner are evident at a distance, and each of these can become potential cues (CSs) for subsequent olfactory, tactile and other cues that serve more as unconditioned stimuli. Considering that sexual conditioning improves the efficiency and effectiveness of copulatory interactions (e.g., Mahometa & Domjan, 2005; Matthews, Domjan, Ramsey & Crews, 2007), it is not a stretch to suggest that sexual conditioning evolved to take advantage of naturalistic conditioned stimuli that

precede copulatory interaction and that is why learning involving such cues is more robust and occurs over longer delays.

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