

Symposium Paper

Appetite Festschrift

Proceedings of a *Fest* on 17 May 1999 at Columbia University, New York
honouring the scientific career of John D. Davis, PhD

Guest Editor: James Gibbs

The history of the “Davis Rig”

J. C. Smith

The Florida State University, Tallahassee, FL32306-1270, U.S.A.

(Published electronically 19 December 2000)

The “Davis Rig” (Fig. 1) was developed at The Florida State University in the early 1990s. It was designed by Ross Henderson for use in my laboratory. As can be seen in Fig. 1, it is an apparatus that allows for the micro-analysis of ingestive behavior of liquid substances in small rodents. It has been described in some detail elsewhere (Rhinehart-Doty *et al.*, 1994; Smith *et al.*, 1992).

Eight (or more) small bottles were fitted with 5/16” diameter stainless steel sipper tubes. These tubes were securely mounted in a row on a teflon bar so that any one of them could be positioned in front of a drinking slot. The positioning of the tubes was controlled by a reversible motor which was monitored by a helipot. In front of the drinking slot a motor driven shutter was positioned so that it could

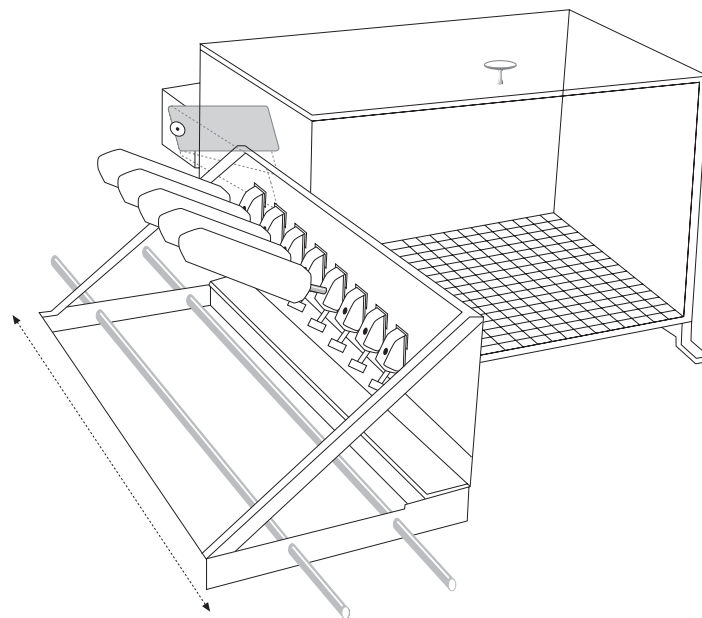


Figure 1. The “Davis Rig”. Any one of the eight drinking tubes can be positioned in front of the drinking port in the rat’s cage. The movement of the bottle rack is controlled by a reversible motor and monitored by a micro computer. The shutter moves from the “closed” position to the “open” position allowing the rat access to the particular drinking port. Licking on any tube is recorded by electronic lick circuits. Programming the access time and the inter-trial intervals is controlled by the micro computer.

either occlude the slot or leave it open so that the rodent could easily lick. The animal's cage was approximately 12 cm wide, 30 cm long and 26 cm tall. Each lick on the tube was recorded by a contact circuit. A micro-computer controlled the shutter and the positioning of the tubes. The experimenter could determine the variables for a testing session such as the number of times each tube was presented, the duration of each presentation, the inter-trial intervals, and the order of tube presentations. The time between each lick was measured to a resolution of 1 ms and these inter-lick intervals were saved in a variable array for later data processing. It has proved to be a valuable apparatus for the study of gustation and ingestive behaviors, especially when brief access to test solutions was desired.

How did the Davis Rig come about and why is it called the "Davis Rig"? That is the topic of this paper.

In 1973 John D. Davis (Jack) published a paper in *Physiology and Behavior* (Davis, 1973) entitled "*The effectiveness of some sugars in stimulating licking behavior in the rat*". This paper was most interesting to many scientists studying ingestive behavior for a variety of reasons. Several of the papers in this tribute to Jack refer to this paper, but my attention was focused on only one aspect of the first Figure in the paper. He had described an experiment where on a given day a rat was presented with a sucrose solution for five 30-sec periods. These presentations were each separated by a 30-sec period. On 6 consecutive days, the rats received water, 0.01, 0.032, 0.10, 0.316 or 1.0 M/l concentrations of sucrose in the on/off sequence described above. The rats were tested in this sequence after having been subjected to food deprivation periods of 0, 30, 45, 90, 240 or 480 min prior to testing. What interested me was the 0 food deprivation condition. I have taken the liberty to re-plot the data for this condition and they are illustrated in Fig. 2. These data were collected over a 6-day period (one concentration per day). As can be seen from the figure, the mean number of licks per 30-sec presentations is a direct function of the concentration of the sucrose. The function is quite similar to intake data from sham feeding rat (Gibbs, 1994, pers. comm.) and from electrophysiological recordings from the greater superficial petrosal nerve (the branch of the facial nerve that innervates the palate of the rat, see Nejad, 1986). I converted the y-axes of these three functions into relative responses using Beidler's taste equation (Smith, 1988) and plotted the functions in Fig. 3. Although the sham feeding data fit a little closer to the electrophysiological data, the function from Davis' curve shows the same increase in relative response to increases in sucrose concentration. I interpreted these data from Jack's paper as measures of gustation that were void of post-ingestional factors. The only disadvantage was that it took 8 days to collect the data.

Meanwhile in my laboratory, we were studying possible changes in gustation as a function of aging in Fischer-344 rats. We had placed special emphasis on "sweet" taste and had collected data on sucrose intake in longitudinal studies from weaning until death, a period of 24–34 months (Smith & Wilson, 1988).

During this time we worked out a method for measuring taste thresholds in rats with a conditioned suppression

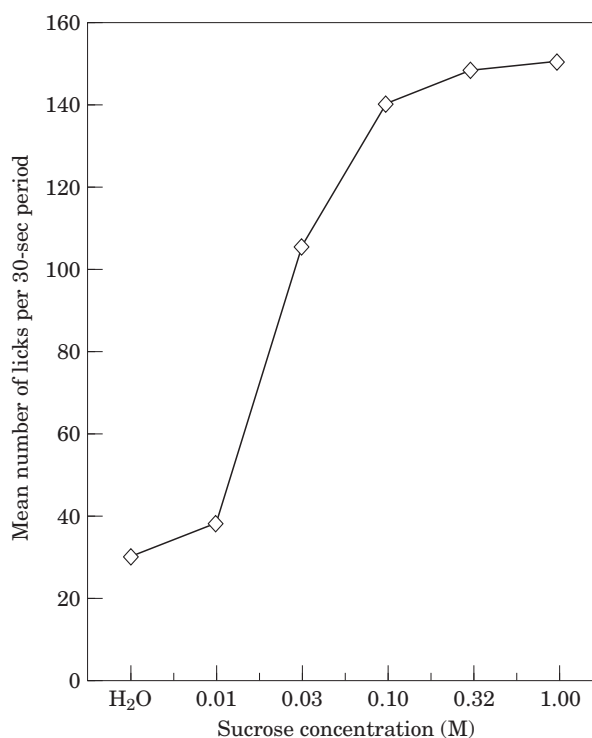


Figure 2. Mean number of licks per 30-sec period over five presentations at each concentration are replotted from Figure 1 (Davis, 1973).

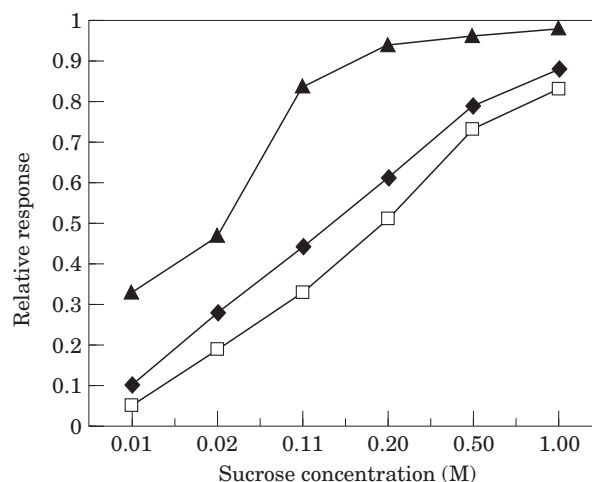


Figure 3. The relative response as a function of sucrose concentration is plotted for electrophysiological recordings from the greater superficial petrosal nerve (GSP REC, (Nejad, 1986); from sham feeding in 30-min trials, (Gibbs, 1994, pers. comm.); from behavioral licking in 30-sec tests, (Davis, 1973). The relative response is calculated using Beidler's Taste Equation (see Smith, 1988). GSP Rec (—◆—); shamfeed (—□—); davis (—▲—).

technique. To make this technique possible, we needed to have a rat drink for 45–50 min with little pausing and not to stop for long periods when he received a foot shock. Ross Henderson and I had made extensive observations on

ingestive behavior as a function of the amount of fluid received per lick. Ross developed a lick circuit that would trip a solenoid valve, allowing a known amount of fluid go through an 18-gauge needle to the opening of a standard lick tube. We started with Stellar’s 4 μl /lick measurement (Stellar & Hill, 1952) and began to systematically decrease the size of the amount obtained per lick to 3, 2 and 1 μl /lick. When we got down to 1–2-range, we observed that licking became much more steady and bursts of licking lasted for a long time without pauses. We figured that by limiting the amount of fluid the rat got per lick would aid in getting a rat to lick for a long time.

A second procedure for getting sustained licking possibly could come from the use of a psychogenic polydipsia procedure (Falk, 1966). John Faulk found that distributing pellets one at a time every minute or so over a period of several hours to a hungry rat markedly increased water drinking when compared to a rat that received all of the pellets in a pile at the outset of the testing period. We developed a rig for

measuring thresholds that incorporated both the restricted drop size and psychogenic polydipsia (Thaw, 1996; Thaw & Smith, 1992). This apparatus is illustrated in Fig. 4.

One of the eight lick tubes which were hooked through solenoid valves could be positioned in front of the drinking port. When the shutter was opened, the rat could be trained to lick water on a certain schedule of reinforcement for a food pellet. When the rat was well trained to lick for the food, some of the reservoirs were filled with a tastant. Upon encountering a tastant, the rat was conditioned to stop licking or receive an electric foot-shock. Quickly, the rat learned that water was safe and anything else was not. By loading the reservoir with varying concentrations of the sweet, sour, salty or bitter tastant, we could find that concentration that the rat could no longer discriminate from water. Kurt Thaw did his Master’s thesis on this rig and published two papers in *Chemical Senses* on the use of this apparatus (Thaw & Smith, 1992; Thaw, 1996).

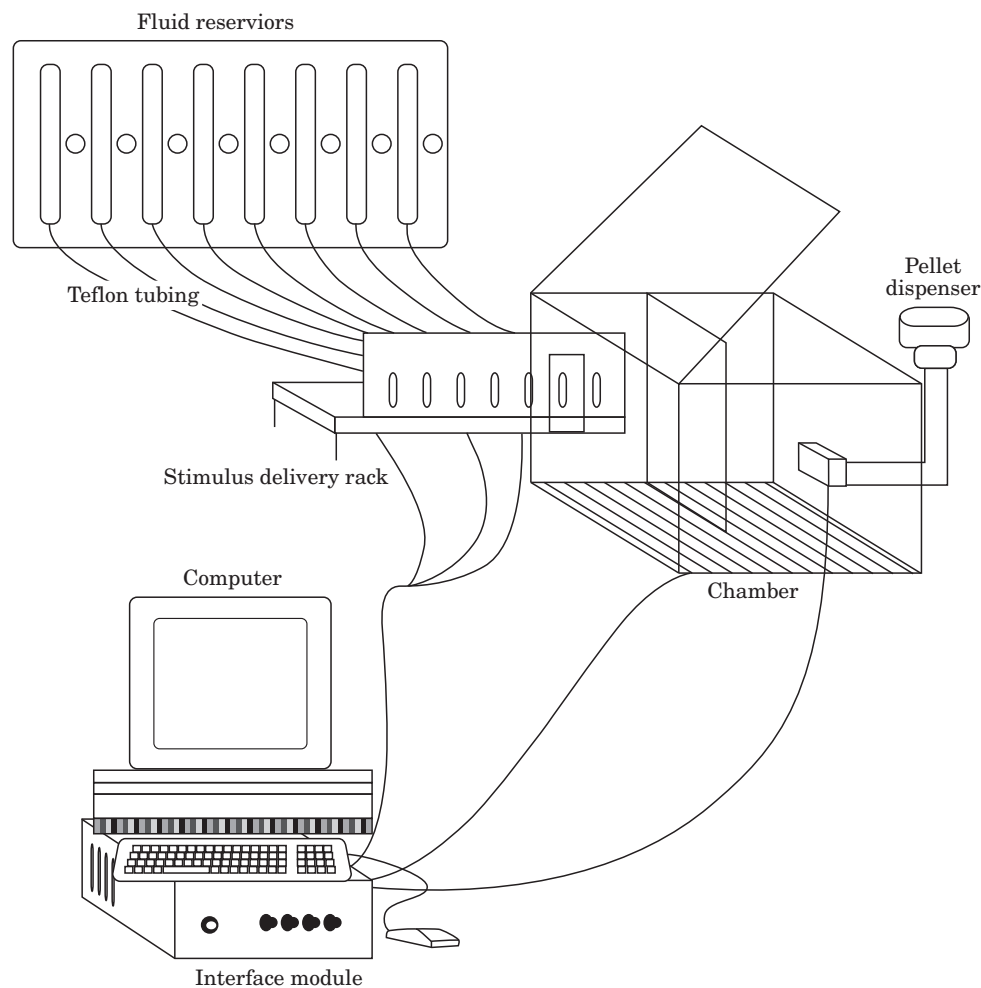
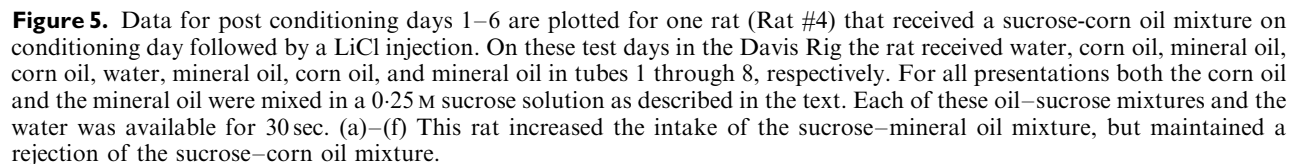


Figure 4. Taste threshold rig (Thaw & Smith, 1992). Any one of eight drinking tubes can be positioned in front of the rat’s drinking port. Licking on water results in a food pellet reinforcement, where licking on a tube containing a tastant results in a mild electric shock. With the conditioned suppression technique the rat is trained to lick freely for water and to suppress licking when he can taste a compound. Thresholds can be determined by measuring the lowest concentration of each tastant that the rat can discriminate from water.

Ross Henderson built for me a rig without the food chamber and the Davis Rig was history. My colleagues and friends saw the advantage of this short-term taste-testing rig that allowed for many daily brief exposures to different concentrations of a particular solution or of solutions of different qualities. Dilog Instruments Company manufactured the Davis Rig and they were widely accepted.

In fact, in 1995, Sandra Frankmann, Thomas Houpt, Timothy Moran and Stephen Cooper organized a symposium



entitled "Looking at Ingestive Consumption and Kinetics Symposium" (better known as the LICKS Symposium) in Pueblo, Colorado and the vast majority of the papers presented there were based on data collected in some variety of the Davis Rig.

I will conclude this history with an illustration of one way that I have used my Davis Rig in the past few months.

It is a wonderful instrument in which to measure a learned taste aversion. The temporal resolution of the licking measurement allows for closely watching the development of the taste aversion. We begin all experiments by training water deprived rats to promptly lick one of the tubes when the shutter opens. We load all eight tubes with water and set the parameters as follows: When the shutter opens, the first lick starts a clock. Some 30 sec after the first lick the shutter closes for 30 sec and then re-opens with a different tube in the licking position. If the rat fails to lick within 60 sec, the shutter closes and after a 30-sec delay the next presentation is made. The rat gets eight water presentations daily for a total of 240 sec of drinking time. We typically give the animals a 30-min supplementary home cage drinking period later in the day. Training on these water days usually takes about four to six sessions to have a rat making 180–200 licks each time the shutter is opened.

For my illustration, I wanted to see if rats conditioned with a sucrose–corn oil mixture could discriminate a sucrose–corn oil mixture from a sucrose–mineral oil mixture in post conditioning tests. Could I condition rats to avoid corn oil mixed with sucrose and subsequently show that they would not generalize this aversion to mineral oil mixed with sucrose? In total, 22 rats were conditioned after the water training by loading all eight tubes with the taste CS (the CS was a mixture of sucrose (0.25 M) and corn oil (16 %) blended with the use of 5 ml of a detergent, Tween-80) and presenting each tube for a 30-sec period. After the rats drank the CS from the eight tubes, half were injected with LiCl and the sham group received an injection of isotonic NaCl. They were tested for aversion in the Davis Rig the next day. On this first post-conditioning day the eight tubes were filled as follows: tube 1, water; tube 2, sucrose + corn oil; tube 3, sucrose + mineral oil; tube 4, sucrose + corn oil; tube 5, water; tube 6, sucrose + mineral oil; tube 7, sucrose + corn oil; tube 8, sucrose + mineral oil. Therefore, they received two water trials and three each of the sucrose–corn oil and the sucrose–mineral oil mixtures.

The details of the results will be presented elsewhere, but data from one rat from each group will illustrate the use of the Davis Rig in showing how the rats discriminated between the two oils. The cumulative licking data during each 30-sec presentation over six post-conditioning days are shown for Rat #4 in Fig. 5. On test Day 1, this rat drank water and showed a strong aversion to the sucrose–corn oil. This aversion generalized to the sucrose mineral oil rats. However, there was a small amount of drinking activity during the three sucrose–mineral oil presentations (10, 36 and 15 licks). As can be seen from the Figure, there was a steady increase in drinking of the sucrose–mineral oil mixture, but the aversion to the sucrose–corn oil remained profound except for a little activity on the fifth post-conditioning day. In summary, the

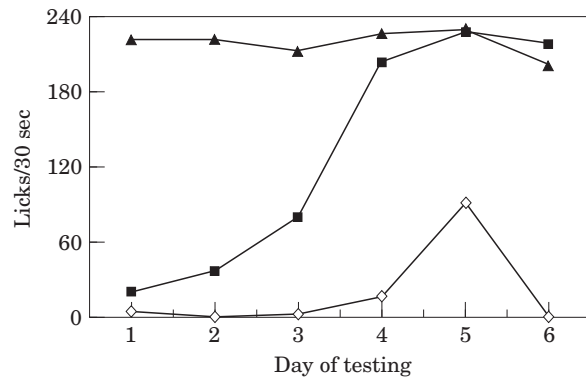


Figure 6. In order to further clarify the rapid discrimination between corn oil and mineral oil made by the LiCl injected rats during the post-conditioning tests, the mean number of licks/30 sec during the corn oil-sucrose, C + S (-◇-); mineral oil-sucrose, M + S (-■-); and water, WAT (-▲-), presentations are plotted over the six post-conditioning days for Rat #4.

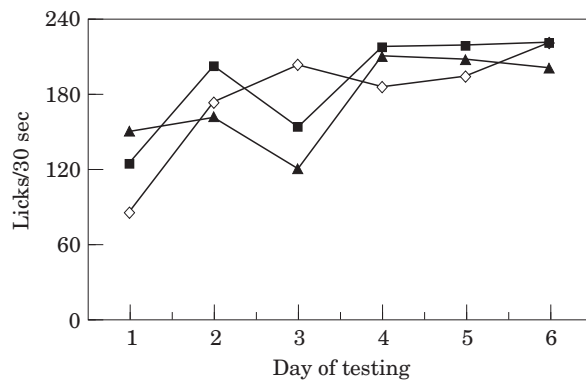


Figure 7. Rat #9 was in the sham group, receiving an injection of isotonic NaCl. As can be seen, he developed no aversion to either of the sucrose–oil solutions. C + S, (-◇-); M + S, (-■-); WAT, (-▲-).

mean licks/30 sec for each presentation across the 6 days of testing are shown in Fig. 6 for Rat #4. These data show more clearly the gradual discrimination of the corn and mineral oil mixtures in the post-conditioning testing. A similar plot is presented in Fig. 7 for one of the saline injected rats (Rat #9). The discrimination between the two oil mixtures became clear after only 240 sec of licking.

Needless to say, the Davis Rig has become a very important instrument for measuring the chemical senses component of ingestion in my laboratory (O'Keefe *et al.*, 1994; Stephan *et al.*, 1999). The 1973 paper of Professor Davis would rank my top 10 scientific articles that markedly influenced my way of thinking. It was a pioneer of articles on the microstructure of short term drinking tests. John D. Davis has made a significant impression on my research life and I am particularly proud to have him as a colleague and as a friend.

- Davis, J. D. (1973). The effectiveness of some sugars in stimulating licking behavior in the rat. *Physiology and Behavior* **11**, 39–45.
- Falk, J. L. (1966). Schedule induced polydipsia as a function of fixed interval length. *Journal of Experimental Analysis of Behavior* **9**, 37–39.
- Nejad, M. S. (1986). The neural activities of the greater superficial petrosal nerve of the rat in response to chemical stimulation of the palate. *Chemical Senses* **11**, 283–293.
- O'Keefe, G. B., Schumm, J. & Smith, J. C. (1994) Loss of sensitivity to low concentration of NaCl following bilateral chorda tympani nerve sections in rats. *Chemical Senses* **19**, 169–184.
- Rhinehart-Doty, J. A., Schumm, J., Smith, J. C. & Smith, G. P. (1994). A non-taste cue of sucrose in short-term taste tests in rats. *Chemical Senses* **19**, 425–431.
- Smith, J. C. (1988). Behavioral measures of the taste of sucrose in the rat. In I. J. Miller (Ed.), *Beidler symposium on taste and smell: a festschrift to Lloyd M. Beidler*. Winston Salem, NC: Book Service Associates.
- Smith, J. C. & Wilson, L. S. (1988). A study of a lifetime of sucrose intake by the Fischer-344 rat. In C. Murphy (Ed.), *Nutrition and the chemical senses in aging: recent advances and current research needs* New York: New York Academy of Sciences. pp. 291–306.
- Smith, J. C., Davis, J. D. & O'Keefe, G. B. (1992). Lack of an order effect in brief contact taste tests with closely spaced test trials. *Physiology and Behavior* **52**, 1107–1111.
- Stellar, E. & Hill, J. H. (1952). The rat's rate of drinking as a function of water deprivation. *Journal of Comparative Physiology and Psychology* **45**, 96–102.
- Stephan, F. K., Smith, J. C. & Fisher, E. M. (1999). Profound conditioned taste aversion induced by oral consumption of 2-deoxy-D-glucose. *Physiology and Behavior* **68**, 221–226.
- Thaw, A. K. (1996). Changes in taste threshold over the life span of the Sprague–Dawley rat. *Chemical Senses* **21**, 189–193.
- Thaw, A. K. & J. C. Smith. (1992). Conditioned suppression as a method of detecting taste thresholds in the rat. *Chemical Senses* **17**, 211–223.