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PREFERENCE DIFFERENCES FOR SUCROSE SOLUTIONS IN YOUNG AND
AGED SQUIRREL MONKEYS

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PREFERENCE DIFFERENCES FOR SUCROSE SOLUTIONS IN
YOUNG AND AGED SQUIRREL MONKEYS

by

Raenel Ruth Michels Neitz

A Thesis Submitted to the Faculty of the
DEPARTMENT OF PSYCHOLOGY
In Partial Fulfillment of the Requirements
For the Degree of
MASTER OF ARTS
In the Graduate College
THE UNIVERSITY OF ARIZONA

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STATEMENT BY AUTHOR

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ABSTRACT

Licking patterns and molarity preferences, elicited by two sets of sucrose solutions (0.0 to 1.75 M and 1.0 to 3.0 M), were measured in six young and six aged squirrel monkeys. Additionally, sucrose preference thresholds were determined for each group using sucrose concentrations from .025 to .1 M.

Age had no effect on sucrose preference thresholds. Consumatory activity in all monkeys increased monotonically with increasing sucrose concentrations, from 0.0 to 1.0 M. However, aged monkeys continued to increase consumption until sucrose concentrations exceeded 1.5 M. All monkeys increased consumption by increasing number of licks, number of licking bursts and length of licking bursts.

Compared to young monkeys, aged monkeys displayed greater within animal variability of tongue contact times, exponentially decreasing rates of licking at high molarities, constant consumption efficiency decrements, and consistent negative correlations between tongue contact and following tongue-off times.

CHAPTER 1

INTRODUCTION

Licking at a sipper tube is a high speed, rhythmic pattern of tongue, jaw and throat movements (Yamamoto, Matsuo, Fjuiwara, & Kawamura, 1982). Under constant conditions, the movements of the tongue are highly stereotyped (Halpern, 1975) and can be divided into several temporal components: duration of tongue contact with the sipper spout (tongue contact time), time from off set to following onset of tongue contact with the sipper spout (tongue off time), and tongue movement pattern fluctuations (rate of licking, duration of licking bursts and pauses, etc.). Temporal patterns of licking have been analyzed in the laboratory rat (Halpern, 1975), cat (Schaeffer & Huff, 1965), opossum (Cone, Cone, Golden, & Saunders, 1973), hamster (Faull & Halpern, 1972), gerbil (Pierson & Schaeffer, 1975) and squirrel monkey (King, Hsiao, & Leeming, 1986). The mean licking rates in mammals range between 3.4 and 6.5 licks/second (see Halpern, 1977, for review). The supposition that within-species licking parameters are relatively constant has been widely accepted and supported by experimental evidence (Hulse & Suter, 1970; Weijnen & Mendelson, 1977).

Within a species, licking behavior may be modified by accessibility of the sipper spout (Marowitz & Halpern, 1973), chemical characteristics and viscosity of the stimulus solution (Davis, 1973; Cone, Wells, Goodson, & Cone, 1975), and several organismic and

methodological variables such as gender, developmental age, time of testing and experience with the sipper spout (see Cone, 1974, for review). Despite the sensitivity of licking behavior to experimental manipulation, demonstrations of within species licking behavior variations have never revealed parameter changes that exceed 20% of median control values (Hernandez-Mesa, Mamedov, & Bures, 1985).

Recently, an unusual within species parameter variability was shown in the squirrel monkey (Saimiri sciureus) (King et al., 1986). Aged (over 15 years old) squirrel monkeys displayed about 50% greater variability in tongue contact times than did young (3 to 5 years old) monkeys when licking in response to sucrose solutions. This variability was not accompanied by significant age differences in mean tongue contact times, mean tongue off times or rate of licking. King et al. (1986) suggest that the inability to maintain constancy of tongue contact times in the aged monkeys may represent a partial loss of timing control of the tongue muscles during licking.

When licking in response to reinforcing stimulus solutions, such as sucrose water, the amount of fluid consumed is determined by the subject's gustatory threshold for detection of the stimulus, motor performance capability and gustatory preference for a particular concentration of the stimulus. All of these organismic characteristics may be affected by age. In the following sections, evidence for such age related effects and their possible mechanisms will be considered.

Gustatory Anatomy and Sensory Thresholds

Most studies of gustatory responses report that detection and preference thresholds increase with age (see Schiffman, 1979; and Schiffman & Covey, 1984, for reviews). Age related changes in taste thresholds could result from diminished functioning of taste receptors, reduction in the number of taste receptors, or alteration in neural transmission at any level along the gustatory pathways. The following is a description of gustatory anatomy and age dependent changes in taste thresholds. The description of gustatory anatomy is modified, in large part, from Bloom and Faucett (1975) and Schmidt (1978).

The primate tongue contains elevated structures called papillae, within which taste buds (chemoreceptor organs) are located. Three types of papillae--fungiform, foliate and circumvallate--contain taste buds. Each taste bud is composed of 30 to 60 sensory cells and each papilla may contain up to 250 taste buds. Non-papilliform taste buds are found on the soft palate and palatal arches, posterior wall of the pharynx, upper larynx and on the posterior surface of the epiglottis.

The fungiform, foliate and circumvallate papillae are distinctly distributed on the surface of the tongue (Fig. 1). In most primates, the foliate and circumvallate papillae occur in consistent, restricted regions of the tongue (Halpern, 1977). The foliate papillae are arranged on the lateral surface of the posterior part of the tongue, while the circumvallate papillae, numbering only ten to twelve in man, appear as posterior protuberances in a V-shaped area on the

Fig. 1. Papillae Distribution on the Primate Tongue

back of the tongue. The fungiform papillae are usually scattered singly on the dorsal surface of the front two-thirds of the tongue.

Taste buds are nested in the epithelium of the papillae, beneath a small opening called a taste pore. The taste bud is composed of two cell types: supporting cells and neuroepithelial taste receptor cells. The latter are arranged between the supporting cells, are rod shaped and have a short taste hair that protrudes through the taste pore on the surface of the tongue. The proximal end of the taste receptor cell is innervated by a sensory nerve fiber.

Four primary tastes have been determined: sweet, sour, salty and bitter. Each type of papilla, and the taste buds within a papilla, may subserve more than one primary taste. Each taste bud responds to multiple primary taste stimuli, but is maximally responsive to only one taste stimulus. There are no morphological differences among the taste buds that respond maximally to different taste stimuli; however, the taste buds are topographically represented in distinct, overlapping areas of the tongue (Fig. 2). Taste buds located on the lateral regions of the tongue respond preferentially to sour substances, those on the back of the tongue to bitter substances and those on the anterior dorsal surface of the tongue to sweet and salty substances (Guyton, 1976).

The notion of a patterning code for taste was introduced by Pfaffman (1941) and later expanded by Erickson (1963). The proposal states that each primary stimulus evokes a particular rate of discharge from each of a large number of neurons, establishing a pattern of

Fig. 2. Taste Stimuli Receptive Topography on the Primate Tongue

activity that is unique to the quality and intensity of the stimulating chemical. The topography of the response, read across neurons in a specified order, encodes stimulus quality, whereas the cumulative discharge rate represents stimulus intensity. This proposal is supported by recent electrophysiological evidence (Yamamoto, Yuyama, & Kawamura, 1981). The pattern of signal strengths from various taste buds results in the recognition of taste and taste discrimination. Taste recognition, but not taste reflex, requires cortical integration of sensory input (Pfaffman, 1977).

Taste receptors are served by cranial nerves VII (facial), IX (glossopharyngeal) and X (vagus). The receptors on the anterior two-thirds of the tongue, bearing the fungiform and more lateral foliate papillae, are innervated by the sensory root of the VII cranial nerve, while the posterior third of the tongue, bearing circumvallate papillae, is innervated by the X cranial nerve.

Neurons receiving input from taste receptors are located in the inferior ganglia of cranial nerves IX and X (petrosal and nodosal respectively) and in the geniculate ganglion for cranial nerve VII. Taste fibers from the tongue reach the geniculate ganglion via the chorda tympani and the lingual branch of cranial nerve V. Fibers from the tongue to the petrosal and nodosal ganglia are carried in the pharyngeal and laryngeal branches of the respective nerves.

The central projections of the geniculate, petrosal and nodosal ganglia become part of the tractus solitarius and terminate in parts of the spinal trigeminal nucleus, the first few segments of the spinal

cord, and in the rostral portion of the nucleus solitarius (Norgren, 1981). In primates, the nucleus solitarius has minor projections to the parabrachial nuclei of the dorsal pons, while the primary gustatory fibers synapse directly in the nucleus ventralis posteromedialis paraventricularis (VPMpc) of the thalamus (Norgren, 1984). Long ascending projections from the nucleus solitarius to the frontal cortex are present in rats and cats but not primates. Cells in the VPMpc of primates project to the insular and opercular regions of the cortex, while the neurons of the parabrachial nuclei distribute to the hypothalamus and amygdala (Norgren, 1985) (Fig. 3). The gustatory cortex is closely related to the somatosensory area for the tongue and subserves the conscious recognition of taste. Input to the hypothalamus and amygdala is important for autonomic control of feeding behavior (Heimer, 1983). For a complete review of central nervous system gustatory projections, see Yamamoto et al. (1981).

Many studies report differential performance of young and aged subjects in psychophysical taste tests. The concentrations at which humans can distinguish between a stimulus solution and plain water (detection thresholds) are higher in aged than young subjects for a variety of compounds; analogously, in two-bottle-choice paradigms, the concentrations at which animals consume 75% more of a stimulus solution than water increase in the aged (see Schiffman, 1979, 1984, for reviews). Sucrose detection thresholds have been reported to increase in humans after critical ages that range from 60 (threshold = .03M) (Cooper, Bilash, & Zubek) to 80 years (threshold = .018M) (Dye &

Fig. 3. Peripheral and Central Nervous System Taste Pathways in the Primate

Kosiatek, 1981). Other studies report no change in sucrose detection thresholds in the aged (Hyde & Feller, 1981; Nilsson, 1979; Weiffenbach, Wolf, & Baun, 1981). These contradictory reports may be due to many uncontrolled subject variables such as gender, alcohol use, nutritional state and medical history.

Gustatory responses of senescent animals have received little attention. Cicala and McMichael (1964) demonstrated lower quinine aversion thresholds for adult Wistar rats (95 to 105 days old) than for infant animals (22 days old), but found no significant difference between mature and aged rats (300 or more days old). When given a saccharin solution and water simultaneously for 15 to 30 minutes, following fluid deprivation for 23 to 24 hours, senescent and adult rats display similar saccharin preferences (Ingram & Peacock, 1980; Martinez & Rigter, 1983). In two-bottle preference threshold tests lasting longer than 30 minutes, no significant age differences were found for saccharin (Guanowski, Misanin, & Riccio, 1983; Martin & Fuchs, 1985) or glucose (Martin & Fuchs, 1985) in rats.

Few studies of age related differences in taste bud and papillae number exist, and the results of these studies are contradictory (see Mistretta & Baum, 1984, and Schiffman, Orlandi, & Erickson, 1979, for reviews). Early literature reported a loss or atrophy of taste buds and papillae with age (Schiffman, 1984); however, the methods described in these studies were inconsistent and, sometimes, untenable. For example, Moses et al. (1967) is often cited as evidence for decreased fungiform papillae in aged humans. Moses et

al. actually reported a reduction in the number of fungiform papillae per square inch on the human tongue between the ages of 4 and 45. A decrease in papillae number per square inch should be expected, but does not necessarily represent an age-related loss. The tongue approximately doubles in area between 4 and 18 years of age (Cohen & Vig, 1976). Additionally, Moses' report, together with many other publications on taste bud and papillae number, lacks statistical analysis and gives incomplete subject profiles and methods description. Subject profiles and methods description are imperative because taste buds and papillae can be physically altered by variables such as mechanical trauma, pathology, medication use, smoking, post mortem age, dental condition and methods of tissue preservation (Mistretta, 1984). Recent, well-controlled and analysed studies report no decrease in taste bud and papillae number with age in rodents (Mistretta & Baum, 1984), monkeys (Bradley, Stedman, & Mistretta, 1985), and humans (Arvidson, 1979).

Taste thresholds could also be affected by alterations in cell receptor membranes. Age related changes in cell receptor membranes would presumably be reflected in altered electrophysiological responses from peripheral taste nerves. Responses were recorded from the chorda tympani nerve, in young and aged Fischer 344 rats (McBride & Mistretta, 1983). Even in the oldest rats, large responses were obtained from the whole nerve during lingual stimulation with salts, acids, sucrose and quinine hydrochloride. However, in aged rats, responses to very high molar concentrations of salt were smaller than in young rats. As a

consequence, the ratio of stimulation by sweet, sour and bitter substances increases in comparison to salty substances with age. If this ratio change affects the complex patterning code of stimulation, qualitative judgments about gustatory stimuli could be affected.

Little is known about age related changes in the central nervous system pathways for taste. Degenerative changes in the brain structures involved with feeding behavior are suggested by the finding of neurofibrillary tangles in the amygdala and progressive dendritic loss in the hypothalamus (Schiffman et al., 1979). No work has been done to indicate that there are age related changes in the opercular cortex; however, changes in the cortices of the temporal, parietal and frontal lobes are well documented (see Cotman & Holets, 1985, for review).

In summary, the gustatory system is composed of peripheral, topographically distinct, taste receptors, midbrain projections capable of moderating gustatory reflexes, and higher projections to limbic and cortical structures which moderate feeding and taste discrimination respectively. Changes in gustatory thresholds with age are dependent on many variables including species and life history of the subject. When organismic and life history factors are held constant, receptor number and function appear to remain intact with age. However, the neural activity produced by suprathreshold salty stimuli is altered in comparison to other gustatory stimuli in the aged rat. The impact of this alteration on gustatory thresholds is unclear. There is little evidence that this change in ratio of stimulation effects thresholds

for sweet, sour or bitter substances, however, it may be reflected by increased gustatory thresholds for salt (Hyde & Feller, 1981). The central processing of the patterning code for gustation is not well understood and, although age related changes undoubtedly occur in the central nervous system, the effect of these changes on taste thresholds remains relatively unexplored.

Motor Control of Licking

Licking behavior is often assumed to be stabile and automatic because it is rhythmic. However, rhythmic licking actually requires highly complex motor coordination, and this coordination is subject to modification by changes in both neuronal input and muscular integrity. The changes in motor coordination that accompany advanced age should, consequently, also be observed in the motor coordination of licking. The following is a summary of the mechanisms regulating licking behavior and an overview of age related changes that affect these mechanisms.

At any moment during the execution of licking behavior, tongue position is a direct resultant of extrinsic, intrinsic and hypobranchial muscle tension (Doran & Baggett, 1972). The intrinsic muscles of the tongue (superior longitudinal, inferior longitudinal, transverse and vertical muscles) have both their points of origin and points of insertion within the tongue. These muscles change the shape of the tongue and modify tongue movement. The extrinsic muscles of the tongue (styloglossus, genioglossus, hypoglossus, and, in man, the palatoglossal muscles) have their points of origin on the bones of the

skull and hyoid apparatus; their points of insertion are mainly in the connective tissue of the tongue and onto the intrinsic muscles. The extrinsic muscles function primarily to protrude and retract the tongue. The hypobranchial muscles (mylohyoid, geniohyoid, sternohyoid and omohyoid muscles) have extralingual points of origin and insertion; they influence tongue position through manipulation of the hyoid bone which is the attachment point for many of the extrinsic muscles. For an expanded review of tongue and mouth anatomy in mammals, see Halpern (1977).

All of the intrinsic and extrinsic muscles of the tongue, except the palatoglossal muscle in man, are innervated by the hypoglossal nerves (cranial nerve XII). The hypoglossal nerves originate in the hypoglossal nuclei of the medulla and are located dorsal to the inferior olivary nuclei (DeArmond, Fusco, & Dewey, 1976). Wiesenfeld, Halpern and Tapper (1977) recorded rhythmic single and multiunit activity in the hypoglossal nuclei that was synchronous with, and briefly continuing after cessation of, overt licking for water in rats. Each lick was accompanied by a burst of hypoglossal activity which had modal periods (140 to 160 ms) similar to the interlick interval lengths (duration from the offset of tongue contact to the onset of the following tongue contact with the sipper tube). Wouters and Weigen (1985) recorded neural activity in the hypoglossal nuclei of rats licking water from sipper spouts. Neural activity in the dorsal portion of the hypoglossal nuclei was related to tongue retraction, while activity in the ventral portion was related to tongue protrusion.

The neural oscillatory activity in the hypoglossal nuclei, that is related to licking behavior, is commonly referred to as the hypoglossal oscillator: a rhythmic generator of licking behavior (Wiesenfeld, Halpern & Tapper, 1977). The hypoglossal oscillator represents the most peripheral central nervous system innervation of the tongue.

Tongue movement can be influenced by input from the central nervous system superior to the hypoglossal nuclei. The cortico-bulbar tract synapses directly onto the cells of the hypoglossal nuclei; however, rhythmic tongue and jaw movements can be demonstrated in decerebrate animals indicating that the pacemaking circuits for licking are probably located subcortically (Grill & Norgren, 1978; Lund, 1976; Yamamoto et al., 1982).

Pharmacological and surgical techniques have been useful in demonstrating specific brainstem regions that affect licking. Reduced tongue extension and lap volume results following lesions to the zona incerta, globus pallidus, central amygdaloid complex and lateral hypothalamus (Brimley & Mogenson, 1979). Treatment of the above brainstem areas with 6-hydroxydopamine produces a significant reduction in tongue extension and lap volume. Additionally, spiroperidol, a dopamine (DA) receptor blocker, causes a dose dependent decrease in tongue extension and lap volume when injected into the nucleus accumbens of the rat (Jones & Mogenson, 1979). These brainstem structures, and several other DA-rich brainstem regions, are important in the oral motor control of licking.

Only a limited number of studies have been carried out to describe brainstem structural changes in aged animals. The extent of degenerative change varies in the different brainstem and brain nuclear structures. In the hypoglossal nuclei of the aged mouse, less than 5% of the neurons appear atrophied (neuronal retraction, basophilic cytoplasm loaded with lipofuscin, and pyknotic nuclei); however, severe changes occur in the neuronal and dendritic morphology of the hypothalamus and substantia nigra (Machado-Salas, Scheibel & Scheibel, 1977a, 1977b). Little or no cell loss is seen in the inferior olivary nuclei of aged humans (Monagle & Brody, 1974), while the locus coeruleus (Brody & Vijayashankar, 1977) and putamen (Bugiani, Salvarania, Perdelli, Mancardi, & Leonardi, 1978) of aged humans shows significant decreases in neuronal density.

Dopamine is widely distributed in the central nervous system, primarily through the tuberoinfundibular, incerto-hypothalamic and medullary paraventricular pathways and through the long projections of the ventral tegmental and substantia nigral DA cell groups to neostriatal and limbic targets (Fig. 4) (Kandel & Schwartz, 1981). Changes in striatal DA content, synthesis and receptors are indicated in several movement disorders that involve oral motor control changes, such as tardive dyskinesia and Parkinsonism (Casey, 1984). Some of the dopaminergic pathways and motor control disorders are profoundly affected by the aging process.

Age related decreases in DA content have been reported in the striatum, diencephalon and brainstem of many animal species (see

Fig. 4. Unilateral Representation of the Nigrostriatal and Ventral Paraventricular Dopaminergic Pathways in the Squirrel Monkey (modified from Felten and Sladek, 1983)

Simkins, Muller, Huang, & Meites, 1977, and Morimasa, Doi, Shohmori, & Kohsaka, 1982, for reviews). The overall number of binding sites for DA decreases progressively during adult life, with a loss of about 40% during the average life span of humans (Severson & Finch, 1980). In the striatum and basal ganglia, DA receptor losses have been reported to be as high as 83% in the aged rat (Govoni, Memo, Saiani, Spano, & Trabucchi, 1980) and 63% in the aged human (Lee, Seeman, Rajput, Farloy, & Hornykiewicz, 1978). Age related decreases in DA receptors in the striatum have been documented in many species, including rabbits, mice, rats and man (see Rogers & Bloom, 1985, for review).

Several steps in the synthesis of DA are affected adversely by age. Dopamine synthesis requires the enzymes tyrosine hydroxylase, which functions in an initial and rate-limiting step to convert tyrosine to dihydroxyphenylalanine (DOPA), and DOPA decarboxylase, an aromatic amino acid that catalyses the conversion of DOPA to DA. Activity of tyrosine hydroxylase decreases with age in several human and rat brain structures, including the striatum, caudate, putamen, substantia nigra and nucleus accumbens (see Finch & Schnieder, 1985, for review). Dihydroxyphenylalanine decarboxylase depletion has been observed in aged human amygdala, putamen, caudate, substantia nigra and nucleus accumbens (McGeer & McGeer, 1976; see Rogers & Bloom, 1985, for review). This age related deterioration in DA synthesis is accompanied by decreased DA turnover, uptake, catabolism and general function (Rogers & Bloom, 1985).

Motor performance deteriorates rapidly with age, especially when tasks require prolonged or strenuous, coordinated movements (Marshal & Berrois, 1979; Ingram, London, Waller, & Reynolds, 1983). Poor performance of aged animals cannot be solely attributed to peripheral factors such as diminished muscle mass or increased adiposity (Marshal & Berrois, 1979). In particular, poor motor performance of aged animals is linked to age related changes in DA transmission; especially changes in striatal tyrosine hydroxylase activity (McGeer, McGeer, & Suzuku, 1977).

In summary, age appears to be correlated with central nervous system changes in DA transmission that affect motor control. As mentioned in the previous section, King et al. (1986) have shown that the variability of tongue contact time with a sipper tube is significantly higher in aged than young squirrel monkeys. Tongue extension toward a sipper tube is regulated by activity in the ventral portion of the hypoglossal nuclei and by the striatum. Drastic changes in dopaminergic systems with age are most pronounced in the striatal region and result in an interference with motor performance. This interference with motor performance undoubtedly affects licking behavior and may be evidenced by a greater variability in tongue contact times in aged subjects.

Gustatory Preferences and Hedonic Affect

Hedonic assessment of gustatory stimuli is vulnerable to alteration by the subject's physical state, degree of satiety and previous experience with the gustatory stimulus. It is also a function

of stimulus intensity. Early studies suggested that preference ratings are biphasic with stimulus intensity; as stimulus intensity rises above threshold, pleasantness ratings increase to a peak, level off, and then turn down through indifference to increasing unpleasantness (see Pfaffman, 1969, for review). A change in hedonic assessment, from pleasant to unpleasant as stimulus intensities increase, has been documented for salty, bitter and sour substances; however, responses to sweet stimuli do not always follow this pattern (see Pfaffman, 1982, for review). If subjects ingest successive sweet stimulus portions, judgments of pleasantness decrease throughout the trials. If portions are tasted and rated, but not swallowed, the rating of pleasantness increases with stimulus intensity to a stable plateau (Cabanac, 1979). Thus, postingestional effects seem to play a significant role in affective judgments of sweet stimuli.

Hedonic concepts have been criticized as explanations for positive responses toward stimuli by nonhuman species because the ratings of pleasantness are not direct. A number of behavioral measures have been used to assess hedonic affect in animals. The classic method is the two-bottle preference test developed by Richter and Campbell (1940) in which an animal is provided with two calibrated drinking tubes, one containing taste solution and the other plain water, for 24 consecutive hours. The magnitude of preference for a suprathreshold concentration is given by the relative amounts of the stimulus solution consumed over water intake. In this experimental paradigm, preference functions for sweet stimuli are biphasic with

stimulus intensity; however, postingestional effects cannot be excluded as an explanation for the decline in preference at high molarities. If a sweet stimulus is presented alone, and intake is restricted by limiting access to the stimulus, designing short test sessions or performing an esophagogastrotomy on the subject, preference functions do not decrease as sugar concentration increases (Pfaffman, 1982). These results seem to indicate that the presence of a biphasic preference function for sweet stimuli is a result of postingestional effects. An alternative explanation is that the highest stimulus intensities used in testing are not extreme enough to expose a biphasic preference function. The stimulus solutions used are generally restricted to within 0.03 and 1.00 M concentrations.

Very little research has focused on changes in hedonic evaluation with age. Dye and Koziateck (1981) reported that while young and aged humans rated suprathreshold sucrose solutions the same in intensity, their evaluations of pleasantness were significantly different. Young subjects rated sucrose solutions from 0.125 to 0.250 M concentration of increasing pleasantness and ratings dropped off monotonically as sucrose intensities increased beyond the 0.25 M concentration. This contrasted with the judgments of aged (over 65) subjects who continued to rate solutions increasingly pleasant until concentrations exceeded 1.00 M. It is unlikely that these biphasic preference functions are due to postingestional effects because test sessions were very short and the total volume of stimulus solution consumed never exceeded 5 ml.

Animal research on age dependent changes in preference for reinforcing gustatory stimuli has been limited to the rat. Bloomquist and Candland (1965) measured number of tongue licks and bar presses in response to sucrose, hydrochloric acid, sodium chloride and quinine hydrochloride solutions in young and aged rats who had been water-deprived for 15 hours. In all test conditions, the aged rats made fewer responses than the young rats. These results are difficult to interpret because the age differences may be due to differential motivation or performance capabilities. The results are also confounded by the extended water deprivation period. Extended water deprivation could affect the age groups differently because of activity and metabolic differences.

Martin and Fuchs (1985) tested young (8-10 month) and aged (31-33 month) rats in several four-day, two- and three-bottle preference tests. No significant age differences in the pattern of long term intake of several concentrations of glucose or saccharin solutions were observed. Both age groups increased number of responses as stimulus intensity increased. Even though the test sessions were very long, glucose consumption was not affected by postingestional factors. There were no age differences between the preference functions for glucose or saccharin; however, the stimulus concentrations never exceeded 1.00 M.

Hedonic evaluation may be mediated by central nervous system dopaminergic pathways (Wise, 1982). The anhedonia hypothesis, proposed by Wise, Spindler, deWit, and Gerber (1978), suggests that normal

functioning DA neurons are necessary for the motivational phenomena of reinforcement and for the subjective experience of pleasure which usually accompanies these phenomena. In experiments involving intracranial self stimulation, drug self administration, and operant conditioning or extinction paradigms with natural reinforcers, neuroleptics blunt the hedonic impact of rewards. At very low doses, this blunting of hedonic impact may occur without causing any significant impairment of the motor performance capabilities of the animal. This suggests that if the animal can respond, failure to do so must reflect a failure of reward to sustain response willingness.

The most likely dopaminergic neurons to be involved in reward mechanisms project from the midbrain to limbic and association cortical regions. Ventral tegmental dopaminergic cells project, in a topographical fashion, to the septal nuclei, amygdala and the frontal, cingulate and entorhinal cortices. The dorsal dopaminergic cells in the substantia nigra also project to limbic forebrain structures (Fallon, Riley, & Moore, 1978). Lesioning the ventral tegmental terminals in the nucleus accumbens seems to block the reinforcing characteristics of cocaine self administration (Roberts, Koob, Klonoff, & Fibiger, 1980) and intracranial self stimulation (Crow, 1972). These results indicate that the release of DA in various nonstriatal forebrain structures is involved in the mechanisms of reward.

As previously mentioned, age related deficits in central nervous system DA activity have been well documented. These deficits could contributed to the hedonic evaluation changes seen in the aged

human. However, motor performance deficits could also result from central nervous system dopaminergic changes. Any model of hedonic change with age must account for possible performance deficits in the aged subjects.

An animal model of age related hedonic change has not been developed because the subjects, rather than directly rating stimulus pleasantness, must produce a respondent that is operationally defined as the effect of pleasure. Differences in response frequency and duration in the age groups may be interpreted as differences in motivation or, more simply, differences in performance capability.

In summary, pleasure, response affect or hedonic judgment is difficult to evaluate. The most likely neurons to be involved in a reward mechanism are the midbrain dopaminergic neurons which project to midbrain and association cortical regions. This system is undoubtedly affected by aging and may, consequently, alter hedonic evaluations. Controversy exists over whether preference functions for sweet stimuli are biphasic with stimulus intensity. Some data suggest that preference for sweet stimuli increases with the concentration of the stimulus, reaches a plateau, but does not decrease again as it does with salty, bitter and sour substances. This stable plateau may be an artifact of the limited range of stimuli used to evaluate hedonic judgments. With the use of stimulus concentrations ranging from 0.125 to 2.000 M, a biphasic preference function for sucrose is seen in humans (Dye & Koziateck, 1981). Additionally, the peak of this function is significantly different for young and aged subjects. A shift in

hedonic evaluation is seen in the age groups, from a preference for the 0.25 M sucrose solution in young subjects to a preference for the 1.00 M solution in aged subjects. This shift in hedonic affect is similar to that seen after the administration of neuroleptic drugs in animals.

Rationale for Experiments

The foregoing sections have detailed variables that influence licking behavior in response to gustatory stimuli. The purpose of this study is to partition and describe the effects of these variables on licking by young and aged squirrel monkeys. With the use of sensitive and precise measures of licking behavior, an animal model of age-related changes in oral motor performance and hedonic affect may be developed.

Regulation of overall fluid ingestion in the rat (Smith, Castanguay, Foster, & Bloom, 1980) and squirrel monkey (King et al., 1986) is mainly accomplished through macrobehavioral changes (length of, number of and pauses between bursts). However, some research has indicated that lick rate, a microbehavioral measure, helps regulate fluid ingestion and may be used as an indication of preference for test stimuli in rats (Cone, 1974). This change in lick rate will not necessarily occur in all animals. King et al. (1986) showed that young and aged squirrel monkeys, licking in response to sucrose solutions that ranged in concentration from 0.30 to 1.00 M, demonstrated a constant lick rate within and between test sessions. Lick rate remained constant across all molarities, despite macrobehavioral

evidence of preference changes. However, it is important to note that constant lick rates do not necessitate constancy of other microbehavioral measures. Aged squirrel monkeys display significantly greater tongue contact variability than young animals. Additionally, there is no evidence to indicate that rate constancy requires the relationship between tongue contact and tongue off times to be uniform or predictable. Therefore, analysis of all micro- as well as the macrobehavioral components of licking is necessary for a full description of fluid consumption regulation.

The experiments described in this paper will extend the work done by King et al. (1986) and demonstrate micro- and macrobehavioral characteristics of licking by young and aged squirrel monkeys in response to both low and high molarity sucrose solutions. Age differences in gustatory preference thresholds for sucrose will be evaluated in phase I of the research, using a two-bottle choice procedure similar to that developed by Richter and Campbell (1940). Following this, licking responses to sucrose solutions will be measured in two separate experiments: one with low (phase II) and one with high (phase III) molarity sucrose concentrations. In order to disclose a possible biphasic preference function, the low intensity concentrations will range from 0.00 to 1.75 M and the high intensity concentrations will range from 1.00 to 3.00 M. Postingestional variables will be controlled by minimizing the length of test sessions and by measuring number of grams of sucrose, as well as volume of fluid, consumed in each molarity condition. Changes in the magnitude of micro- and

macrobehavioral licking measures across all test conditions will be used to interpret motor performance capabilities. A detailed composite of tongue movement patterns will be obtained with a computerized lickometer, accurate to within 1 ms. Gustatory preferences will be inferred from the peaks in overall consumption, licking efficiency and macrobehavioral licking measures.

CHAPTER 2

METHODS

The following is a description of subjects, apparatus and procedures used in the three phases of research.

Subjects

Subjects were two groups of six squirrel monkeys (Saimiri sciureus), consisting of three males and three females. One group was aged adults (estimated ages over 15 years) and the other group was young adults (ages between 3 and 6 years). The same monkeys were used in all phases of the research. Throughout the experiment the monkeys were housed individually and kept on a 12:12 hour light:dark cycle.

Apparatus

Phase I

Sucrose taste preference threshold measurements were taken in monkeys' home cages. A 30 by 30 cm screen was mounted on the front of each cage. Two graduated water bottles (10 ml units), with stainless steel sipper spouts, were attached to the screen on the outside of the cage. The sipper spouts were inserted into the cage through two holes 10 cm apart and 28 cm above the cage floor.

Phases II and III

All lick measurements were taken from three lick stations. Lick stations were conventional animal cages (69 by 46 by 71 cm stainless steel mesh) with a sheet of 3.2 mm thick plexiglass 28 cm above the cage floor. A 50 ml graduated glass buret (0.1 ml units) was vertically mounted on the outside of the cage so that its stainless steel sipper spout (1.6 mm diameter opening) was positioned 6 mm beyond the hole in the plexiglass shield. This forced the monkeys to extend their tongues at least 9.2 mm to contact the sipper spout, but prevented mouth contact with the spout.

Contact between the animal's tongue and the metal sipper spout completed an electrical circuit through which $0.25 \mu\text{A}$ passed (5 VDC open circuit voltage, $22 \text{ M}\Omega \pm 10\%$ output impedance, resistive). This is well below the threshold of detection in rats (Weijnen, 1977). The changes in current flow were recorded by a Data General Micronova computer, giving tongue contact and tongue-off times to an accuracy of 1 ms.

Procedure

Phase I

Before the start of testing, all monkeys were trained over a one-week period to lick sucrose solutions from graduated water bottles mounted on their home cages. This training included adaptation to the four sucrose molarities used in phase I of the experiment.

Sucrose taste preference measurements were taken for 16 days. The monkeys' regular water bottles were removed at the beginning of

each test session. Each test day, two calibrated water bottles were attached to the subjects' home cages for 6 hours: one contained tap water, the other contained either a 0.025, 0.05, 0.075 or 0.100 M sucrose solution. A different presentation order for the four molarities was used for each subject within a group, with the same sequences used for both groups. The presentations were randomized with the restriction that no experimental condition be repeated on two successive days. Each sucrose concentration was presented four times to each subject. Sucrose solutions were mixed with tap water and presented at room temperature (25°C). Fluid intake was measured every hour and fresh solutions were provided as necessary. All monkeys were fed one half of their daily ration of moist monkey chow 2 hours before testing. After each test, each monkey received a small portion of fruit, vegetable or egg and one half their daily ration of moist monkey chow.

Phase II

Three monkeys were randomly selected and housed individually in the lick stations for 8 training days and 16 testing days. Before the start of testing, all monkeys were trained over an 8-day period to lick sucrose solutions from burets mounted on the lick stations. This training included adaptation to the eight sucrose molarities used in phase II of the experiment. All monkeys had previous experience licking sucrose solutions in the lick stations.

Lick measurements were taken using sucrose concentrations of 0.0, 0.25, 0.5, 0.75, 1.0, 1.25, 1.5, and 1.75 M. Sucrose solutions were

mixed with tap water and presented at room temperature (25°C). Tests were conducted at 8:00 a.m. and 3:00 p.m. 5 days a week. Each of the sucrose solutions was presented on two morning tests and two afternoon tests for each monkey. The presentation was randomized with the restriction that the same molarity not be presented to any monkey in two consecutive tests. Additionally, no two monkeys received the same molarity sucrose solution during a given test.

All monkeys were fed one half of their daily ration of moist monkey chow 2 hours before the 8:00 a.m. test. Following the 3:00 p.m. test, monkeys were given a small portion of fruit, vegetables or egg and one half of their daily ration of moist monkey chow. The monkeys' water bottles were removed 1 hour before each test and replaced after each test.

Ten minutes before each test, burets were filled to a height of 50 cm above the tip of the attached sipper tube. The burets were then installed on the lick stations with the sipper spouts turned away from the monkeys and the solution levels recorded. The test was initiated by turning the sipper tubes toward the monkeys and starting recording from the lickometers. Testing continued for 20 minutes, after which liquid levels in the burets were again read.

Phase III

The conditions in phase II remained basically the same as those in phase II with the following exceptions. Lick measurements were taken with sucrose concentrations of 1.0, 1.5, 2.0, 2.5, and 3.0 M. Each trio of monkeys was housed in the lick stations for 5 training

days and 10 testing days. Before the start of testing, all monkeys were trained over a 5-day period to lick sucrose solutions from burets mounted on the lick stations. This training included adaptation to the five sucrose molarities used in phase III of the experiment.

CHAPTER 3

RESULTS

In phases II and III, tongue contact responses were defined as tongue contacts with the sipper tube lasting no longer than 500 ms. Contact durations longer than 500 ms constituted less than 1% of all responses and resulted largely from artifacts, such as finger contact with the sipper tube. King et al. (1986) has shown that, in the squirrel monkey, frequency distributions of tongue off times have a mode of about 80 ms with a sharp decrease in frequencies of higher times. Tongue off times greater than 300 ms are clearly not part of the distribution of tongue off times within a burst, but instead indicate a break in the rhythm of licking. Therefore, a burst of licking was defined as three or more tongue contacts with less than 300 ms between each contact. Tongue off times exceeding 300 ms were defined as a pause in licking. Single and double licks were included in data for computation of means and standard deviations of tongue contact and tongue off times.

The standard deviations of tongue contact times, standard deviations of tongue off times, correlations between tongue contact and following tongue off times, and correlations between tongue off and following tongue contact times were obtained for each monkey and then used as additional dependent variables for analysis of variance.

Phase I

A sucrose taste preference threshold for each monkey was defined as the estimated molarity at which 75% of the test solutions consumed was sucrose water and 25% was plain water. To determine this threshold with maximum accuracy, the proportions of sucrose water consumed by each monkey, at each molarity, were converted to z scores. Graphs, for each monkey, of the relationship between the resulting z scores and sucrose molarities were highly linear: a result consistent with the phi-gamma hypothesis (Gilford, 1954). The linear function will occur if the relation between untransformed percentages and molarity is approximated by a normal ogive. The best fitting straight line was calculated and used to estimate the molarity corresponding to a 75% preference threshold ($z = 0.6745$) for each monkey.

Young and aged monkeys did not differ significantly in taste preference thresholds for sucrose (mean of aged = 0.033 M, mean of young = 0.049 M; $t(10) = 1.058$, $p > 0.2$). There was also no significant age difference in the slopes of the regression lines used to estimate these thresholds (mean slope of aged = 13.29, mean slope of young = 17.44; $t(10) = 1.106$, $p > 0.2$) or in the correlations of z scores with their corresponding sucrose molarities (mean r of aged = .8154, mean r of young = .8732; $t(10) = 0.909$, $p > 0.2$).

Phase II

Neither sex of the monkey nor time of testing had a significant effect on any of the dependent variables. Therefore, sex and testing time were not included as variables in the following analysis.

Motor Performance

While age had no significant effect on the correlations of tongue off with following tongue contact times, the correlations of tongue contact with following tongue off times was significantly stronger in the aged (mean $r = 0.24$) than the young (mean $r = -.09$) monkeys ($F(1,10) = 5.41$, $p = .0423$). In aged monkeys long tongue contacts were followed by short tongue off times and vice versa. The correlations of tongue contact with following tongue off times were significantly higher than the correlations of tongue off with following tongue contact times in the aged ($t(5) = -8.49$, $p < .001$) but not in the young monkeys ($t(5) = -2.32$, $p > .05$). In other words, the only strong correlation was between tongue contact and following tongue off times in the aged monkeys.

The aged monkeys displayed significantly larger standard deviations of their tongue contact times than the young monkeys (mean of young = 29.6 ms, mean of aged = 42.8 ms; $F(1,10) = 5.44$, $p = .0419$). Note that these are the mean standard deviations of tongue contact times within monkeys, not the standard deviations across monkeys, within groups. Additionally, as sucrose concentration increased, the standard deviations of tongue contact times increased in the aged monkeys more than the young animals yielding a significantly age by molarity interaction ($F(7,70) = 2.91$, $p = .009$) (Fig. 5). The two age groups did not differ significantly in mean rate of licking (4.45 lick/sec) (Fig. 6), mean tongue contact time (141.5 ms), mean

Fig. 5. Mean Standard Deviations of Within Subject Tongue Contact Times for Young and Aged Monkeys in Phases II and III

Fig. 6. Mean Licks per Second (Rate) by Young and Aged Monkeys in Phases II and III

tongue off time (80.2 ms) or standard deviation of tongue off time (26.3 ms). These variables were also unaffected by molarity.

Consummatory Performance

The volume of fluid consumed, grams of sucrose consumed, number of licks, number of licking bursts and total time spent bursting increased monotonically for both age groups between the 0.0 and 1.0 M conditions. At concentrations higher than 1.0 M, the aged monkeys' consummatory activity continued to increase, while that of the young monkeys decreased. This disparity resulted in significant age by molarity interactions for volume of fluid consumed ($F(7,70) = 3.12$, $p = .002$) (Fig. 7), grams of sucrose consumed ($F(6,60) = 2.86$, $p = .0612$) (Fig. 8), number of licks ($F(7,70) = 2.45$, $p = .0264$) (Fig. 9), number of bursts of licking ($F(7,70) = 2.5$, $p = .0237$) (Fig. 10), and total time spent bursting ($F(7,70) = 2.46$, $p = .026$) (Fig. 11).

Licking Efficiency

Measures of licking efficiency were profoundly impaired in the aged monkeys. Aged monkeys consumed significantly less per lick (mean of aged = 0.003 ml/lick, mean of young = 0.005 ml/lick) ($F(1,10) = 5.64$, $p = .0390$) and less per second of time spent bursting (mean of aged = 0.013 ml/sec, mean of young = 0.022 ml/sec) ($F(1,10) = 9.11$, $p = .0129$) than the young monkeys. As molarity increased, the amount consumed per lick ($F(7,70) = 3.61$, $p = .0022$) (Fig. 12) and per second of time spent bursting ($F(7,70) = 5.84$, $p < .0001$) (Fig. 13) decreased across all

Fig. 7. Mean Fluid Volume Consumption by Young and Aged Monkeys in Phases II and III

Fig. 8. Mean Grams of Sucrose Consumed by Young and Aged Monkeys in Phases II and III

Fig. 9. Mean Number of Licks per Testing Session by Young and Aged Monkeys in Phases II and III

Fig. 10. Mean Number of Licking Bursts by Young and Aged Monkeys in Phases II and III

Fig. 11. Mean Length of Licking Bursts by Young and Aged Monkeys in Phases II and III

Fig. 12. Mean Amount of Fluid Consumed During Each Lick by Young and Aged Monkeys in Phases II and III

Fig. 13. Mean Amount of Fluid Consumed During Each Second of Licking by Young and Aged Monkeys in Phases II and III

monkeys. The interaction between age and molarity was not significant for any licking efficiency measures.

Phase III

As in phase II, neither sex nor time of testing had a significant effect on any of the variables. Therefore, sex and time of testing were not included as variables in the following analysis.

Motor Performance

Consistent with the results found in phase II, molarity and age had no effect on mean tongue contact times (mean = 152.9 ms), mean tongue-off times (mean = 73.0 ms), standard deviations of tongue-off times (mean = 26.2 ms) or correlations between tongue-off and following tongue contact times (mean = $-.061$). Aged monkeys continued to display significantly higher standard deviations of tongue contact times (mean of aged = 55.8 ms, mean of young = 31.5 ms [Fig. 5]; $F(1,10) = 9.82$, $p = .0106$) and stronger correlations between tongue contact and following tongue-off times than young monkeys (mean r of aged = $-.236$, mean r of young = $-.021$; $F(1,10) = 15.53$, $p = .002$). A significant difference between the correlations of tongue contact with following tongue-off times and tongue-off with following tongue contact times was seen only in the aged monkeys ($t(5) = 11.77$, $p < .001$).

Unlike the results in phase II of the research, age and molarity significantly influenced licking rate. As molarity increased, the rate of licking decreased more in the aged than the young monkey,

yielding a significant age by molarity interaction ($F(4,40) = 3.31$, $p = .0197$) (Fig. 6).

Consummatory Performance

Age and molarity affected the volume of fluid consumed, grams of sucrose consumed and number of licking bursts. As molarity increased, young monkeys displayed a steady decrease in consumption and number of bursts, whereas aged monkeys displayed an increase in these variables. This resulted in a significant age by molarity interaction for volume of fluid consumed ($F(4,40) = 2.78$, $p = .039$) (Fig. 7), grams of sucrose consumed ($F(4,40) = 3.24$, $p = .021$) (Fig. 8), and number of licking bursts ($F(4,40) = 3.81$, $p = .010$) (Fig. 10).

Unlike the results in phase II, increases in molarity produced mildly significant decreases in total time spent bursting ($F(4,40) = 2.60$, $p = .046$) (Fig. 11), and in the total number of licks ($F(4,40) = 3.88$, $p = .009$) (Fig. 9) across all monkeys.

Licking Efficiency

Age and molarity had no effect on the amount consumed per lick or the amount consumed per second of bursting. This differs from the results of phase II, in which aged monkeys exhibited profound efficiency impairments when compared to young monkeys (Figs. 12 and 13).

CHAPTER 4

DISCUSSION

In this experiment, young and aged squirrel monkeys displayed strikingly different sucrose molarity preferences. Taste preference thresholds were remarkably similar in the two age groups. At low sucrose concentrations, young monkeys exhibited higher macrobehavioral consumption measures (number of licks, bursts of licking, milliliters of fluid and grams of sucrose consumed, and length of bursting) than the aged monkeys. This effect was reversed in the high molarity conditions. Consumption by young monkeys increased as molarities increased from the 0.0 to 1.0 M condition, but consumption decreased in conditions that exceeded the 1.0 M concentration. This contrasts with the behavior of the aged squirrel monkeys, whose consumption increased until sucrose solutions exceeded the 1.5 to 2.0 M concentrations. The profound increase in preference displayed by aged monkeys toward high molarity sucrose solutions resulted in the exhibition of several macrobehavioral consumption measures that were greater than any of those displayed by young monkeys at any molarity. Since taste preference thresholds were independent of age, the shift in preference at high molarities may be attributed to changes in hedonic evaluation. If Wise (1982) is correct in assuming that normal functioning CNS dopaminergic neurons are necessary for the subjective experience of pleasure, this change in hedonic evaluation by the aged monkeys may

indicate that age dependent decreases in DA are blunting the hedonic impact of reinforcement.

Macrobehavioral consumption measures clearly showed age dependent preference functions that were not monotonically increasing to a stable plateau. The peaks in consumption undoubtedly resulted from hedonic preference rather than some ambiguous postingestional factor, such as satiation. This is confirmed by the finding of age dependent inverted U-shaped preference functions for total grams of sucrose consumed across molarity conditions. If postingestional factors were solely responsible for reduced fluid intake in the high molarity conditions, the number of grams of sucrose consumed across these conditions should have remained relatively constant. In the present case, both age groups consumed significantly fewer grams of sucrose when solutions exceeded the 2.0 M concentration. One possible explanation for the reduction in grams of sucrose consumed at molarities exceeding 2.0 M is that the viscosity of high molarity sucrose solutions interfered with fluid ingestion. However, a reduced number of licks in the high molarity conditions demonstrates that decreased consumption measures are a function of diminished effort to obtain fluid, rather than impeded fluid access resulting from changes in fluid viscosity. Additionally, at the testing temperature (25°C), all sucrose molar concentrations used in the experiment flowed freely from the sipper spouts.

Both age groups increased their fluid consumption by increasing number of licks, number of licking bursts and total time spent licking.

However, the fluid consumption measures which indicate a preference shift in the aged monkeys are remarkable considering the age dependent motor performance changes that are exacerbated in the high molarity conditions. Consistent with the findings of King et al. (1986), rate of licking was not impaired in the aged monkeys for low molarity sucrose solutions (phase II). However, in the high molarity conditions, lick rate was significantly lower in aged than in young monkeys. Aged monkeys also showed more variability in tongue contact times and this variability increased with sucrose concentration. In other words, in aged monkeys, the licking cycle (tongue contact to following tongue contact) duration increased, the variability of tongue contact times within this cycle were greater, and the magnitude of both these measures was positively related to sucrose concentration. These microbehavioral changes were conspicuously absent in the young monkeys.

The effect of decreased rate of licking by the aged monkeys on sucrose consumption is unclear. Changes in licking rate are controversially interpreted as indicating changes in preference for stimulus solutions (Halpern, 1975). In the present case, if licking rate were used to define preference, young monkeys would show a peak preference for the 0.5 M sucrose concentration. Aged monkeys would show a peak preference for water, with a generally linear decrease in preference for all sucrose solutions as concentrations increased. In view of the taste preference threshold results from phase I of the experiment, and considering the increased consumption measures produced by the aged monkeys in high molarity conditions (phase III), the licking

rate interpretation of preference is clearly invalid for squirrel monkeys.

The cause, as well as the effect, of licking rate changes in the aged squirrel monkey is difficult to interpret. Rate changes may result from fatigue that is exacerbated by the increased viscosity of high molarity sucrose solutions. However, viscosity induced fatigue would also be antagonistic to the expression of a preference for high molarity sucrose solutions. Aged monkeys consume more, lick for longer periods of time and produce a greater number of licks in high than in low molarity conditions. These increased consumption measures are inconsistent with fatigue as an explanation for rate change. Additionally, although aged monkeys showed deficits in measures of consumption efficiency (amount drunk per lick and drunk per second of bursting) in low molarity conditions (phase II), there were no age differences in efficiency measures in the high molarity conditions (phase III). This could indicate that, for the aged monkeys, lower licking rates actually facilitate licking efficiency.

The increased tongue contact variability and deficits in licking efficiency produced by aged monkeys may be related to age dependent changes in central nervous system dopaminergic pathways. Because the monkeys were required to extend their tongues at least 9.2 mm to make contact with the sipper tube, variability in tongue contact with the tube could result from difficulty in tongue extension. Licking efficiency might also be disrupted by changes in tongue extension. As stated in the introduction, changes in tongue extension and impairments

in licking efficiency accompany lesions to the zona incerta, globus pallidus, central amygdaloid complex and lateral hypothalamus. Treatment of these same areas with 6-hydroxydopamine also produces a reduction in tongue extension and licking efficiency (Brimley & Mogenson, 1979). Since dopaminergic activity is impaired in the aged, it is possible that the changes in tongue contact variability and licking efficiency in the aged monkeys resulted from functional dopaminergic alterations in one of the aforementioned systems. The relationship between tongue extension capability, tongue contact variability and licking efficiency should be further investigated.

Aged monkeys differed from young monkeys on one motor performance measure that was not affected by sucrose molarity: the correlation of tongue contact with following tongue off times. Tongue-off times were not correlated with following tongue contact times in any of the monkeys and, in young monkeys, tongue contact time was uncorrelated with following tongue off time. In aged monkeys, a significant negative correlation between tongue contact and following tongue off times was produced in every test session, by every monkey. A relationship between tongue contact and following tongue off time was conspicuously absent in the young monkeys.

When the correlation of tongue contact with following tongue off times is considered simultaneously with the other age dependent motor performance changes, an interesting pattern of licking behavior is defined in aged squirrel monkeys. Regardless of the tongue contact duration exhibited by the aged monkey, the lick cycle (tongue contact

to following tongue contact time) remained constant within each test session. In other words, when tongue contact time was long, the following tongue off time was short and vice versa. This relationship held true for all molarities and, thus, for all rates of licking (cycle lengths) and all variabilities of tongue contact time.

The persistent negative correlation between tongue contact and following tongue off times in the aged monkeys is difficult to interpret. Given a specific tongue contact duration, the following tongue off time was fairly obligatory in the aged monkeys. It follows that, if a licking cycle exists, this cycle begins with tongue extension and lasts until the following tongue extension. The duration of the intervening events, between tongue extensions, is limited by the cycle length. It is possible that the correlation between tongue contact and following tongue off times indicates an obligatory licking cycle present in all monkeys, but that is masked by some voluntary or cortical control mechanisms in the young monkeys. Evidence for rhythmic behavioral generators that can be overridden or masked by higher order neural processing exist in many animals (see Delcomyn, 1980, for review).

It would be interesting to evaluate the effects of viscosity, independent of hedonic quality, on micro- and macrobehavioral licking measures. A nonviscous sweetener could be used to evaluate hedonic effect independent of viscosity; however, to evaluate viscosity, without any interaction of taste quality, would require a stimulus solution thickened by a tasteless, odorless chemical. This requirement seems

forbidding. As an alternative, one could use a non nutritive thickening agent and a non viscous sweetener to design an experiment which partitions the effects of viscosity from the effects of hedonic quality. Four stimulus conditions could be used, such as plain water, water thickened with the non-nutritive agent, water sweetened with the non-viscous sweetener and water that is both sweetened and thickened. A comparison of these four conditions would give a better understanding of the effects of viscosity and hedonic quality on licking behavior.

Further investigation of dopaminergic effects on hedonic evaluation and motor performance is an obvious successor to the present experiments. Hedonic preference shifts are clearly indicated by horizontal displacement of the preference curves to encompass either higher or lower molarity solutions. Motor performance deficits are reflected by decreased magnitude in the preference functions. Administration of neuroleptics, in a paradigm similar to the present one, would indicate if CNS changes in DA were responsible for the hedonic shift seen in aged monkeys. The comparison of neuroleptic induced, with age induced, motor performance changes would be enlightening. Microbehavioral measures of licking could be a potentially sensitive measure of tardive dyskinesia.

In summary, the lickometer apparatus used in the present set of experiments makes it possible to separate the effects of motor performance from the effects of preference on licking behavior. Aged monkeys displayed both hedonic and motor performance differences from young monkeys when licking in response to sucrose solutions ranging in

intensity from 0.0 to 3.0 M concentrations. These differences were independent of taste preference thresholds for sucrose. The cause of the age dependent changes seen in licking behavior are unclear; however, altered functioning of CNS dopaminergic systems is a possible explanation and should receive further research.

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