Changes in Taste Threshold over the Life Span of the Sprague–Dawley Rat

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Abstract

Taste thresholds for sucrose, NaCl, QHCl and citric acid were examined over the lifetime of seven rats. Significant yet subtle decreases in taste sensitivity were observed in the oldest subjects only. **Chem. Senses 21: 189–193, 1996.**

Introduction

Changes in taste perception due to aging have been investigated by a number of researchers using both human and animal models (Richter and Campbell, 1941; Cooper *et al.*, 1959; Murphy, 1977, Grzegorczyk *et al.*, 1979; Dye and Koziatek, 1981; Moore *et al.*, 1982; Weiffenbach *et al.*, 1982; Weiffenbach, 1984). Yet it is still controversial as to whether or not an actual change in taste occurs. Secondary influences affecting the perception of a tastant may be responsible for some of the reported decreases found in aged subjects. These influences include methodology, general health, dentures, medication, salivary function and especially olfaction.

One popular method used to detect taste sensitivity is the threshold test. While many researchers have developed various threshold procedures, few have examined changes in taste threshold over the life span of their subjects. A number of cross-sectional experiments have been conducted comparing the sensitivity of a sample of young versus old human subjects (Richter and Campbell, 1941; Harris and Kalmus, 1949; Cooper *et al.*, 1959). Kalmus and Trotter (1962) conducted one of the few longitudinal studies of human taste threshold. They used sensitivity to PTC as their tastant and tested subjects 10–15 years after they had

originally been tested. Results showed an average threshold increase of 3% annually.

Recently, better methods of testing taste thresholds have been developed (Grzegorczyk *et al.*, 1979; Moore *et al.*, 1982). In the forced choice method, a subject is required to sample solution from two cups, one containing distilled water and the other the solution. The subject then must determine which solution had a 'taste' and which did not. Thorough rinsing of the oral cavity is performed between each sample. Subjects continue to compare paired solutions of water and tastant in a descending and ascending series until the approximate threshold is determined. The above-mentioned investigators found an age-related decrease in sensitivity for sucrose, as well as NaCl, while other researchers have found no such decrement (Weiffenbach *et al.*, 1982).

While animals have been used to develop many taste threshold procedures (Blough, 1958; Carpenter, 1958; Koh and Teitelbaum, 1961; Morrison and Norrison, 1966; Shaber *et al.*, 1970; Slotnick, 1982; Brosvic and Slotnick, 1986; Spector *et al.*, 1990), they have been noticeably absent from studies comparing changes in taste threshold over their life span. Comparisons between the physiology and anatomy of the peripheral taste system of young versus old rats, monkeys

and mice have been conducted in an attempt to locate areas of deterioration that may contribute to the taste decrements observed in humans (Hill *et al.*, 1982; McBride and Mistretta, 1986; Mistretta and Oakley, 1986). However, there are no studies which monitor changes in taste threshold that may occur during the life span of a particular subject. The present paper is a longitudinal study of changes in taste detection thresholds using Sprague–Dawley rats. A recently developed taste threshold procedure (Thaw and Smith, 1992) employing a modified method of conditioned suppression was used in an attempt to provide evidence for increased taste thresholds in aging rats and to determine when such increases occur.

Methods, results and discussion

Seven male Sprague–Dawley rats (Charles River Breeding Laboratories) served as subjects. They were housed individually in wire-mesh cages (Hoeltge) and maintained on a 12:12 light:dark cycle with a constant room temperature of 72°F. Subjects were food deprived to 85–80% of their *ad libitum* weight when training/testing. They received water *ad libitum* and supplemental Purina rat chow blocks (5012) if their weight fell below 80% of its *ad libitum* normal free-feeding value. Subjects were housed with *ad libitum* food and water between testing.

The rats were tested in an apparatus containing eating and drinking compartments separated by a partition. Any one of eight sipper tubes could be moved in front of an opening in the drinking area. Each tube was mounted in a Plexiglas block with an infra-red beam in front of it to detect licks. The opening could be occluded by a shutter. Noyes pellets were delivered to the food area by a Gerbrands (model D-1 #0906) pellet dispenser. A photo beam placed in front of the food area indicated when the animal's head was in the hopper. The rats were free to move from one area to the other. All data were collected using a microcomputer that stored the data on disk for later analysis. A line drawing of the apparatus can be seen in Figure 1.

Training

The subjects were trained to lick water from the sipper tubes for pellet reinforcements. In order to obtain a steady rate of licking for testing periods up to an hour, the rats were trained to work on a variable interval schedule of reinforcement with a mean interval of 17.5 s. In order to reach this ultimate schedule the subjects were initially trained on a fixed ratio schedule of reinforcement. The ratio was increased until the rats were licking 50 times for each pellet. The subjects were

then placed on a variable ratio (VR) schedule that increased from a VR 50 to a VR 60 and then to a VR 70. Finally, each subject was switched to the variable interval schedule. At this time, testing was initiated.

Testing

On the first day of testing four of the sipper tubes contained various concentrations of tastants while the others contained water. The concentrations of the tastants used were selected on the basis of pilot studies conducted in the apparatus that revealed concentrations that were readily detected by each subject. When a rat licked a water tube the normal VI schedule of reinforcement was in effect. After a food pellet delivery, when the rat returned to the drinking compartment and encountered a tube containing a tastant, a mild electric shock would be delivered through the bar floor of the apparatus if the subject licked 20 or more times on the tube. Tastant tubes were presented for 10 s. The shock was not delivered until the 10 s had elapsed. The subjects quickly learned to sample each tube and continue licking only the ones containing water. If all of the tastants were detected, the concentrations were lowered for the next day (in such a way that the lowest concentration from the previous day was the highest). This process continued until some of the tastants were detected and others were not. The concentrations were then made so as to include the lowest that was detected and the highest that was not detected. Experimentation continued between these two levels until a precise measure had been made to determine the animal's threshold.

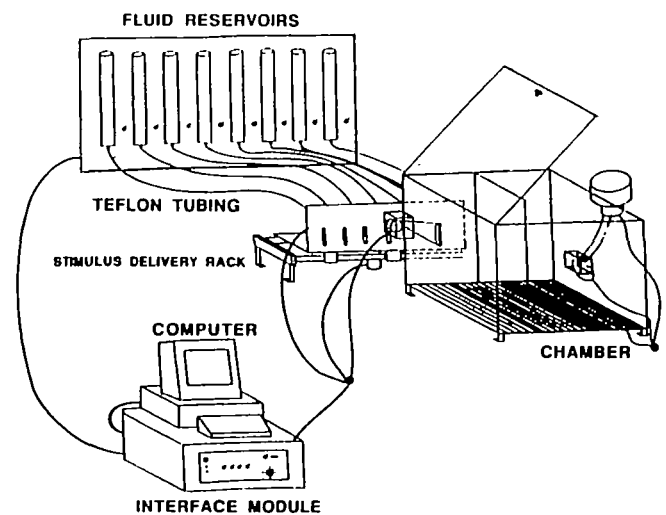Suppression was quantified in the following manner. The

Figure 1 Line drawing of the conditioned suppression apparatus.

number of licks that occurred in the last 5 s of a tastant presentation were recorded and compared to the average number of licks in the last 5 s of the water presentations. The suppression ratio was calculated as follows:

$$SR = W - S / W + S$$

where W = the average number of licks for the last 5 s of

Table 1 The age and test session that each rat survived to and mean age of death for the group

Test session (age in months)	1 (4)	2 (9)	3 (13)	4 (18)	5 (23)	6 (28)
Subjects participating	1	1	1	1	1	1
	2	2	2	2	2	2
	3	3	3	3	3	3
	4	4	4	4	4	
	5	5	5	5	5	
	6	6	6	6	6*	
	7					

*Rat 6 completed his sucrose testing only
Mean age at death = 24.3 months.

all water presentations during a session and S = the average number of licks for the last 5 s of the presentation of a particular solution.

A suppression ratio was calculated for each presentation of each solution. Each concentration in the test array was presented a minimum of six times. Only one compound was used in each daily session until threshold was determined. An average of all suppression ratios for each concentration during a single test session was calculated to determine the threshold, which was the value obtained when S was exactly half of W ($SR = 0.333$). This threshold procedure was repeated every 4–5 months throughout the animals' life.

Since this was a longitudinal study it followed that the subject pool would decline as time went on. Table 1 indicates the last test session that each subject was able to complete. This provides observation of the lifespan of each subject as well as a mean life expectancy for the group.

Suppression ratios were averaged for all rats at each concentration. A graphic representation of the groups threshold for each of the four tastants has been produced in Figure 2.

Though only three of the original subjects survived beyond 23 months, repeated measures ANOVA statistical analysis
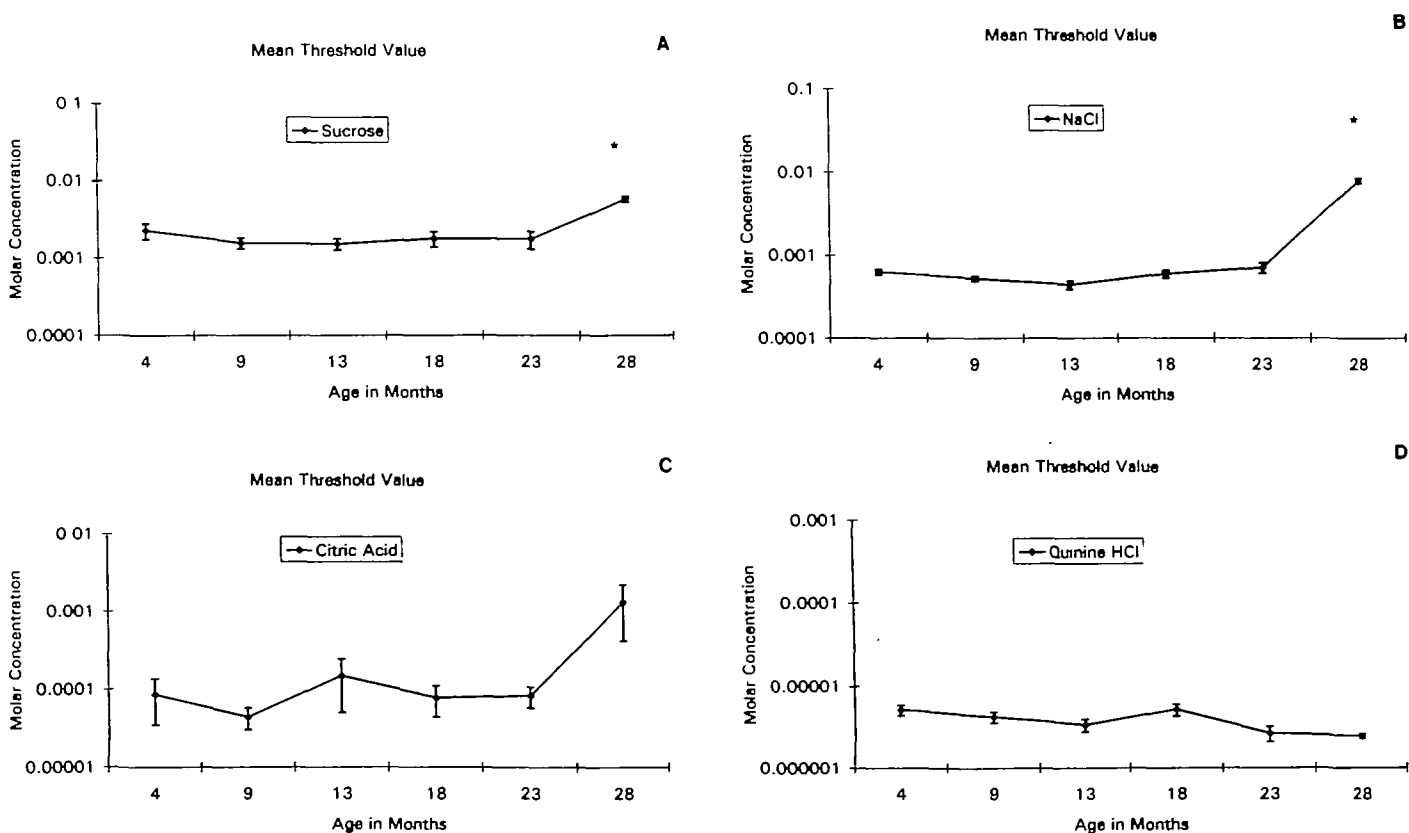
Figure 2 Mean threshold (SE) for each tastant: **(A)** sucose; **(B)** NaCl; **(C)** citric acid; **(D)** quinine HCl. * = significantly different from the other scores (repeated measures ANOVA, $P < 0.01$).

of these subjects reveal significant differences in threshold values for two of the four solutions. For sucrose and NaCl the threshold of the subjects at 28 months of age was significantly different from the other test dates: $F = 11.25$ (sucrose), 229.67 (NaCl), d.f. = 5,10, $P < 0.01$; post-hoc Fischer's LSD for repeated measures ANOVA, $t = 5.22$ (sucrose) and $t = 25.85$ (NaCl), $P < 0.01$. No other comparisons produced significant differences.

This study is the first longitudinal analysis of taste thresholds in rats. The results confirm findings from cross-sectional studies that indicate decreased taste sensitivity with advanced age. This study reveals that such increases in threshold are manifest in only the oldest subjects. In fact, subjects had to be beyond the mean life expectancy of the group before any decrements were detected.

Of interest is the fact that the decline in sensitivity is not a generalized decrement, but rather specific for sucrose and NaCl. This is in accord with other findings that show altered sensitivity to sucrose and NaCl. Especially interesting are the comparable physiological results obtained by McBride and Mistretta (1986) who compared chorda tympani responses from young and old Fischer 344 rats. They report significantly different response ratios for sucrose and citric acid relative to NaCl in the oldest age group (30 months versus 6 months). Additionally, the response/concentration function of NaCl was significantly different for the old groups (24 and 30 months) as compared to the young group (6 months). There was no change in the response to quinine.

Reasons for the decline in sensitivity are unclear. Speculation of loss of taste buds in aged subjects has been previously examined (Mistretta and Oakley, 1986). However, even in the oldest subjects examined at least 90% of all fungiform papilla still contained a taste bud (Mistretta, 1984). Therefore, a general loss of receptor organs is not likely responsible for the decrease in taste sensitivity. Other possibilities for the changes include: taste cell turnover rate or membrane changes, afferent fiber characteristic changes, hormonal changes or even changes in central taste areas. Few studies have investigated any of the above-mentioned possibilities with regards to the taste system.

It should be noted that while significant differences in taste threshold are reported in this paper, the subjects were still able to perform the task. Since this test requires behavioral responses based on taste, it must be concluded that the taste system functions relatively well, even in the oldest subjects. In fact, all of the concentrations detected in this study were well below those normally encountered in everyday foods. Therefore, complaints of taste changes in elderly adults may not necessarily be due to decrements in taste sensitivity (Weiffenbach,1984).

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