HEDONICS OF TASTE-ODOR MIXTURES IN HUMANS:

A STUDY OF FLAVOR PERCEPTION

By

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A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

DOCTOR OF PHILOSOPHY (1995) McMASTER UNIVERSITY

(Psychology) Hamilton, Ontario

TITLE: Hedonics of Taste-Odor Mixtures: A Study of Flavor Perception

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NUMBER OF PAGES: xi, 135

ABSTRACT

Most research done on taste and smell has examined the two systems in isolation. This is unfortunate since it is the combination of taste and smell that determines flavor, perhaps the most salient characteristic of food for humans. Furthermore, assessment of flavor pleasantness is integral to food choice and intake. Yet, despite the importance of the hedonic dimension of flavor, most empirical studies of flavor have focused on the intensity of taste-odor mixtures, not their hedonic value. Thus, the experiments that comprise this dissertation focused on the pleasantness of taste-odor mixtures.

Three food odors (chocolate, raspberry, and popcorn) at five concentrations were utilized as stimuli. Experiment 1 replicated the psychophysical functions that have been reported in the literature relating stimulus strength, perceived intensity, and perceived pleasantness with these three odors. Experiments 2 and 3 demonstrated that a negative taste experienced concomitantly with odor reduces odor pleasantness ratings. Experiment 4 established that it is unlikely that this effect results from a general negative affective state since an aversive non-gustatory stimulus did not produce a similar reduction in odor pleasantness.

Subjects in Experiments 1 through 4 were required to report odor pleasantness. However, in these studies it was not clear whether subjects were reporting a downward shift in odor hedonics, a negative hedonic response to taste, or their hedonic response to the taste-odor mixture. Experiment 5 required subjects to be analytical about their hedonic response to taste-odor mixtures. They were instructed to report their independent hedonic response to the odor, taste, and overall sensation. Experiment 5 demonstrated that when subjects are explicitly required to be analytical

about the hedonic experience of flavor, they can differentiate between a taste they do not like an odor that is neutral or pleasant to them. However, when not instructed to be analytical, subjects tend to fuse the components into a whole percept or "gestalt."

Metabolic changes modulate the pleasantness of sensation, a phenomenon known as alliesthesia. It is clear that hunger increases the pleasantness of sweet taste relative to the sated state, but the effect of metabolic state on odor hedonics is unclear. Thus, in Experiment 6, I first replicated alliesthesia for sweet taste and demonstrated that aversive tastes are not made more pleasant by hunger. More importantly, though, Experiment 6 showed a clear odor alliesthesia effect; that is, a reduction of odor pleasantness when subjects are full relative to hungry.

It has been suggested that odor hedonics are more labile than taste hedonics. Since no studies have empirically compared the modulation of taste-odor mixtures by hunger and satiety, it is not known whether alliesthesia is greater for the taste or odor component of flavor. Experiment 7 required subjects to be analytical about their hedonic experience of taste-odor mixtures when hungry and full. General alliesthesia was observed, that is, hedonic ratings of all stimuli were lower in the hungry state relative to the sated state. The alliesthesia effect did not depend on whether subjects rated odor alone, taste alone, or a taste-odor mixture. Thus, no distinction could be made between taste or smell in terms of degree of hedonic modulation by metabolic state.

The main goal of these experiments was to explore the hedonics of taste-odor mixtures in humans. These examinations increase our understanding of the chemical senses in general and may be particularly pertinent to understanding the relationship between food hedonics and ingestive behavior. Future work should concentrate on whether food hedonics as studied psychophysically in the manner of the experiments comprising this dissertation predict food preferences or intake. Additionally, the influence of cognitive factors (e.g. identification of the odor as food related) on the hedonics of taste-odor mixtures should be determined.

ACKNOWLEDGMENTS

Putting aside all schmaltz, I must thank the following people:

To Harvey Weingarten: Thanks for being a mensch. I appreciate your efforts and hope that your daughters receive treatment similar to that which you bestowed upon me.

To Ron Racine and Shep Siegel (members of my supervisory committee): Thank you for your helpful suggestions and contributions to my thinking around this thesis.

To Psychology Department Staff (to numerous to mention by name, but too important to forget): I think those guys in the wine commercial said it best: "I thank you for your support."

Thanks to Jean Dumond at International Flavors and Fragrances Canada for her generous donation of the odors used in this dissertation.

There is a comfort in the strength of love;
'Twill make a thing endurable, which else
Would overset the brain, or break the heart.
William Wordsworth

To Family and Friends (and darlings, you know who you are): It is certain that my brain would be 'overset' and my heart broken if not for the love of family and friends. I hope that I have shown gratitude and thoughtfulness toward you every day. Thanks for...well, everything. And now for something completely different.

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GENERAL INTRODUCTION

Experiments in physiological psychology examine the relationship of, and attempts to show causal links between, biological and behavioral variables. Our understanding of eating behavior has been strongly influenced by the physiological psychology tradition. Researchers have found it useful to divide eating behavior into food choice (what is eaten) and intake (how much is eaten). It is acknowledged that food choice and intake are influenced by metabolic signals originating from the physiological states of repletion or depletion (Striker, 1984). Researchers have also acknowledged the impact of experience with food on ingestive behavior. A specific type of experience with food, evaluation of sensory properties, can exert a strong control over eating behavior. The importance of a food's sensory properties may seem self-evident to food lovers everywhere, but it has not been dealt with empirically to any appreciable extent.

The sensory properties of food, sight, taste, smell, texture, and temperature are major aspects that dominate the experience of eating (Bartoshuk, 1991b). Two of these, taste and smell, have been studied extensively, but not by researchers interested in eating. The scientists who have studied taste and smell have tended to come from the psychophysics tradition, which addresses the relationship between the physical and perceived world. Also, chemosensory psychophysics has tended to utilize simple tastes and odors rather than the more complex stimuli of food mixtures. In addition, that field has tended to focus on perceived intensity, whereas hedonics has received less attention. A great deal of what is known about taste and smell comes from the field of psychophysics. To understand how taste and smell influence food choice and intake, one must understand the biological and behavioral variables that control ingestion, the physiology of the chemical senses, the psychophysics of chemosensory mixtures, and perception of taste-odor mixtures in humans. The remainder of this chapter will attempt to review literature that "bridges the gap" between what is known about the physiological psychology of eating and chemosensory perception.

I. INFLUENCES ON FOOD CHOICE AND INTAKE

A variety of factors influence ingestive behavior. A complete review of the control of eating is beyond the scope of this dissertation. However, the experiments reviewed here serve to introduce some important concepts and terminology. The section that follows briefly reviews literature on the biological, experiential, and sensory factors that control ingestive behavior that will be relevant to the specific experiments in this dissertation.

A. Biological Influences

1. Innate Hedonic Response to Taste : An important biological determinant of food choice in omnivores (including rats and humans) are innate responses to certain taste qualities. Taste has been suggested to act as a "gateway" (Scott, 1991) into the body, and as such, some have argued that an innate acceptance of nutritive substances and rejection of toxic substances would be adaptive for omnivores (Beauchamp & Mason, 1991). While some differences exist among species, most neonate mammals readily receive sugar solutions into the oral cavity (see Kare &

Beauchamp, 1984 for a review). Human neonates show sucking, positive facial expressions and increased intake of sugar solutions compared to water (Desor, Maller, & Turner, 1973; Steiner, 1977; Rosenstein & Oster, 1988). Some researchers have suggested that unlearned acceptance for sweet taste reflects evolved calorie-recognition (Jacobs, Beauchamp, & Kare, 1978).

In nature, bitterness is often correlated with toxicity. Thus, the unlearned rejection of bitter tasting substances demonstrated by most species is thought to reflect an evolved toxin-detecting mechanism (Beauchamp & Mason, 1991). Human neonates show tongue protrusions and other signs of active rejection when a bitter taste is in their mouth (Steiner, 1977; Rosenstein & Oster, 1988). Responses to sour and salty tastes at birth are less clear (Crook, 1987). Innate taste biases are not fixed, however. Experience and context shape acceptance and rejection of taste in children and adults (see Beauchamp & Cowart, 1985 for a review of taste preference development).

2. Repletion / Depletion: An important biological determinant of food intake is metabolic state. Nutritional repletion induces peripheral signals that contribute to the psychological state known as "satiety" (fullness). Peripheral satiety signals include gastric distention, intestinal absorption of nutrients, hepatic storage of nutrients, and alterations in insulin / blood glucose levels (Stricker, 1984). Many of the peripheral satiety signals are transmitted to the central nervous system via the vagus nerve (tenth cranial nerve) and neuroendocrine events that are not yet fully understood. It is believed, however, that sensory afferents from the periphery are integrated in a synergistic fashion as a negative feedback signal that controls amount eaten at a particular meal (Smith, Greenberg, Corp, & Gibbs, 1990).

Nutritional depletion induces an opposite psychological state, hunger. In the post-absorptive state, short-term energy stores are spent, and the organism seeks to correct the energy deficiency by initiating a meal. The biological mechanisms underlying hunger are not as well understood as those of satiety. A specific dynamic of blood glucose, (specifically, a transient dip and then rise) has been shown to be causally related to meal initiation in the spontaneously eating rat (Campfield & Smith, 1990). While energy depletion and transient declines of blood glucose are clearly causally linked to eating, not all instances of meal initiation are explained by these physiological states. Organisms often initiate eating before states of nutritional need (Weingarten, 1990). This observation has led to the examination of the role of other variables, especially experience and learning, in the control of eating.

B. <u>Experiential Influences</u>

1. Social Learning: Food preferences and avoidances are socially conveyed in animals (see Galef & Beck, 1990) and in our own species. Social influence and values are mechanisms which establish preferences and avoidances in humans (Rozin & Vollmecke, 1986). Families and cultures directly and indirectly transmit attitudes about what is edible (Rozin & Fallon, 1980), what foods are appropriate at certain points during the day (Birch, Billman, & Richards, 1984), and what is generally eaten or avoided by an individual (Rozin, 1988). Foods and beverages that are initially unpleasant (coffee, chili-pepper, alcohol) often become an "acquired taste" because of their association with adulthood in the culture (Rozin & Vollmecke, 1986). Children also acquire preferences for foods associated with a respected other (Birch, Zimmerman, & Hind, 1980). Therefore, through direct exposure (or lack thereof), indirect attitudinal shaping, and instrumental social rewards, human food choice is heavily influenced by social learning (see Rozin & Schulkin, 1990 for a full review).

2. Post-Ingestive Consequences: Experience with the consequences of a food also influences food selection. Pairing a flavor with calories causes that flavor to become preferred over other flavors associated with foods lacking calories (Mehiel, 1991). Similarly, pairing a flavor with a pleasant, even if non-caloric, taste will also cause rats (Fanselow & Birk, 1982) and humans (Zellner, Rozin, Aron, & Kulish, 1983) to choose that flavor in the future. Therefore, positive experiences with a food, be they based in post-ingestive consequences or sensory pleasure, influence subsequent food choice. Negative experiences also influence food selection. Foods associated with the aversive post-ingestive consequence of nausea are generally not selected in the future (Garcia, Henkins, & Rusiniak, 1974; Garb & Stunkard, 1974).

Additionally, learning about a food's post-ingestive consequences determines how much of that food may be eaten. Rats (Bernstein & Goehler, 1983) and humans (Bernstein & Webster, 1980) who associate nausea with the ingestion of a particular food subsequently consume less of that food. This type of learning, called conditioned taste aversions (CTA) is a very robust learning phenomenon (Garcia, Henkins, & Rusiniak, 1974) and represents one of the most powerful experiences humans have with food (Garb & Stunkard, 1974).

An association of a food with positive consequences, such as calories, also determines future intake. Rats (Booth, 1972) and humans (Booth, Mather, & Fuller, 1982) demonstrate "conditioned satiety." Conditioned satiety is produced when one flavor is paired with high calories while another flavor is paired with low calories. Upon reversal of the flavor cues, subjects consume more of the flavor associated with low calorie food (Booth, 1972; Booth, Mather, & Fuller, 1982). Conditioned taste aversions and conditioned satiety are just two phenomena suggesting that animals and humans learn about post-ingestive consequences of foods and can adjust how much they eat according to experience.

C. Sensory Influences

A third variable that influences ingestive behavior, and the one most relevant to the experiments in this dissertation, is a food's sensory properties. Even though the relationship between a food's sensory properties and eating behavior has not been the dominant focus of eating research, the literature that exists describes some compelling phenomena that underscore the importance of understanding the role of sensations in ingestive behavior.

1. Palatability: The evaluation of food's sensory properties along the dimension of pleasantness is known as palatability. Palatability affects whether a food is ingested or rejected. As mentioned previously, the case for innate acceptance of sweet and rejection of bitter substances is fairly strong (Steiner, 1977; Rosenstein & Oster, 1988). The addition of a non-caloric sweetener to food increases meal size or 24-hour cumulative intake of free-feeding rats (Williams & Campbell, 1961). Conversely, adulterating a food with a bitter substance will reduce intake (Ramirez, Tordoff, & Friedman, 1989) although not when physiological need is great (Naim, Brand, Kare, Kaufmann, & Kratz, 1980).

The "cafeteria diet" effect demonstrates that the sensory properties of food can have a dramatic effect on both food choice and intake. A cafeteria diet is composed of a variety of highly palatable foods presented simultaneously. Increased food intake leading to obesity can be induced in the rat by simply exposing the animal to a cafeteria diet (Sclafani & Springer, 1976). Similar effects are seen in humans (Rolls, 1979). The potency of the cafeteria diet for the induction of overeating and obesity may be based in both palatability and post-ingestive consequences and the extent to which each contributes is the subject of some controversy (Sclafani, 1989).

2. Variety: When presented with a variety of chows that only differ in odor, rats will eat more than when one type of chow is available (LeMagnen, 1967). Similarly, rats given four different flavors of wet mash successively will eat significantly more than rats given four separate presentations of unflavored wet mash (Clifton, Burton, & Sharp, 1987). The above studies demonstrate that food intake in rats is influenced by sensory variety.

Studies utilizing human subjects indicate that sensory variety increases intake via hedonic-motivational mechanisms. As humans eat a food, its pleasantness tends to decline (Rolls, 1990). A general decline in sensory pleasantness due to a change in metabolic state is called alliesthesia (Cabanac, 1971) and will be discussed in Chapter Eight. When a food is consumed to satiety, subjects report a decline in the pleasantness of the specific sensory characteristics of that food (Rolls, 1990). This phenomenon is known as sensory specific satiety. Conversely, pleasantness ratings of food increase when sensory variety characterizes a meal (Rolls, Rowe, & Rolls, 1982).

The reductions in pleasantness of the particular sensory aspects of food upon consumption do not reflect simple sensory adaptation since minimal changes in the food intensity are reported (Rolls, Rowe, & Rolls, 1982). Nor is the alliesthesia effect due strictly to physiological satiety cues since alliesthesia can be observed before significant nutritive absorption (Rolls, 1990). Additional support for a cognitive basis for alliesthesia comes from the observation that visual aspects of food are sensitive to sensory specific satiety (Rolls, Rowe, & Rolls, 1982). It is unlikely that visual characteristics of food are affected by chemosensory adaptation or metabolic state.

The effects of palatability and sensory variety on eating behavior suggest that the sensory properties of food have the capacity to drive food choice and intake. Survey data imply that sensory aspects of food are most important to eating behavior (Spitzer & Rodin, 1981; Shepherd, 1989). Additionally, laboratory studies in which humans can eat freely from many different foods have demonstrated that hedonic ratings of a food's taste and smell predict the amount of that food eaten (Rolls, Rolls, Rowe, & Sweeney, 1981). Before the impact of taste and smell on ingestive behavior can be reviewed, it is appropriate to digress briefly on the two sensory modalities, taste and smell, most relevant to eating control.

II. TASTE AND SMELL PERCEPTION

A. Taste Perception

Gustation or taste is a specialized sensory system that brings information about chemicals from outside the body to the viscera and the central nervous system (Everett, 1971). The taste system begins at the oral cavity and acts as a "gateway" into the body (Scott, 1991). Therefore, some have argued that taste is evolved to analyze the quality of chemical stimuli and mediate ingestion through communication with the visceral senses (Scott, 1991). Information from the viscera feedback on to the taste system, modifying perception and behavior (Cabanac, 1971). Regulation of nutrient intake appears to be the only function of the taste system (Bartoshuk, 1989a; Scott, 1991).

1. Taste Primaries: When food is placed into the oral cavity, salivation is elicited reflexively. Enzymes in saliva initiate the breakdown of food into smaller molecules. Once mixed with saliva, these molecules interact with the taste system and a physiological cascade begins that ultimately results in gustation. Psychological sensations evoked by taste stimuli are categorized into four primaries or qualities (sweet, sour, salty, and bitter). Classification of taste qualities not only describes human perception, but it has also guided our exploration of the transduction of taste.

i. Sweet: Many different chemical substances can evoke a sweet taste, indicating a multiple receptor system for the sweet quality. The necessary chemical component for sweet perception is a hydroxyl group most often found in organic compounds such as alcohols, sugars, glycols, aldehydes and ketones (Bartoshuk, 1988). While many different chemical substances will elicit a sweet taste, there are fairly wide differences in the quality of the sweet percept. For example, artificial sweeteners are perceived by humans to be intensely sweet, but also elicit a bitter aftertaste (Bartoshuk, 1988). Aftertastes may be caused by the binding of the substance to the taste receptors for the other qualities (Bartoshuk & Beauchamp, 1994).

Psychophysical procedures have often been used to elucidate properties of the perceptual system controlling taste. For example, the fact that a panel of well trained tasters cannot distinguish between sucrose, fructose and glucose when these natural sugars are matched for intensity suggests that the underlying physiological structure responsible for a sweet percept are the same for these substances. Another natural sugar, maltose, can be distinguished from sucrose, fructose, and glucose, therefore the receptors responsible for the transduction of its sweet taste must be different (Bartoshuk & Beauchamp, 1994). As yet we do not know how many subsets of sweet receptors exist or what the biological differences are between them.

ii. Bitter: Like sweet taste perception, bitter taste is mediated by several different receptor types. Many chemically distinct stimuli are perceived as bitter by humans, but two classes of substances are especially likely to evoke bitter taste: long chain organic molecules with a nitrogen group and alkaloids (Bartoshuk & Beauchamp, 1994). Bitterness positively correlates with lipid solubility (Kurihara & Koyama, 1972).

iii. Sour: The necessary chemical component for the sour quality is the hydrogen ion. Concentration of hydrogen ions in solution explains sour quality and intensity perception. That is, the lower the pH, the more sour the taste (Bartoshuk, 1988).

iv. Salty: In solution, salts are separated into cations (positively charged ions) and anions (negatively charged ions). The chemical component necessary for perception of salty taste is a cation (such as Na^+). Anions are inhibitory, dampening cell response to cations. Sodium chloride produces the purest salty quality because the Cl^- anion is the least inhibitory, allowing Na^+ to evoke a strong cell response (Bartoshuk, 1988). Many salts evoke other taste qualities, a characteristic related to chemical properties of the substance. For example, whether a salt is perceived as bitter depends on the size of its anion (Bartoshuk, 1988).

2. Anatomy: Most gustatory receptors are embedded in the surface of the lingual epithelium in small bumps called papillae. There are four kinds of papillae, one related to mechanical (i.e. the breakdown of food) and three to the perception of taste qualities. The three sensory papillae types are located on specific areas of the tongue and tend to be more sensitive to one of the four taste qualities (Bartoshuk, 1988). Some taste buds are located on the back on the of the soft palate, pharynx (throat), larynx, and esophagus, but most are on the tongue (Bartoshuk, 1988).

i. Receptors: A taste bud is made of receptors (taste cells) along with supporting cells in a formation very much like sections of an orange. With a diameter of 1/30 mm and a length of 1/16 mm, between thirty and eighty taste receptors are found within a single taste bud. There is a small opening where taste cells come together at the surface of the tongue called the taste pore. Coming out of the taste pore are microvilli (taste hairs), which are stimulated by saliva. Microvilli are thought to provide the receptor site for taste. Taste buds develop out of neuroepithelial tissue and rejuvenate approximately every ten days in humans (Bartoshuk, 1988).

ii. Taste Transduction: Like all sensory receptors, the internal environment of a taste cell is negatively charged relative to the outside of the cell. Researchers currently believe that adsorption of a stimulus molecule to the receptor changes the physical characteristics of the membrane so that the cell is made more permeable to ions. The cell is then depolarized by an influx of sodium into the receptor so that the cell transmits an electrical signal (Bartoshuk & Beauchamp, 1994). The activity of taste receptors is summated along taste nerve fibers. Taste fibers form the major cranial nerve trunks, which go to the brain stem of the central nervous system.

iii. Innervation of Taste: Taste fibers are interwoven among taste cells in the papillae located on the different areas of the tongue. Taste sensations, in the form of electrical signals, are carried by four cranial nerves (Guyton, 1986). Other cranial nerves provide motor control and proprioception for the oral cavity, but they will not be discussed here.

The chorda typani branch of the facial nerve (cranial nerve VII) innervates the tip and sides of the anterior tongue. The greater superficial petrosal branch of the facial nerve carries information from the front two-thirds of the tongue. Sensory fibers of the glossopharyngeal (cranial nerve IX) innervate back two-thirds of the tongue. The vagus (cranial nerve X) is responsible for visceral muscle movement and swallowing. Taste buds on the epiglottis (the epithelial flap that closes the trachea off during swallowing) are innervated by the superior laryngeal branch of the vagus. However, the innervation of other taste buds not located on the tongue is uncertain (Tortora & Anagnostakos, 1984).

A specific type of oral cavity stimulation, irritation and temperature, is carried by three branches of the trigeminal (cranial nerve V). The opthalmic branch runs over the eyes to the lacrimal gland. The maxillary branch innervates the mucosa of the nose, palate, upper teeth, upper lip, cheek, and lower eyelid. The mandibular branch innervates the front two-thirds of the tongue, lower teeth and side of the head. Irritation sensations transmitted by the trigeminal nerve elicit protective reflexes of crying and sneezing (Tortora & Anagnostakos, 1984). It has also been suggested that the trigeminal nerve could be a mechanism for the interaction of taste and odor (Hornung & Enns, 1989).

iv. Central Projections of Taste Nerves: It is apparent that taste nerves are distinct in that they innervate different regions of the oropharynx and have different paths to the brain stem. All taste fibers synapse in various sections of the nucleus of the solitary tract (NTS) in the medulla portion of the brain stem. Taste information is sent via the secondary afferent pathway for taste, which runs from the NTS in the medulla to the posteromedial ventral nucleus of thalamus (the central relay for sensory information). From the thalamus, gustatory pathways project to the cortex, specifically, the lower tip of the post central gyrus in the parietal lobe. Another major projection goes to the opercular-insular cortex. Both of these cortical areas are located deep in the sylvian fissure (a groove that runs along the side of the brain). Cortical areas responsible for processing of taste sensations are superimposed on the somatic pathways of the tongue. Taste information is also projected to the amygdala of the limbic system, which is believed to account for the emotional response to taste. One strong gustatory projection is to the lateral hypothalamus, an area which is involved in feeding regulation (Guyton, 1986).

3. Coding: Translation of electrical signals from receptors to a meaningful perception is called coding. Sensory coding is related to the two ways our nervous system represents information. *Spatial (line-specific) coding* represents a particular dimension of the stimulus as the activity of a "line" or a particular chain of neurons from receptor to brain. By monitoring the patterns of neuronal activity, researchers can observe a code and test the link between cell activity and behavior. *Temporal coding* suggests that the brain reads the timing of receptor firing, but temporal coding is more complicated than response rate. A good analogy for temporal coding is Morse Code, in which a complex temporal pulse is transmitted over a single pathway.

Theories of taste coding try to link knowledge from electrophysiological studies with knowledge of human taste perception. An early theory, the across-fiber pattern theory, promoted the idea that taste is coded spatially. As such, the overall activity level across multiple neurons is responsible for taste rather than firing from a single response pathway. Pfaffman (1941) found taste fibers in the cat responded to acid-salt and acid-quinine mixtures rather than single taste qualities. Based on this evidence, Pfaffman reasoned that the overall pattern of activity was read by the taste system. However, Pfaffman's studies and subsequent experiments supporting the across-fiber pattern theory were technically limited. With better equipment, a new set of evidence was gathered and another taste coding theory emerged.

The labeled-lines theory argues that the taste of a stimulus is comprised of responses by taste fibers specific to that quality. Electrophysiological evidence supports the existence of taste fibers that respond best to specific taste qualities, called best-type fibers (Frank, 1973). The taste quality activating a fiber predicts a lower response to the other taste qualities (Boudreau, 1974). Further studies at the level of the nerve, NTS, and parabrachial nucleus, have shown that coding by quality is the rule throughout the system (Travers & Smith, 1979; Smith, Van Buskirk, Travers, & Bieber, 1983). Neurons of the central nervous system respond less specifically than peripheral neurons. However, readers of the literature should be aware of species differences in taste neuron responding (Bartoshuk, 1988).

B. Odor Perception

1. Nutritive Functions of Odor: The role of smell in nutritive choice and intake is less apparent than that of taste. For example, while taste is easily categorized into primaries that may be directly related to the nutritive value of the substance, odor is not (Cain, 1987). Animals learn to easily perform instrumental responses when taste, but not odor, is used as a reward (Long & Tapp, 1967). In addition, olfaction appears to be the more plastic modality between the two chemical senses (Bartoshuk, 1991a). Hedonic response to some tastes is innate, but hedonic response to all odors appears to be learned (Engen, 1979; 1982). Thus, while taste may have a very specific and direct influence on ingestive behavior, the influence of smell may be more subtle. Those subtle influences involving odor and food intake that have been studied are reviewed below.

i. Role of Odor In Food Identification: In a classic study, Mozell and colleagues (1969) compared subjects' ability to identify common foods with their noses open and blocked. Identification was very poor when nasal patency was impeded. In this experiment, a liquefied food was delivered directly to the tongue and subjects were required to swirl the food around their mouth for thirty seconds before identification. Taste alone was not sufficient for the identification of many foods presented (Mozell, Smith, Smith, Sullivan, & Swender, 1969). Even identification of substances with a strong and distinctive taste or trigeminal input (e.g. lemon juice, vinegar) was impaired without nasal patency (Mozell et al., 1969). A later study estimated that food recognition with odor alone is accurate about 35% of the time and increases to only 46% with both taste and smell (Schiffman, 1977).

ii. Learning of Post-Ingestive Consequences: A second role of odor in food intake involves learning to associate an odor tag with the ultimate post-ingestive consequences of that food. It has been proposed that odor hedonics provides the chemical senses with a labile component to permit quick and specific learning of the post-ingestive consequences of food (Bartoshuk, 1989a; 1991a). For example, there is some evidence to suggest that conditioned taste aversions may be more specific to the odor component, as opposed to the taste, of a flavor. Bartoshuk and Wolfe (1990) found that subjects reporting aversions rated the odor of the food as more unpleasant than its sight or texture. Furthermore, the aversion often generalized to items with the same odor (Bartoshuk & Wolfe, 1990). Observations in the area of alcohol aversion therapy support the hypothesis that odor quality rather than taste quality is associated with negative post-ingestive consequences. If the taste quality of alcohol, which is mostly bitter, is affected by nausea, then one would expect that all types of alcohol would be avoided after association with illness. After becoming ill by one type of alcohol, however, many patients will simply switch to a type of alcohol with a different odor tag (Garb & Stunkard, 1974).

Pairing an odor with positive experiences modifies the hedonic value of the odor. Pairing of calories with a distinct odor tag produces a conditioned preference (Mehiel, 1991). An animal can learn to avoid a flavor associated with a thiamin-deficient diet and prefer a flavor associated with a thiamin-rich diet because of the effects of these diets on the body (Rozin, 1967). Therefore, negative and positive post-ingestive consequences can affect the hedonics of associated odors. The extent to which taste and odor hedonics are modified by physiological state will be discussed in more detail in Chapter 8.

iii. Effects of Olfactory Deficits: Mozell's (1969) method of blocking nasal patency was an excellent acute experimental preparation to examine the role of odor in food identification. However, questions about the role of odor in food preference and intake are elucidated by consideration of a population that suffers chronically from reductions in odor perception. One such population is the elderly.

The elderly often complain that foods "taste flat" (Cohen & Gitman, 1959). But it is clear that this reported reduction in food hedonics is, in most cases, caused by deficits in olfaction rather than taste. Substantial olfactory deficits are demonstrated by the elderly when odors are delivered prenasally (Stevens & Cain, 1985) and retronasally (Stevens & Cain, 1986). Given the earlier results of Mozell (1969), it is not surprising that reduced ability to identify foods is seen in the elderly (Schiffman, 1977). In contrast, taste perception in the elderly is quite robust. The taste perception of elderly people allowed to sample a taste using the whole mouth (rather than placing a tastant on a specific area of the tongue) is not very different from that of young people (Bartoshuk, 1989b). Thus, it has been proposed that olfactory rather than taste losses may reduce the flavor experience of the elderly and this has been suggested to be a partial account of the nutritional risk of that population (Schiffman & Warwick, 1988).

There is support for the hypothesis that olfactory losses in the elderly reduces the hedonic tone of flavor and contributes to anorexia (Schiffman & Warwick, 1988). Flavor enhancement involves chromatographic analysis of food substances, selection of odor molecules that best represent that food, and production of a chemical form of these odor molecules. Such a chemical, known as a flavor enhancer, is then added back to the original food. Thus, flavor enhancers increase the amount of volatile molecules reaching the olfactory system. The addition of flavor enhancers to food increases preference and intake in the elderly (Schiffman & Warwick, 1988). Taken together, food identification studies (Mozell et al., 1969; Schiffman, 1977) and the flavor enhancement effect in the elderly (Schiffman & Warwick, 1988) suggest that odor contributes significantly to our ability to identify a food and that odor also affects food preferences and intake.

The previous section described two nutritive functions of odor. First, odor is the primary sense used to identify and distinguish among foods. Second, odor is a sensory tag that can be associated with the consequences of ingestion. To understand the mechanisms by which odor may mediate these two important roles, it is necessary to digress, again, to a review of the anatomy and physiology of the olfactory system.

2. **Anatomy:** The particular chemical properties necessary for specific olfactory sensations are not known. However, all olfactory stimuli do have three physical characteristics in common. First, all olfactory stimuli are somewhat volatile so that their molecules can be actively sniffed into the nostrils. Second, olfactory stimuli must be water-soluble in order to pass through mucus that coats the olfactory epithelium. Third, olfactory stimuli are lipid-soluble and can penetrate olfactory cilia, the long, hair-like structures composed of lipids that emanate from olfactory receptors (Guyton, 1986). Most olfactory stimuli are organic molecules. In spite of the constraints on molecules in order for them to act as olfactory stimuli, it is estimated that half a million odors can be detected and discriminated by humans (Cain, 1988)!

In terms of its non-sensory function, the nose has been likened to an air conditioner that heats / cools, filters, and moistens air (Cain, 1988). The respiratory epithelium lining the nose performs these functions and has nothing to do with olfaction. Olfactory epithelium (also called the olfactory mucosa or olfactory membrane) is physiologically and functionally very different than the respiratory epithelium. The olfactory epithelium is located very high up in both nostrils and covers a surface area of 2-4 square centimeters in each nostril. For olfactory stimulation to occur, air must be forced upward into the superior region of the nostril so that receptors can be reached, an action called sniffing. Olfactory epithelium consists of basal cells, sustentacular cells (supporting cells), the glands of Bowman (which secrete mucus onto the olfactory membrane), and receptor cells (olfactory cells). Basal cells are the foundation of the mucosa. Interspersing sustentacular cells form a tight seal around the base of olfactory cells, isolating the receptors functionally and anatomically (Guyton, 1986).

i. Receptors: Approximately 100 million olfactory receptors are present in the epithelium. Olfactory receptors are bipolar nerve cells, and therefore derived from central nervous system tissue. A long, hair-like structure (cilium) comes out of each olfactory cell into the mucosa. Cilia lack inherent motility and only move in response to air flow into the superior region of the nasal cavity. Cilia are critical to olfaction since they are the portion of the cell that reacts with odor molecules (Guyton, 1986).

Once odor molecules are present in the upper region of the nostril, they become embedded in the mucus where they meet with the proteinacious receptor sites on cilia. Upon receptor stimulation, the cell depolarizes and the subsequent action potentials are transmitted as a nerve impulse. Axons from olfactory receptors join as a bundle of approximately 1000 fibers, forming the olfactory nerve (cranial nerve I). Unlike other sensory systems, no synapse intervenes between olfactory receptors and the axon of the nerve that transmits olfactory information (Cain, 1988).

ii. The Olfactory Bulb: The bundles of axons that form the olfactory nerves exit the nasal cavity through the ethmoidal foramen, the small holes in the ethmoid bone of the skull, and up to the olfactory bulb (Cain, 1988). The synapse of olfactory nerves and dendrites from mitral and tufted cells in the olfactory bulb form a glomerulus. About ten thousand glomeruli exist and as the functional units of the olfactory system, they relay signals from the periphery to the olfactory bulb (Guyton, 1986).

In humans, the olfactory bulb is small in comparison to the rest of the brain. It is located right beneath the frontal lobe. Like the cerebral cortex, the olfactory bulb is symmetrical and receives its projections ipsilaterally. Dendrites of mitral and tuffed cells of the olfactory bulb receive electrical signals from the periphery. Axons from mitral and tufted cells form bundles of myelinated fibers connecting the olfactory bulb with the rest of the brain. Fibers from the olfactory bulb to the rest of the brain form the olfactory tract (Everett, 1971).

iii. Central Projections of Olfaction: Nerve impulses are carried from the olfactory bulb to the olfactory cortex by secondary olfactory fibers which form the primary olfactory tract. The primary olfactory tract terminates in the lateral and medial olfactory areas. The lateral olfactory area, including the prepyriform cortex, the pyriform cortex and the amygdaloid nuclei. The medial olfactory area is comprised of serval nuclei (including the olfactory nuclei, olfactory tubercle and parts of the hypothalamus) and is located in the midbrain anterior to the hypothalamus (Guyton, 1986).

From the lateral and medial olfactory areas, secondary olfactory tracts project to the limbic system, the dorsomedial nucleus of the thalamus, and various brain stem nuclei. The lateral olfactory area in particular projects to the amygdala of the limbic system and pyriform and prepyriform cortex (Guyton, 1986).

3. Lack of Evidence for Olfactory Primaries: Throughout the history of research on smell, many have proposed various schemes for primary odor qualities (Cain, 1978). In contrast to the taste system where four taste primaries are acknowledged, the classification of odors into primaries such as burnt, floral, pungent, and repulsive is quite arbitrary (Cain, 1987). Within such categories humans can readily make distinctions between a large number of odors. Lack of primaries makes olfaction unique among the other senses, which all have clear cases of basic qualities. The quality classification that currently exists in the olfactory literature is acknowledged to exist for practical reasons rather than reflecting any solid psychophysical or physiological evidence (Cain, 1988).

4. Coding: The lack of olfactory primaries presents a problem to those who wish to understand olfactory coding. Currently, we lack a thorough understanding of olfactory quality coding at the receptor level. As such, an understanding of central olfactory coding is even more difficult to obtain. However, the following theories have been proposed.

Amoore (1962) put forth the stereochemical theory, which stated that receptors in the nose are preferentially sensitive to particular odors of a certain shape in a "lock and key" fashion. Amoore's theory is only important for historical reasons, since molecules that possess similar shape often do not smell the same. As well, chemicals that are very similar in odor are often very different stereochemically, Finally, the non-specificity of peripheral receptors makes the stereochemical theory an unlikely explanation for olfactory coding (Cain, 1988).

Among the spatial theories of olfactory coding is the across-fiber pattern theory. According to this theory the brain reads the pattern of firing, including cell location and frequency of firing, so that every odor elicits a unique activity pattern. A classic study by Døving and Pinching (1973) supports the across-fiber pattern theory for mitral cells in the olfactory bulb. When animals were exposed to one odor for an extended period of time, the mitral cells of their olfactory bulbs showed a specific pattern of degeneration (Døving & Pinching, 1973). Similarly, studies utilizing 2-DG to "label" active cells, showed patterns of mitral cell firing after exposure to a particular odor (Stewart, Kaur, & Shepherd, 1979). Therefore, at the level of the olfactory bulb, there is some evidence for across-fiber pattern coding of olfaction.

Recording of neuronal activity in the orbitofrontal olfactory cortex of monkeys demonstrates a more specific response to particular odor stimuli (Tanabe, Iino, & Takagi, 1975). Neurons in the cortex did not respond to as many odors as neurons in the olfactory bulb. A diffuse response pattern in the limbic system and a narrow response pattern in the cortex suggests that it is only at the cortical level that the olfactory experience is analyzed (Cain, 1988). Studies utilizing positron emission tomography show increased cerebral blood flow at the junction of the inferior frontal and temporal lobes on both sides of the brain upon olfactory stimulation. Blood flow also increases to the pyriform cortex upon olfactory stimulation, but only on the right side of the brain (Zatorre, Jones-Gotman, Evans & Meyer, 1992). Despite a general understanding of the cortical areas involved in olfactory perception, coding in the cortex remains a mystery at this time.

C. Flavor Perception

Flavor refers to the combination of taste and odor (Bartoshuk, 1990). Hence, the perception of flavor depends on the interaction of taste and smell. The anatomy which permits taste-smell interaction and the perceptual experience that results are discussed next.

1. Anatomy: There are two routes for olfactory input, prenasal and retronasal. Holding something up to your nose and sniffing involves prenasal olfaction. In prenasal olfaction, an odor enters via the nares, travels through the nasal cavity, and stimulates receptors located at the top of the nasal cavity (Cain, 1988). However, experiencing the strawberry component of a flavored seltzer, for example, involves retronasal olfaction. In the retronasal route, olfactory volatiles enter the nasal cleft via the nasopharynx in the back of the mouth (Geldard, 1972). That is, in a normal condition of nasal patency, odorant molecules move around the soft palate to the back of the mouth and continue to flow to the space in the nasal cavity above olfactory receptors.

2. Perception of Retronasal Olfaction: When humans experience retronasal olfaction a very curious perception tends to occur. Subjects report that they are experiencing a "taste" even though no taste qualities are present (Cain, 1988). The confusion of taste and smell has been known for over a hundred years (Cain, 1978). Rozin (1982) examined the extent to which language separates the retronasal and prenasal olfactory experience. In English, as well as in seven of nine languages represented in the study, there was an overall tendency to use the word "taste" as a description for an edible substance in the mouth (Rozin, 1982). One may wonder if taste-smell confusions are purely semantic. A review of the literature on taste-smell confusions supports the view, however, that taste-smell confusions have a perceptual basis. Furthermore, characteristics of taste-smell confusion elucidate some of the properties of flavor perception.

3. Olfactory Referral: The most common type of taste-smell confusion is olfactory referral (Cain, 1988). When a pure odorant is present in the oral cavity, its volatiles are transmitted into the nasal cavity and eventually to the olfactory mucosa by diffusion and convection (Hornung & Enns, 1989) and by chewing and swallowing movements (Burdach & Doty, 1987). Even though the stimulation is purely in the olfactory modality, subjects perceptually "refer" to the sensation as a taste coming from the mouth. Thus the above phenomenon is called "olfactory referral" and the resulting perception is a "referred taste" rather than an actual taste (Cain, 1988).

An important characteristic of olfactory referral is that the phenomenon disappears if nasal receptors are blocked, i.e. if nose is pinched or otherwise obstructed (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980). Everyone has experienced the loss of olfactory referral. A simple headcold will temporarily impede nasal patency, resulting in a decrement of our food's "taste." Doty and Kimmelman (1986) report that individuals who lack a sense of smell (anosmics) perceive losses in "taste." Technically, it is the odor component that is lacking, thereby reducing the flavor of food. Recall the decrement in flavor identification upon blockage of nasal patency demonstrated by Mozell and colleagues (1969). Thus, retronasal olfaction is the mechanism by which odor is confused as taste.

4. Taste Referral: Taste-smell confusion is a general term that also describes the less common experience of a pure taste sensation mistaken as an olfactory stimulus (Rozin, 1982). The resulting sensation is a "referred odor." Textbooks on sensation (Geldard, 1972) will often mention taste-smell confusions, but these allusions are almost exclusively to olfactory referral rather than taste referral. The fact that olfactory referral is more common (along with the psychophysical data to be reviewed shortly) may indicate that the interaction between taste and smell is not symmetrical. The possible asymmetrical nature of taste-smell confusion has important implications for how taste and smell are unified by the perceptual system into a concordant gestalt known as flavor.

We have seen in the previous discussion that a pure odor is often perceived as a taste, a phenomenon called olfactory referral. Less often, a pure taste is perceived as an odor. When a taste and odor mixture are presented together in the oral cavity, taste-smell confusion occurs, affecting perception of both the components and the flavor gestalt. Thus, flavor must be discussed as a taste-odor mixture. The methods, terms, and perceptual rules described by the mixture psychophysics literature is briefly reviewed in the following section and informs the experiments presented in this dissertation.

III. MIXTURES

The goal of classical psychophysics is to understand the relationship between the physical characteristics of a stimulus and the perception of that stimulus along a particular psychological dimension (intensity, quality, or pleasantness). For ease of experimentation and interpretation, the use of simple or univariate stimuli has dominated the field of psychophysics. However, most stimuli encountered by humans are complex and multivariate. That is, we deal with stimuli that are mixtures of pure simple stimuli. A review of the experimental approaches and perceptual rules governing stimuli that represent chemosensory mixtures is presented next.

A. Approaches to the Study of Mixtures

Chemical senses scientists use two approaches to study taste-odor mixtures. In the first approach, the experimenter presents a mixture to subjects and obtains a measure of overall stimulus perception on some dimension, usually intensity. In a different session or block of judgments, the components are presented in isolation, and their intensities are rated. Overall intensity is then compared to the component intensities (e.g. Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980; Hornung & Enns, 1984). The goal of this approach is to describe the rules of mixture perception in terms of how the components add to or subtract from the overall intensity. This approach has tended to dominate the psychophysics literature.

In the second approach, the experimenter presents a mixture to subjects and obtains a measure of one of the components on some dimension. For example, if citric acid is mixed with sucrose, the experimenter may ask the subject for a sweetness rating. The goal of this approach is usually to examine the effect of one component on perception of the other. This approach has tended to dominate the field of sensory evaluation that typically is driven by the quite pragmatic concerns of food technology. Both approaches have illuminated different aspects of mixture perception and a review of the literature follows.

B. Relationships Between Components and Overall Sensation

The psychophysical approach to chemosensory mixtures has yielded several models that describe the relationship between component perception and overall sensation. Historically, many relationships between components and mixture have been proposed (see Frijters, 1987), but for the purposes of this dissertation only models with good empirical support will be discussed. These models have been developed mostly on the basis of studies measuring perceived intensity of binary mixtures. Therefore, these findings may not generalize to the quality or hedonics of mixtures, or to mixtures made up of more than two components.

1. Additivity: The additivity model predicts that the intensity of a mixture is the sum of the intensities of the components experienced in isolation. Additivity is usually interpreted to mean that the components of the mixture are processed independently, perhaps by separate receptor populations or different neural systems (Frijters, 1987).

2. Hypoadditivity (Subadditivity): It is rare that a mixture is perceived as the exact sum of the components. Most often, when components are heterogeneous, i.e. remain distinct when mixed, overall intensity is somewhat less than additive (McBurney, 1978). That is, perception of the mixture is hypoadditive, or slightly less than the sum of perceived intensities of the unmixed components. The reason for hypoadditivity is not currently known. In the case of taste mixtures, hypoadditivity has been referred to as "mixture suppression," the perception of qualities as less intense when in a mixture than when encountered in isolation (Bartoshuk, 1988).

Hypoadditivity has also been described with odor mixtures, a phenomenon that has been termed counteraction (Cain, 1975). Hypoadditivity is seen for odors mixed in the liquid or vapor phase (Cain, 1975) and for odors presented environmentally rather than in a laboratory (Cain & Drexler, 1974). Hypoadditivity is also observed for dichorinic mixtures, in which Odor A is presented to one nostril and Odor B is presented to the other nostril (Cain, 1975). Hypoadditivity in dichorinic odor mixtures eliminates the possibility that molecules are competing for the same receptor sites and suggests that processing must occur above the receptor level (Engen, 1982). As a relationship that approximates additivity, hypoadditivity is usually interpreted to mean that the components of the mixture are processed independently (Frijters, 1987).

3. Hyperadditivity (Synergy): There are some reports of hyperadditivity in the literature. That is, the perception of the mixture is greater than the sum of the individual components. Hyperadditivity is rare, however, instances of true taste synergy do exist (e.g. monosodium glutamate) (Bartoshuk, 1988). In olfaction, the only case where hyperadditivity has been observed is when a hypo-threshold odor is mixed with a suprathreshold odor (Engen, 1982).

4. Enhancement: Related to hyperadditivity is the concept of enhancement. Enhancement describes a perceptual rule in which the presence of Component A increases the perceived intensity of Component B. Here it is critical to mention that "enhancement" is often used loosely. For example, monosodium glutamate (MSG) is called a "taste enhancer." However, MSG actually adds its own intensity to the mixture in a synergistic fashion rather than enhancing the other component *per se*. If MSG had no perceived intensity on its own, but made another taste quality more intense, then it would be a true taste enhancer. True taste enhancers do exist and contribute to our understanding of taste perception, but a discussion of them is beyond the scope of this review (Ugawa, Konosu, & Kurihara, 1992).

5. Averaging: Another rule that can describe the relationship between perception of a mixture and the components experienced in isolation is averaging. That is, the mixture could be perceived as the average of the two component intensities. In odor mixtures, this relationship is called compromise (Engen, 1982). Some have discussed the concept of a "weighted average" in which this case, one component's contribution is greater than the other, even though the lesser component can still be perceived (Moskowitz & Klarman, 1975). In odor mixtures, such a relationship is called masking (Engen, 1982).

Two approaches to the study of chemosensory mixture intensity were surveyed. The relationship between components perceived in isolation and mixtures has been described by five models. The models discussed above have been based almost exclusively on intensity. But these approaches and models can also be used to describe the relationship between the pleasantness of the components in isolation and mixture hedonics. Very little work has been done to determine the model that best describes mixture hedonics. A review of the existing literature on mixture hedonics follows.

D. Mixture Hedonics

Those who have examined taste-taste mixtures or odor-odor mixtures all converge on a weighted averaging model. Moskowitz and Klarman (1975) examined hedonic perception of artificial sweeteners (sodium and calcium saccharine and cyclamate). The bitter component of the artificial sweeteners suppressed sweetness and changed the overall character of the mixture to bitter. Klitzner (1975) obtained similar results with apple juice - quinine sulfate mixtures. The negative taste of bitter was more salient at the low concentrations of apple juice, making the overall hedonic tone of the mixture unpleasant. In mixtures of sucrose and quinine sulfate, the affectively negative component, whether it was bitter or extremely sweet, mostly determined the overall hedonic tone of the mixture (Lawless, 1977). Therefore, an unpleasant component has more salience in a taste-taste mixture than a pleasant component.

A weighted averaging model has also been described for odor mixtures. Spence and Guilford (1933) had subjects rate the pleasantness of individual odors and their mixtures. The hedonic tone of odor mixtures tended to fall in between the hedonic value of the two components (Spence & Guilford, 1933). Many years later, the observations of Spence and Guilford (1933) were replicated. In the context of ambient odors, Cain and Drexler (1974) examined the ability of a pleasant deodorizer to counteract a malodor. If the malodor is of a weak concentration, then a deodorizer is effective at reducing its negative hedonic tone. However, adding a deodorizer to a very strong malodor can increase the overall mixture intensity and makes the olfactory ambiance more unpleasant (Cain & Drexler, 1974). Another experiment which delivered odor stimuli in sniff bottles rather than environmentally also replicated the findings of Spence and Guilford (1933). Lawless (1977) presented subjects with mixtures of pleasant and unpleasant odors at various concentrations. The pleasantness of the mixture was dominated by the unpleasant component (Lawless, 1977). Thus, regardless of whether odors are presented environmentally or in a laboratory, a negative odor will tend to dominate a mixture.

It is acknowledged that the studies presented in this review examined mixtures with one pleasant and one unpleasant component. Two unpleasant components and two pleasant components may follow different rules of hedonic integration. However, in pleasant-unpleasant mixtures, in both the taste and odor modalities, the overall hedonic value of a mixture tends to be the average of its components judged in isolation weighted more by the unpleasant component.

The previous section reviewed perception of taste-taste mixtures and odor-odor mixtures. Mixture intensity tends to follow a hypoadditivity rule, i.e. mixture intensity is slightly less than the sum of the isolated component intensities (McBurney, 1978;

Cain, 1975). Mixture hedonics tends to follow a weighted averaging rule, i.e. mixture pleasantness is dominated by the unpleasant component even though the pleasant component can still be distinguished (Moskowitz & Klarman, 1975; Lawless, 1977).

Very few studies have examined taste-odor mixture perception. This is disappointing for two reasons. First, as discussed previously, taste and odor combine to form flavor, a salient aspect of food choice and intake (Bartoshuk, 1991b). The rules that govern taste-odor mixture perception, particularly in the hedonic realm, may contribute to our understanding of the role of flavor in ingestive behavior. Second, as discussed previously, the properties of taste-smell confusion may be further defined by the study of taste-odor mixtures (Rozin, 1982). Thus, the examination of taste-odor mixtures may reveal the rules that describe flavor perception and the characteristics of taste-smell confusion. The following section reviews the literature on taste-odor mixtures.

E. Taste-Odor Mixtures

1. Studies Demonstrating Intensity Hypoadditivity: When the intensity of a taste-odor mixture is judged relative to each stimulus in isolation, hypoadditivity is generally observed. In this way, taste-odor mixtures are similar to taste-taste and odor-odor mixtures (Frijters, 1987). Murphy, Cain, and Bartoshuk (1977) had subjects estimate the intensities of taste, smell, and overall sensation of taste-smell mixtures in separate sessions. Overall intensity of taste-smell mixtures demonstrated slight subadditivity (i.e. overall intensity was 93% of the sum of the unmixed components). Because overall intensity was very close to additive, the authors concluded that taste and smell act independently when combined. Other researchers have found similar results (Murphy & Cain, 1980; Gillan, 1983).

The studies mentioned above (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980) utilized physically combined taste-odor mixtures which are presented in medicine cups and sipped by the subject. Such stimulus presentation (called "medicine cup delivery method") is useful for examining taste-smell confusion and the effect of retronasal olfactory input on taste. To obtain a complete picture of taste-odor interaction, it is nccessary to understand the integration of stimulus input from different anatomical routes (prenasal rather than retronasal olfaction). Hornung and Enns (1984) devised an apparatus that permits independent manipulation of taste and odor. In this device, taste and odor are presented concomitantly, but separately. Their two-module delivery system is essentially two bottles, one with an odorant and one with a tastant, on top of each other. The tastant container is on the bottom of the apparatus and has a glass straw extending from it. The odorant container is on the top and has an opening whereby subjects can sniff an olfactory stimulus while simultaneously sampling the tastant. Both bottles are covered by a polyurethane sleeve to minimize visual input (Hornung & Enns, 1984).

After devising this apparatus, Hornung and Enns (1984) compared perception of taste, smell, and overall intensity using the two-module and medicine cup delivery systems. No difference was found between the two delivery methods in terms of component additivity to overall intensity (Hornung & Enns, 1984). It was found that the overall intensity ratings were slightly less than the sum of the component intensities. Therefore, regardless of whether taste-odor combinations are presented in a physically mixed or separate form, hypoadditivity is demonstrated for the intensity dimension of taste-odor mixtures (Enns & Hornung, 1985; Hornung & Enns, 1986).

Even though overall intensity of a taste-smell mixture is hypoadditive compared to the intensities of the isolated components summed, taste and smell are often thought to act independently, especially since the quantitative data usually approximate complete additivity (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980; Hornung & Enns, 1984). The fact that other chemosensory mixtures are additive (McBurney, 1978; Berglund, Berglund, Lindvall & Swensson, 1973; Cain & Drexler, 1974) has reinforced the view that similar perceptual laws describe taste-odor mixtures. However, a different approach to studying taste-odor mixtures, suggests enhancement of the taste component by the odor component. A discussion of that approach, along with data it has yielded, follow.

2. Studies Demonstrating Enhancement: In the second approach to studying taste-odor interaction, the experimenter presents a taste-odor mixture to subjects and measures the effect of one component on the perception of another. For example, a sucrose-strawberry odor mixture is presented and subjects are asked to rate sweetness in the presence of odor compared to sweetness in the absence of odor. This method has been termed *modality specific judgments* since the experimenter asks for ratings of one modality only (e.g. taste) as opposed to component and mixture ratings. When asked for modality-specific intensity estimates, it is apparent that ratings of individual components differ when a sensation in the other modality is present. This section will present studies demonstrating the enhancement of taste intensity by odor and studies demonstrating the enhancement of odor intensity by taste.

i. The Effect of Odor on Taste Perception: Using the medicine cup delivery method, Frank, Ducheny, and Mize (1989) have found that strawberry odor, but not red color, enhances the sweetness of sucrose solutions. Similar findings were demonstrated in non-aqueous stimuli (Frank & Byram, 1988). Physical separation of taste and odor does not alter the ability of odor to enhance perceived taste intensity. Using the two-module delivery system described previously, Enns and Hornung (1985) examined the effect of odor on taste intensity. Odor background changed taste intensity ratings for distilled water, but did not alter the intensity of almond extract in the mouth (Enns & Hornung, 1985). A different experiment showed that taste magnitude of both distilled water and sucrose are increased by the presence of an odorant (ethyl butyrate) in the nose (Hornung & Enns, 1986). In the above studies, increased taste intensity ratings due to odor are eliminated when the nose is pinched, indicating that olfactory referral is the mechanism underlying this effect.

When subjects are asked to make modulus specific judgments of taste intensity, subjects report that taste is more intense with odor compared to the taste alone. Some have termed this effect "odor-induced taste enhancement" (Frank & Byram, 1988; Frank et al., 1989). However, several questions emerge from the above literature and they are addressed in turn.

ii. Is Stimulus Congruity Required for Odor-Induced Taste Enhancement? In the literature on taste-odor mixtures, stimulus congruity refers to the qualitative similarity of the taste and odor (Frank & Byram, 1988). For example, sweet and strawberry are thought to be congruous because most subjects would associate strawberry with a sweet taste quality. The hypothesis that odor-taste congruity is necessary for odor-induced taste enhancement has been examined in a series of experiments by Frank and colleagues. Frank and Byram (1988) found that taste intensity enhancement by odor is odorant specific. Subjects rated whipped cream-sucrose stimuli significantly sweeter in the presence of strawberry but not peanut butter odor. However, subjects rated whipped cream-sodium chloride stimuli significantly saltier in the presence of peanut butter but not strawberry odor (Frank & Byram, 1988). Further investigation of the hypothesis that odor-induced enhancement of taste depends on stimulus congruity has revealed a fairly strong predictive relationship between odor-taste similarity ratings and enhancement of taste (Frank, Shaffer & Smith, 1991). However, no models have been developed to test causality and direction (enhancement or suppression) of taste-odor interaction.

iii. Is Odor-Induced Taste Enhancement True Enhancement?: Odor-induced taste enhancement is observed when modality-specific judgments are required of subjects. That is, when an experimenter asks the subject to judge the intensity of taste in the presence of odor, the subject rates the taste as more intense than when odor is not present. This result could be due to a true enhancement of taste by odor. Alternatively, it could be that subjects are actually reporting the intensity of the taste-odor mixture rather than sweet intensity *per se*. It has been demonstrated that odor-induced taste enhancement is not observed when subjects are instructed to partition overall intensity into individual qualities, such as sweetness and fruitiness (Frank, Wessel, & Shaffer, 1990; Frank, van der Klaauw, & Shifferstein, 1993). Thus, in previous studies (Frank & Byram, 1988; Frank, Ducheny, & Mize, 1989) it may be that subjects were rating the intensity of the mixture rather that taste intensity. Therefore, odor may not be a true taste enhancer, but simply a contributor to the perceived intensity of a mixture.

iv. The Effect of Taste on Odor Perception: Fewer studies have examined the effect of taste on perceived odor intensity. Using the two-module delivery system, Hornung and Enns (1986) looked at the influence of a taste on odor perception. Subjects were asked to estimate odor intensity for five concentrations of almond odor with each of three concentrations of almond tastant in the mouth. A high concentration of almond extract in the mouth altered odor intensity estimates of distilled water vapor delivered to the nose (Enns & Hornung, 1985). Since the tastant used in the experiment above was actually a flavoring extract with some olfactory input, the observed effects on component intensity are most likely due to retronasal input (Enns & Hornung, 1985).

The effect of a purely gustatory stimulus on perceived odor intensity is variable. Some experimenters have found no effect of taste on odor (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980). However, others have found that sucrose in the mouth increased the intensity estimates of ethyl butyrate delivered into the nasal cavity, even though sucrose has no odor (Hornung & Enns, 1986). Sucrose in the mouth did not alter odor intensity estimates of water vapor delivered to the nose (Hornung & Enns, 1986).

Studies examining perceived intensity of taste-odor mixtures reveal the following: First, like some other chemosensory mixtures, taste-odor mixture intensity is hypoadditive compared to the sum of components judged in isolation (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980). Second, a hypoadditivity rule is observed regardless of whether taste-odor mixtures are presented in a physically mixed fashion using the medicine cup delivery method or physically separate fashion using the two-module delivery system (Hornung & Enns, 1984). Thus, the psychophysical rules that govern taste-odor mixtures are similar to those which describe taste-taste and odor-odor mixtures.

Modality-specific judgments of taste-odor mixtures reveals the following: First, reports of taste intensity are increased in the presence of odor compared to taste alone (Frank, Ducheny, & Mize, 1989). The enhancement of taste by odor depends on retronasal olfaction since pinching the nose eliminates the enhancement seen (Frank, Ducheny, & Mize, 1989). Cognitive factors, for example the congruity or similarity of the taste and odor, have been shown to influence whether odor increases taste intensity ratings (Frank, van der Klaauw, & Shifferstein, 1993). Upon further analysis, "odor-induced taste enhancement" may not be true enhancement, but a report of mixture intensity (Frank, Wessel, & Shaffer, 1990).

Even though the elevation of taste intensity ratings by the presence of odor may actually reflect the overall intensity of the mixture, the modality-specific judgment studies are interesting because they demonstrate that taste-smell confusion is asymmetrical. It is clear that different odors across a range of concentrations will produce olfactory referral (Murphy, Cain, & Bartoshuk, 1977; Murphy & Cain, 1980). However, only a high concentration of a sweet taste has been shown to produce taste referral (Murphy, Cain, & Bartoshuk, 1977) and not all studies consistently demonstrate taste referral (Hornung & Enns, 1989). The robustness of olfactory referral and the inconsistency of taste referral points to the asymmetry of taste-smell confusion. However, whether the asymmetry of taste-smell confusion contributes to flavor hedonic perception is not known. Very little work has been done on the hedonic perception of taste-odor mixtures, but a review of the work that has been done follows.

3. Hedonic Perception of Taste-Odor Mixtures: Enns and Hornung (1987) presented taste and odor simultaneously, but physically separate in the two-module delivery system. Subjects rated the pleasantness of odor, taste, and the "overall pleasantness of the odorant-tastant combinations." The authors reported the percentage of subjects who gave negative, positive, or neutral responses to the mixtures based on hedonic tone of the components. When the taste and odor components are both hedonically positive, the mixture is pleasant. When the taste and odor components are both hedonically negative, the mixture is unpleasant. In the more complicated case of a negative and a positive component, hedonic value of the mixture depends on the dominant component (the component with the greater absolute hedonic value). However, if the absolute hedonic value of both components was equal, then the flavor tended to be dominated by the negative component (Enns & Hornung, 1987).

Chappell (1953) had subjects rate their hedonic response to various taste solutions (sucrose, maltose, lactose, glucose, and sodium chloride). Addition of odors (lemon, orange, and vanilla) to the basic tastes increased pleasantness ratings of the solutions. Furthermore, it was observed that a strong, pleasant odor could mask an unpleasant salty taste (Chappell, 1953). One problem with this study is that the hedonic tone of the odors was assumed, not directly rated.

Moskowitz (1977) obtained psychophysical functions describing the relationship between concentration, perceived intensity, and pleasantness for glucose. The hedonic breakpoint of glucose, the concentration at which the pleasantness of the taste starts to decline, is 1.0 M. However, the addition of a cherry odor, which is perceived as more pleasant with increasing concentration, to glucose increased the hedonic breakpoint of glucose. That is, higher concentrations of glucose were more acceptable if mixed with a pleasant odor (Moskowitz, 1977).

Murphy (1982) examined the hedonic value of sodium chloride-citral odor mixtures over repeated exposures. The study's major finding was affective habituation or reduced hedonic ratings upon multiple exposures. However, it was also observed that citral solutions were more pleasant by themselves than when sodium chloride was present (Murphy, 1982). Only mixture and citral alone solutions were rated, so we do not directly know that subjects found the sodium chloride taste unpleasant. However, the sodium chloride component made some contribution to mixture hedonics. One possibility is that subjects found the taste unpleasant, thereby reducing the hedonic value of the mixture. Alternatively, the interaction of sodium chloride and citral could contribute to the unpleasantness of the mixture.

A study of sucrose-strawberry odor mixtures by Looy, Callaghan, and Weingarten (1992) suggests that an unpleasant taste can be made less unpleasant by the addition of an odor. The effect of odor on taste hedonics depended on subjects' hedonic profile to sweet. Sweet dislikers (subjects who find concentrated sucrose unpleasant) gave higher hedonic ratings to sucrose with odor than plain sucrose, though solutions were still unpleasant. Sweet likers (subjects who find concentrated sucrose pleasant) gave equal hedonic ratings to sucrose with odor and plain sucrose (Looy, Callaghan, & Weingarten, 1992).

Thus, it is not clear that hedonic integration of taste-odor mixtures is similar to that of taste-taste and odor-odor mixtures. While the presence of an odor can affect perceived hedonics of a sweet taste (Moskowitz, 1977; Looy, Callaghan, & Weingarten, 1992), it is not clear whether all taste qualities are affected by odor or whether all subjects demonstrate odor-induced taste enhancement. Furthermore, it is not known if hedonic perception of taste is truly affected by odor or if subjects report mixture hedonics.

The paucity of research on taste-odor mixture perception is disappointing since the combination of taste and odor form flavor, an important aspect of food. Currently, most studies of taste-odor mixtures have tended to concentrate on perceived intensity in an attempt to determine which psychophysical model describes component interaction. However, those interested in the relationship between flavor perception and ingestive behavior will tend to focus on hedonic perception of taste-odor mixtures.

Several studies suggest that the hedonic value of a taste is altered by the presence of an odor (Chappell, 1953; Moskowitz, 1977; Looy, Callaghan, & Weingarten, 1992). However, no studies have examined whether the hedonic value of an odor is altered by the presence of a taste. This is surprising for two reasons. First, it has been suggested that odor is more hedonically modifiable than taste. Second, there is some indication that odor is the more hedonically salient component of food (Doty & Kimmelman, 1986; Pelchat, 1993). Thus, the experiments in this dissertation explore the effect of taste on odor perception, particularly along the hedonic dimension.

Experiment 1 describes the basic relationship among concentration, perceived intensity, and perceived pleasantness for the three food odors selected for study in the experiments comprising this dissertation. In Experiment 2, the effect of a taste on perceived odor intensity and hedonics was examined. This represents the attempt to observe whether the odor enhancement of taste described in the literature generalizes to taste on odor. Experiments 3 and 4 reveal the properties of the taste enhancement of odor. As reviewed before, a major issue has been the degree to which enhancement represents "true" enhancement or reports of mixture perception. Experiment 5 required subjects to report their hedonic response to the components and overall sensation of a taste-odor mixture in order to examine this issue. Experiments 6 and 7 represent attempts to generalize the above findings closer to ingestive behavior. Hedonic perception of taste and smell is inexorably linked to ingestive behavior (Bartoshuk, 1989a; 1991b) and Cabanac (1979) has put forth the idea that the hedonic tone of odor is modifiable by internal state. Experiments 6 and 7 examine the effect of hunger and satiety on taste and odor hedonics.

Chapter Two

GENERAL METHOD

The procedures described in this chapter were used consistently in the experiments that follow. Differences in procedure for individual experiments will be detailed in the Methods sections of individual experiments.

Subjects: Both males and females participated in these experiments. Subjects were primarily undergraduate students in a General Psychology class. Some students from other Departments also volunteered their services. The Psychology students received course credit for their participation. Students from outside the Department were paid $5 / hour for their participation. All subjects gave informed consent prior to testing.

Chemosensory studies must consider the effect of cigarette smoking on taste and smell perception. There is conflicting literature concerning the detrimental effect of smoking on odor perception. Some studies find reduced sensitivity in smokers (Ahlstrom, Berglund, Berglund, Engen, & Lindvall, 1987), but other research finds no difference between smokers and non-smokers (Pangborn, Trabue, & Barylko-Pikielna, 1967). Some have questioned whether observed differences can truly be attributed to smoking (Hubert, Fabsitz, Feinleib, & Brown, 1980). However, Doty and colleagues (1987) have found olfactory deficits in smokers and noted the importance of excluding ex-smokers from the "non-smoker" category, as there may be long-term effects of smoking on the olfactory system (Frye, Schwartz, & Doty, 1987). Both intensity and hedonic perception of the four taste qualities appears to be unaffected by smoking (Pangborn, Trabue, & Barylko-Pikielna, 1967; Redington, 1984).

Because the literature is unclear about the effect of smoking on olfaction, records were kept of subjects' smoking habits. The majority of our subjects (97.2 per cent) did not smoke at all, smoked only occasionally, or smoked less than 10 cigarettes per day. Additionally, it is well known that age has a larger effect on odor perception than smoking (Frye, Schwartz, & Doty, 1990). Because our sample has a low incidence of heavy smoking and is composed of mostly young people, it is unlikely that the effects of smoking weigh heavily on our results. For these reasons smokers were not excluded.

The stimuli and rating procedures used in this dissertation were not chosen haphazardly. The Appendix describes how the specific odors, concentration range, and rating procedure used in the experiments comprising this dissertation were selected in a series of pilot experiments.

A. STIMULI

Odor Stimuli: Odorants were obtained from International Flavors and Fragrances. Chocolate (TOL 213), raspberry (TOL 96), and popcorn (TOL 132) synthetic fragrances were used in all experiments. 15 ml of the pure odorant was added to 85 ml of heavy mineral oil (Big V Pharmacies Company, Ltd.) for a total volume of 100 ml. From this "stock" solution, a 1/5 dilution series was done. Five concentrations of each odor were made (3/20, 3/100, 3/500, 3/2500, & 3/12500 vol / vol). For ease of graphing, perceived intensity and hedonic functions across concentrations, the concentrations were converted by multiplying the vol. / vol concentration by 10^5 and taking the $\log_{10}$ of this number. Thus, the notation for the five concentrations of odor used in all experiments is, from lowest to highest, 1.38, 2.08, 2.78, 3.48, and 4.18 LOG (vol. / vol. [ ] x 10^5).

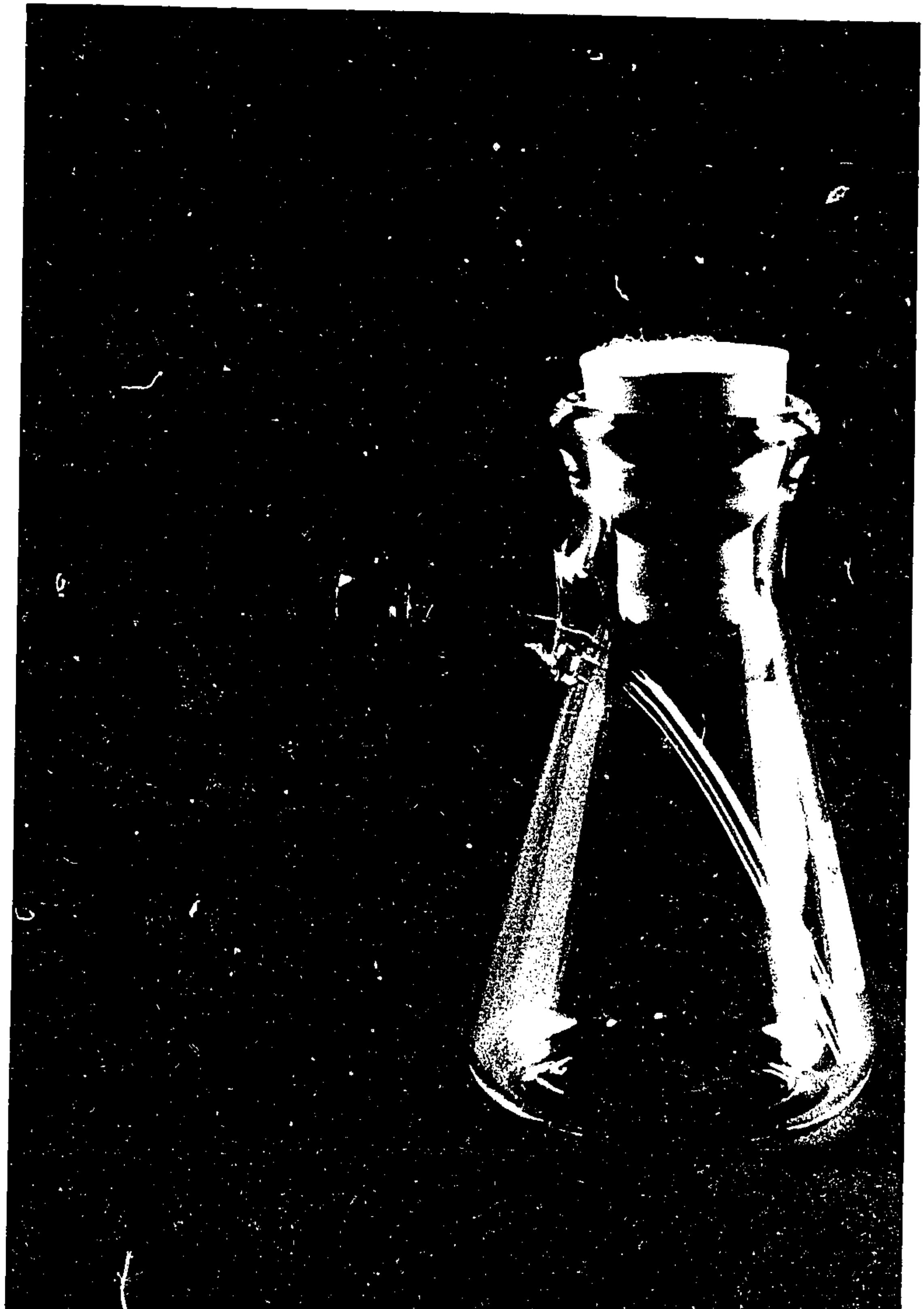
Taste Stimuli: Sweet, salty, and bitter tastants were utilized during the course of these experiments. Sweet solutions were made by dissolving sucrose in distilled water at room temperature (22° C). The concentration of aqueous sucrose presented to subjects concomitantly with odor was 0.8 M. Salty solutions were made by dissolving reagent grade sodium chloride in distilled water at room temperature (22° C). Bitter solutions were made from a stock solution of sucraoctaacetate (SOA). The stock SOA (1×10^{-4} M) was made by dissolving 0.0678 g SOA in 5 ml of 95% ethanol, then topping this solution up to 1000 ml with distilled water. Stock solution was further diluted with distilled water to make concentrations of aqueous SOA that were presented to subjects. All taste solutions were presented at room temperature (22°).

B. APPARATUS FOR DELIVERY OF STIMULI

Odors that are safe to deliver into the mouth (essences or artificial flavorings) are often confounded by the presence of a taste (usually attributable to an alcohol solvent). To avoid this confound, we deliver taste and odor simultaneously without physically mixing. A Two-Module Delivery System (Hornung & Enns, 1984), that allows simultaneous but independent delivery of taste and smell, was used.

In the Two-Module delivery system, tastant is held in a 50 ml Pyrex filtration flask. Approximately 13.0 cm of Tygon tubing (1\16" I.D., 1\8" O.D., 1\32" WALL) runs from the tastant through the tubulation and to the outside of the flask. The Tygon tubing acts as a straw through which subjects sip the tastant. The flask is sealed with an upturned serum stopper (size #4). The upturned serum stopper holds an odorant soaked cotton ball that can be sniffed easily. Subjects were instructed to sniff the odor as they sip the tastant and to continue sniffing the odor while the taste is in their mouth. In this way, odor and taste are delivered simultaneously without being physically mixed (Figure 1).

Figure 1: A photograph of the two-module delivery system, which was used to present taste and odor simultaneously, but independently. This apparatus was used in all experiments involving taste-odor mixtures.



To avoid ambient odor, flasks were kept in a small fume-hood. During a session, odors were taken out by the experimenter, handed to the subject for sampling and ratings, then returned to the fume-hood when not in use. Cotton balls, tastants, and straws were replaced for every subject.

C. METHOD FOR DETERMINING UNDERLYING HEDONIC PROFILE TO SWEET

Prior to the experiment each subject was classified as either a "liker" or "disliker" of concentrated sucrose (Looy & Weingarten, 1992). Subjects were given a block of taste stimuli: 0.0, 0.1, 0.2, 0.4, and 0.8 M sucrose presented in random order. After the subject sampled all concentrations in the block, they were asked: "Which solution do you like the most?" and "Which solution do you dislike the most?" Subjects who liked 0.4 or 0.8 M sucrose and disliked 0.0 M sucrose were classified as a "likers." Subjects who liked 0.0, 0.1, or 0.2 M and disliked 0.4 or 0.8 M sucrose were classified as "dislikers." This procedure was then repeated to ensure subject consistency. The subject had to pick the same concentration as "most liked" twice before they were classified as a sweet liker or disliker. Data from the few subjects who demonstrated non-reliability of hedonic response to sweet was excluded from analysis.

D. STIMULUS RATING PROCEDURE

The magnitude estimation procedure was used to rate stimulus intensity and hedonics. Magnitude estimation is a direct measurement procedure used widely in the field of psychophysics. In magnitude estimation, the subject experiences a standard stimulus. A number (modulus) is given to the standard to represent its magnitude along some dimension. All other stimuli are rated relative to the standard in a ratio fashion.

After a consideration of magnitude estimation procedural effects, Marks (1974) has suggested a method that minimally constrains the subject. In this configuration, called free-modulus magnitude estimation, the subject is free to use any modulus for the first stimulus, and the standard is the middle concentration in the stimulus range. The subject only experiences the standard at the beginning of the session. Also, to give the subject an idea of the range of stimuli, the highest and lowest concentrations are sampled before any judgments are made. As long as the subject is given proper instructions, this method yields psychophysical functions that are not affected by the size of the modulus or the standard being too low or high (Marks, 1974).

After providing signed consent, subjects were told which dimension they were going to rate (intensity or hedonics). Whether the subject rated intensity or hedonics first was counterbalanced across subjects. Subjects were given the following instructions:

INSTRUCTIONS FOR RATING ODOR INTENSITY

In this part of the experiment, I will be asking you to evaluate how strong the odor (what you are smelling on the cotton ball) seems to you while you have the taste in your mouth. You will be using a rating system I will describe to you now.

To describe how strong the odor seems to you, give a numerical estimate. You may give the first stimulus any number you want, as long as you describe subsequent stimuli as a ratio of the first stimulus. For example, say you give the first stimulus 100. If the next one seems 1/4 as strong as the 1st one you would have to give it 25. If the next odor seems twice as strong as the first one, you would have to give that one 200.

INSTRUCTIONS FOR RATINGS ODOR HEDONICS

In this part of the experiment, I will be asking you to evaluate how much you like the odor (what you are smelling on the cotton ball) using the rating system I will describe to you now.

To describe how much you like the odor, give a numerical estimate that describes how strongly you feel about the odor. So, the stronger you feel, the higher the number. You may give the first stimulus any number you want, as long as your describe subsequent stimuli as a ratio of the first stimulus. For example, say you give the first stimulus 100. If you feel twice as strong as the first one, you would have to give that one 200. Now, to let me know if you like or dislike the odor, say "positive" if you like the odor and "negative" if you dislike the odor. If you neither like nor dislike the odor, say "neutral". A "neutral" response receives a number of 0 and is equivalent to having no feeling about the odor.

Once subjects understood the rating system, they were then instructed how to sample stimuli. When taste was presented concomitantly with odor, the sip-and-spit preparation, a procedure in which subjects taste and expectorate a substance, was used. This preparation allows the characteristics of a taste stimulus to be assessed without the confound of ingestion. Ingestion of a stimulus becomes an especially important confound when evaluating hedonic response, since the hedonic value of a substance decreases as more of it is ingested (Cabanac, 1971). The delivery system used in these experiments allows subjects to sip a tastant while sniffing a cotton ball soaked with odor. After sniffing the odor, subjects then expectorate the tastant and rinse with distilled water. A funnel attached to a jug was provided for this purpose. At that time they were asked to rate the stimulus.

After the subject rated the first dimension of all stimuli (either intensity or hedonics), they were given a break ranging from 3 to 5 minutes. Then instructions were given for rating the other dimension. All ratings were recorded by the experimenter. After the subject finished rating all stimuli, they were debriefed as to the purpose of the experiment and instructed not to divulge this information to other students.

E. DATA NORMALIZATION PROCEDURE

Because we do not prescribe a modulus to subjects, ratings must be normalized. Normalization of data eliminates the problem that subjects may use vastly different numbers to describe their experience (e.g. one subject may assign a modulus of 10 while another uses 100). A normalization procedure described by Murphy, Cain, and Bartoshuk

(1977) was used. Each subject's intensity and hedonic ratings were averaged over the replications of stimulus and the median of all an individual subject's rating was taken. All subjects' ratings were pooled and a grand median was calculated. The ratio between the grand median and an individual subject's median was multiplied by ratings to produce normalized data. Once normalized, the data obtained from the magnitude estimation procedure produces ratio scale data and can be legitimately analyzed using parametric statistics (Marks, 1974). For each stimulus, normalized ratings were averaged for all subjects. These averaged data were analyzed using analysis of variance (ANOVAs) and appear in all graphs. Significant F values will be reported for each analysis.

Chapter Three

Experiment 1

THE RELATIONSHIP AMONG ODOR CONCENTRATION, PERCEIVED INTENSITY AND PERCEIVED HEDONICS

The purpose of this experiment was to describe the psychophysical functions for three food odors. There are two reasons why this is necessary. First, psychophysical functions that describe the perception of odor in isolation will be compared to perception of odor in the presence of a taste. In this way, the effect of a taste on odor perception can be determined. Second, the literature describes different types of psychophysical functions among intensity and hedonics for different odors (Moskowitz, 1977). Therefore, it is necessary to understand the intensity-hedonic relationship for each odor in isolation to ensure that the full range of intensity-hedonic relationships are captured by the stimuli used for the experiments in this dissertation.

Taste Psychophysical Functions

The relationship among concentration, perceived intensity and hedonics for taste qualities have been well described (Moskowitz, 1977). A Type I-negative function is characterized by increasing perceived intensity with concentration, but with decreasing estimates of liking. Humans generally generate Type I-negative functions for bitter, sour, and salty solutions (Moskowitz, 1977).

It has been reported that sweet tastes produce a Type II function. Type II functions are characterized by increasing perceived intensity with concentration, and increased liking until the mid-range concentration. At beyond the maximal hedonic point, liking decreases with increasing concentration (Moskowitz, 1977). However, further analysis of individual response functions shows that the averaging of two opposite response types actually makes the Type II function. A subset of the population (sweet dislikers) produces a Type I-negative function for sweet substances (Looy & Weingarten, 1992). A different subset of the population (sweet likers) produces a Type I-positive function for sweet substances. A Type I-positive function is characterized by decreasing pleasantness as concentration increases. When averaged pleasantness ratings are graphed and these two groups are not separated, a Type II function is produced (Pangborn, 1970; Looy & Weingarten, 1992).

Odor Psychophysical Functions

In contrast to taste, the relationship between the hedonic tone of an odor and its intensity and concentration varies immensely (Moncrieff, 1966). With increasing concentration, perceived hedonics of odor can vary depending on the individual (Land, 1979) and the specific odor under examination (Moskowitz & Dravnieks, 1974; Doty, 1975; Moskowitz, Dravnieks, & Klarman, 1976).

After extensive pilot experiments (described in the Appendix), three food odors at five concentrations were chosen as olfactory stimuli. Before the effect of taste on odor hedonics could be examined, I first needed to describe the relationship among odor concentration, perceived intensity, and perceived hedonics for the odor stimuli selected and this is the purpose of the first experiment.

Method

Subjects: Subjects were 18 undergraduate students who participated for course credit. There were 13 males and 5 females with an average age of 19 $\pm$ .58 (SD) years in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, raspberry, and popcorn. Five concentrations, 1.38, 2.08, 2.78, 3.48, and 4.18 (LOG [] x 10^5) of each odor was presented in random order.

Procedure:

Stimulus Delivery: The Two-Module Delivery system (General Method) was used to present olfactory stimuli. Since this experiment utilized no tastant, the straw was removed and subjects simply sniffed the cotton ball in the upper portion of the apparatus.

Ratings: Ratings of intensity and hedonics were obtained using the magnitude estimation procedure (General Method). Subjects rated intensity and hedonics separately. A block of odor stimuli consisted of every concentration presented three times in random order (except for the first stimulus, which was always the middle concentration), for a total of 45 judgments per dimension. The order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating intensity and hedonics. All subjects rated the three odors in separate blocks (randomized order). Subjects were not told the identification of the odor, but they often guessed the odor correctly. After the first odor was rated along both dimensions, the subject was given a 2-3 minute break. The subject was then told that a new odor was being presented. After rating that block of odor stimuli, the subject was given another break and then rated the last block of odor stimuli. Each session lasted approximately one hour.

Results

Within-subject ANOVAs were used to examine the effect of odor concentration on perceived odor intensity and odor hedonics.

Chocolate

Figure 2 (top panel) shows the relationship among chocolate odor concentration, perceived intensity, and perceived hedonics. While intensity ratings increased with chocolate odor concentration ($F(4,68)=57.9$, $p=.0000$), hedonic ratings followed an inverted-U shaped function; hedonic ratings increased with concentration up to a point, but then declined.

Raspberry

Figure 2 (middle panel) shows the relationship among concentration, intensity and hedonics for raspberry odor. Again, intensity ratings increased with odor concentration ($F(4,68)=11.08$, $p=.0000$). However, unlike chocolate, hedonic ratings of raspberry increased with increasing concentrations ($F(4,68)=5.24$, $p=.001$).

Popcorn

Figure 2 (bottom panel) shows the data for popcorn odor. Perceived intensity ratings increased with odor concentration ($F(4,68)=17.52$, $p=.0000$), but popcorn hedonic ratings did not change significantly over concentrations.

Discussion

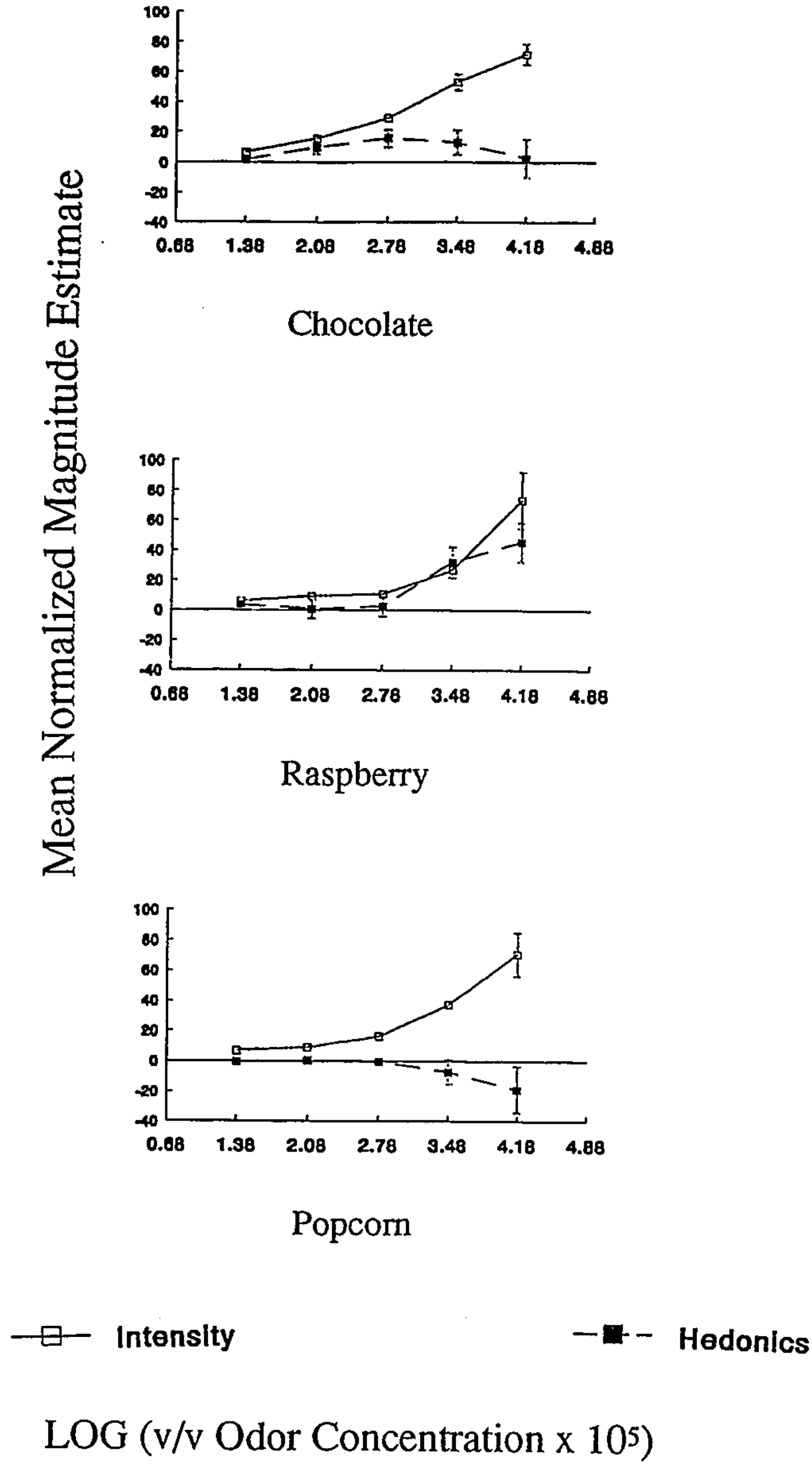
The present experiment shows that the three odors selected for study in this dissertation show different relationships among concentration, intensity and hedonics. The functions cover the range of types (Types I, II, and III) documented in the previous literature (Moskowitz, 1977).

Chocolate odor follows an inverted-U hedonic response pattern over the concentrations used here. That is, like sweet taste substances, hedonic ratings of chocolate odor increase as concentration increases, but then fall at the highest concentration. A function of this shape would be produced if all subjects demonstrated an inverted-U hedonic response pattern to chocolate odor. But a Type II function could also be produced if some subjects reported decreasing hedonic ratings as concentration increased while other subjects reported increasing hedonic ratings as concentration increased. The analysis of an inverted-U function as actually reflecting two populations that have opposite hedonic response patterns has been used to further explain the Type II response for sweet substances (Looy & Weingarten, 1992). However, the Type II function produced by chocolate odor is not due to the averaging of two opposite response functions. In this experiment, the hedonic response to the highest concentrations of chocolate odor was quite variable. However, 9/18 subjects showed an inverted-U hedonic response. Of the remainder, 7/18 showed steadily increasing hedonic ratings with increasing concentration, and only 2/18 showed decreasing hedonic ratings with increasing concentration.

The psychophysical function of raspberry is different from chocolate. Most subjects reported increasing intensity and hedonic ratings with increasing concentration. The psychophysical function of popcorn is distinct from chocolate and raspberry. As popcorn odor concentration and perceived intensity increase, hedonic ratings remain constant. However, this hedonic response pattern is a result of aggregating data from subjects with a negative response (8/18) and slightly more subjects with a flat response (10/18).

Several items are noteworthy about the results of the current experiment: First, over the concentrations used here, subjects can differentiate the experience of odor intensity from odor hedonics. The fact that the three odors produce different intensity-hedonics relationships argues that subjects are not simply repeating magnitude estimates of intensity and hedonics. Second, each odor produces a distinct relationship among concentration, perceived intensity and hedonics and the functions produced by the odors to be used in this dissertation cover the range of such relationships reported previously in the chemosensory literature (Moskowitz, 1977).

Figure 2: Mean (± SEM) intensity ratings (open squares) and hedonic ratings (closed squares) of chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel) odor across five ascending concentrations. (SEMs not visible fall within the symbol).


Mean Normalized Magnitude Estimate
100
80
60
40
20
0
-20
-40
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
Raspberry
Popcorn
Intensity
Hedonics
LOG (v/v Odor Concentration x 10⁵)

Chapter Four

Experiment 2

THE EFFECT OF TASTE ON PERCEIVED INTENSITY AND HEDONICS OF THREE FOOD ODORS

The previous experiment established that the chocolate, raspberry, and popcorn odors used in these studies have distinct relationships among concentration, perceived intensity, and hedonics over the concentrations used here. While all subjects report increasing perceived intensity with increasing concentration, this translates to different hedonic response patterns.

Experiment 2 has two major purposes. The first is to determine if the psychophysical functions of odor described by Experiment 1 are replicable with different subjects in a different experimental context. The second, and a major purpose, is to determine whether the presence of a taste alters the intensity and hedonic perception of odor. In this experiment I use a single taste stimulus, 0.8 M sucrose, that is pleasant to some individuals (sweet likers) and unpleasant to others (sweet dislikers).

As reviewed before, there is a paucity of research on the interaction of taste and odor in the realm of hedonics. Also, most of the studies have been an investigation of the effects of odor on taste. The effect of taste on odor hedonics has been looked at only indirectly in a learning paradigm (Zellner, Rozin, Aron, & Kulish, 1983). The lack of research on odor hedonics as affected by taste is surprising. There is evidence supporting the notion that olfaction is more hedonically modifiable than gustation (Bartoshuk, 1991a). Further, it has been shown that pairing odors with various negative (Bernstein & Webster, 1980; Kirk-Smith, Van Toller & Dodd, 1983) and positive (Booth, Lee, & McAleavey, 1976; Zellner, Rozin, Aron, & Kulish, 1983) experiences can alter their hedonic perception. Given the physiological and perceptual coupling of gustation and olfaction, it is reasonable to hypothesize that taste has an impact on odor hedonics and the current experiment examines this possibility.

Method

Subjects: Subjects were 49 undergraduate students who participated for course credit. There were 16 males and 33 females with an average age of 20.02 $\pm$ 2.67 (SD) years in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, popcorn and raspberry. Five concentrations 1.38, 2.08, 2.78, 3.48, and 4.18 (LOG [] x 10^5) of each odor were utilized in the experiment. Each concentration was judged with no tastant in the mouth or while the subject tasted 0.8 M sucrose. All taste-odor combinations were presented three times in random order throughout the experiment for a total of 30 judgments per dimension. Subjects rinsed with distilled water in between each stimulus.

Procedure:

Stimulus Delivery: The Two-Module Delivery system was used to present gustatory and olfactory stimuli simultaneously, but independently (General Method).

Hedonic Profile Determination: Prior to the experiment, each subject was classified as either a "liker" or "disliker" of concentrated sucrose according to the procedure described in the General Method.

Ratings: Ratings of odor intensity and hedonics were obtained using the magnitude estimation procedure described in the General Method. Subjects rated intensity and hedonics separately. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated only one odor.

Results

Intensity Ratings

Odor intensity ratings were examined using a between-within subjects ANOVA, with "liker/disliker" status as the single between factor and odor concentration and tastant condition as the two within factors. Different ANOVAs were conducted for each odor.

As expected, and as can be observed in Figure 3, odor intensity ratings increased with concentration for chocolate ($F(4,56)=46.2$, $p=.0000$), raspberry ($F(4,68)=41.8$, $p=.0000$), and popcorn odor ($F(4,48)=14.0$, $p=.0000$). Odor intensity ratings were significantly higher when 0.8 M sucrose was in the mouth for both chocolate ($F(1,14)=4.7$, $p=.047$) and popcorn odors ($F(1,12)=6.7$, $p=.023$), but not for raspberry odor. For all three odors, intensity ratings were not significantly affected by hedonic profile to sweet, i.e. whether the subjects were sweet likers or dislikers.

Hedonic Ratings

Odor hedonic ratings were examined using a between-within subjects ANOVA, with "liker/disliker" status as the single between factor and odor concentration and tastant condition as the two within factors. Different ANOVAs were conducted for each odor.

In contrast to intensity ratings, the effect of taste on odor hedonic ratings was significantly effected by hedonic profile to sweet for chocolate ($F(1,14)=10.6$, $p=.0057$), raspberry ($F(1,17)=7.6$, $p=.013$), and popcorn ($F(1,12)=9.36$, $p=.009$) odors. The hedonic ratings of sweet "likers" tended to increase slightly, but not significantly, when sucrose was in the mouth compared to nothing. However, as shown by Figure 4, "dislikers" gave significantly lower hedonic ratings to odor when 0.8 M sucrose was in their mouth. Thus, the presence of sucrose significantly influenced hedonic ratings of odor and this effect is completely accounted for by sweet dislikers.

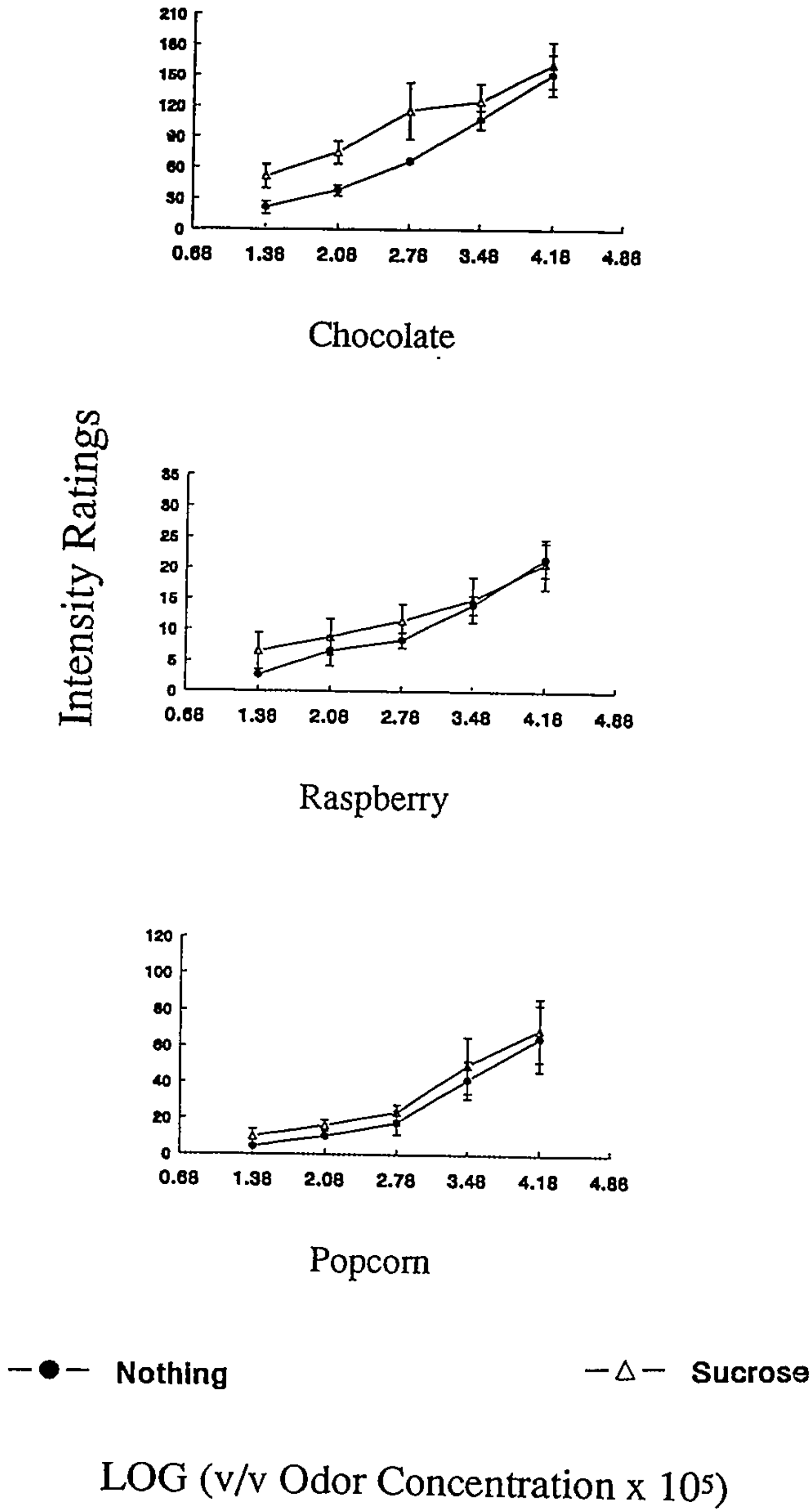
Discussion

The first purpose of this experiment was to determine if the psychophysical functions of odor described by Experiment 1 could be replicated with different subjects. When no taste was present in the mouth, the intensity and hedonic functions of all odors were remarkably similar to the functions demonstrated in Experiment 1. Thus, the stimuli and methods used are internally valid and replicate functions observed in the literature (Moskowitz, 1977).

The second and major purpose of this experiment was to determine whether a taste alters the intensity and hedonic perception of odor. Odor perception was influenced by the presence of taste in the mouth over the concentrations used here. Subjects gave higher intensity ratings to odor when sucrose was in the mouth compared to when nothing was in the mouth. Higher odor intensity ratings in the presence of sucrose have been demonstrated previously (Hornung & Enns, 1986). The extension provided by the current experiment, however, is that the increase in odor intensity ratings due to sucrose in the mouth was demonstrated by all subjects regardless of underlying hedonic profile to sweet. Therefore, taste in the mouth tends to increase intensity ratings of odor regardless of whether the taste is perceived as hedonically negative or positive.

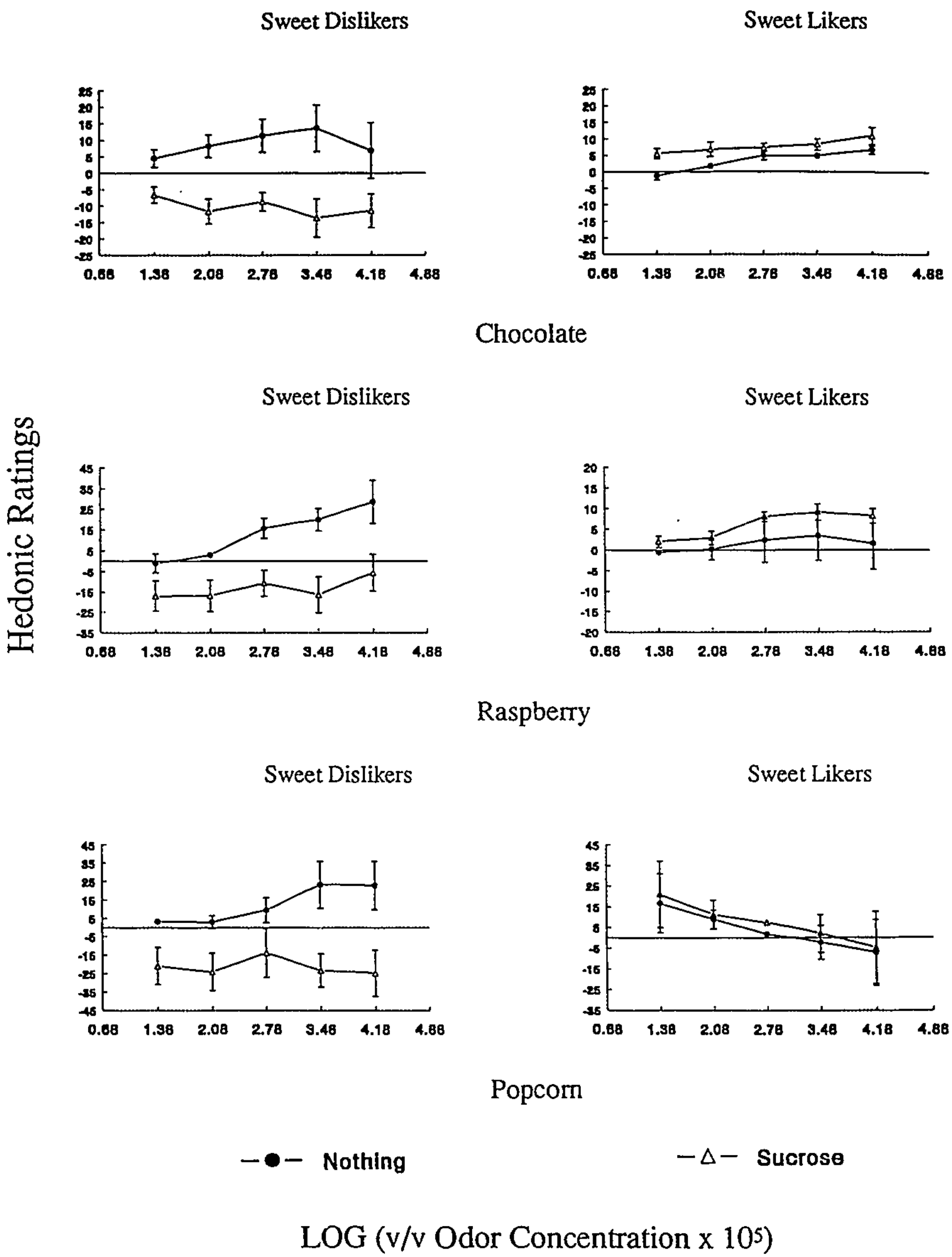
Odor hedonic ratings were influenced by taste in the mouth, but only for subjects who are dislikers of concentrated sucrose. Sucrose in the mouth did not alter ratings of odor hedonics for those who like the taste of concentrated sucrose. Therefore, the main effect of taste is completely accounted for by sweet "dislikers" shifting their hedonic ratings of odor downward. This experiment demonstrates that under the experimental circumstances used here, taste affects odor hedonics, but only when the taste had a negative hedonic tone. This is true for all three odors used in this experiment.

Figure 3: Mean (± SEM) intensity ratings of odor across five ascending concentrations in the presence of nothing or 0.8 M sucrose in the mouth, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). No distinction is made between sweet likers and dislikers. (SEMs not visible fall within the figure).



Intensity Ratings
0
30
60
90
120
150
180
210
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
0
5
10
15
20
25
30
35
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Raspberry
0
20
40
60
80
100
120
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Popcorn
Nothing
Sucrose
LOG (v/v Odor Concentration x 10^5)

Figure 4: Mean (± SEM) hedonic ratings of odor across five ascending concentrations with nothing or 0.8 M sucrose in the mouth for sweet dislikers (left) and sweet likers (right), for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol.)


Sweet Dislikers
Sweet Likers
Chocolate
Sweet Dislikers
Sweet Likers
Raspberry
Sweet Dislikers
Sweet Likers
Popcorn
Hedonic Ratings
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Nothing
Sucrose
LOG (v/v Odor Concentration x 10^5)

Chapter Five

Experiment 3

THE EFFECT OF NEGATIVE TASTE STIMULI OTHER THAN SUCROSE ON ODOR INTENSITY AND HEDONICS

The previous experiment demonstrated that the presence of a taste perceived as unpleasant reduced the reported hedonic ratings of odors. This result could be unique to the population of sweet dislikers. Alternatively, it could be that only tastes perceived as hedonically negative affect hedonic ratings of odor. The purpose of this experiment is to discriminate between these two possibilities by examining the effects of a taste perceived as hedonically negative by both sweet likers and dislikers on odor perception.

Method

Subjects: Subjects were 46 undergraduate students who participated for course credit. There were 10 males and 36 females with an average age of 19.33 $\pm$ 1.5 (SD) years in the study. Of these subjects, 21 were sweet likers and 25 were sweet dislikers.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, popcorn and raspberry. Five concentrations 1.38, 2.08, 2.78, 3.48, and 4.18 (LOG v/v [ ] x 10^5) of each odor were utilized in the experiment. Every concentration was judged with no tastant in the mouth or with a hedonically negative tastant in the mouth. All taste-odor combinations were presented three times in random order throughout the experiment, for a total of 30 judgments per dimension. Subjects rinsed with distilled water in between each stimulus.

Tastants: There were two hedonically negative tastants used, sucrose octaacetate (SOA; $C_{28}H_{38}O_{19}$) and sodium chloride (NaCl). SOA is a bitter substance with a unimodal threshold, and the concentration presented here (16×10^{-6} M) is unpleasant to all subjects (Boughter & Whitney, 1993). Sodium chloride is a salty substance, commonly used in food. But the concentration presented here (.1060 M) has been shown to be unpleasant when presented in the context of a simple solution (Pangborn, 1970; Looy, Callaghan, & Weingarten, 1992).

Procedure:

Stimulus Delivery: The Two-Module Delivery system was used to present gustatory and olfactory stimuli simultaneously, but independently (General Method).

Hedonic Profile Determination: Prior to the experiment, each subject was classified as either a "liker" or "disliker" of concentrated sucrose according to the procedure described in the General Method.

Verification of Negative Response to Tastants: Prior to the experiment, each subject was assigned to one of two possible tastant conditions, bitter or salty. The subject then verified a negative hedonic response to the tastant according to the following procedure.

Bitter: Subjects in the bitter condition were given a block of the following SOA concentrations: 0, 2, 4, 8, & 16×10^{-6} M (random order). After the subject tasted the range of concentrations, they were asked to rank the stimuli from least to most pleasant. The procedure was repeated. For both stimulus blocks, all subjects ranked distilled water as "most pleasant" and 16×10^{-6} M SOA as "most unpleasant."

Salty: Subjects in the salty condition were given a block of the following NaCl concentrations: 0.0, .0068, .0137, .0547, and .1060 M (random order). After the subject tasted the range of concentrations, they were asked to rank the stimuli from least to most pleasant. The procedure was repeated. All subjects ranked distilled water as "most pleasant" and .1060 M NaCl to be "most unpleasant."

Ratings: Ratings of odor intensity and hedonics were obtained using the magnitude estimation procedure described in the General Method. Subjects rated intensity and hedonics separately. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated only one odor.

Results

Intensity Ratings

Odor intensity ratings were examined using a between-within subjects ANOVA, with sweet liker / disliker status and bitter / salty tastant condition as the two between subjects factors and odor concentration and taste condition as the two within subjects factors. Different ANOVAs were conducted for each odor.

As expected and as can be seen in Figure 5, odor intensity ratings increased with odor concentration for chocolate ($F(4,44)=84.12$, $p=.0000$), raspberry ($F(4,44)=7.48$, $p=.0001$), and popcorn odors ($F(4,48)=28.34$, $p=.0000$). Odor intensity ratings were affected by taste for popcorn odor ($F(1,12)=5.96$, $p=.03$), but not chocolate or raspberry odors. Figure 5 (bottom panel) shows that popcorn odor intensity increased in the presence of a high concentration of taste compared to nothing. More importantly, the intensity effect observed for popcorn odor was not affected by underlying hedonic profile to sweet, as evidenced by non-significant Taste x Hedonic Profile interaction.

Hedonic Ratings

Odor hedonic ratings were examined using a between-within subjects ANOVA. Sweet liker / disliker status and bitter / salty tastant condition were the two between subjects factors and odor concentration and taste condition were the two within subjects factors. Different ANOVAs were conducted for each odor.

Hedonic ratings of all odors were affected by the presence of a taste. As shown in Figure 6, hedonic ratings of chocolate ($F(1,11)=10.27$, $p=.008$), raspberry ($F(1,11)=17.5$, $p=.001$), and popcorn odor ($F(1,12)=8.2$, $p=.0014$) all decreased significantly when an aversive taste was in the mouth.

There was no significant interaction between the presence of taste in the mouth and underlying hedonic profile to sweet for any odor presented here. In contrast to the findings of the previous experiment, both sweet likers and dislikers rated odor as less pleasant when a taste perceived as unpleasant was present in the mouth (Figure 6).

Discussion

In the previous experiment, only sweet dislikers decreased their hedonic ratings of odor in the presence of 0.8 M sucrose in the mouth. Two explanations of this result were put forth. It is possible that sweet dislikers are a unique population or that any taste perceived as hedonically negative can reduce reported ratings of odor hedonics. The present experiment showed that sweet likers as well as dislikers demonstrate a negative shift in reported odor hedonics due to the immediate experience of a hedonically negative taste in the mouth. The last two studies lead to the conclusion that all subjects will report lower hedonic ratings of odor when a taste perceived as unpleasant is in the mouth. The effect of a negative taste on hedonic ratings generalizes to other taste substances is not limited to dislikers of concentrated sucrose.

However, gustation may not be the only modality that affects odor perception. It is possible that presenting *any* negative stimulus concomitantly with odor would reduce reported hedonic ratings of odor. Perhaps experiencing an aversive sensation induces a negative mood, which is then reflected by a reduction in odor pleasantness.

Figure 5: Mean (± SEM) intensity ratings of odor across five ascending concentrations with nothing or an aversive taste in the mouth, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). No distinction is made between sweet likers and dislikers. (SEMs not visible fall within the symbol).

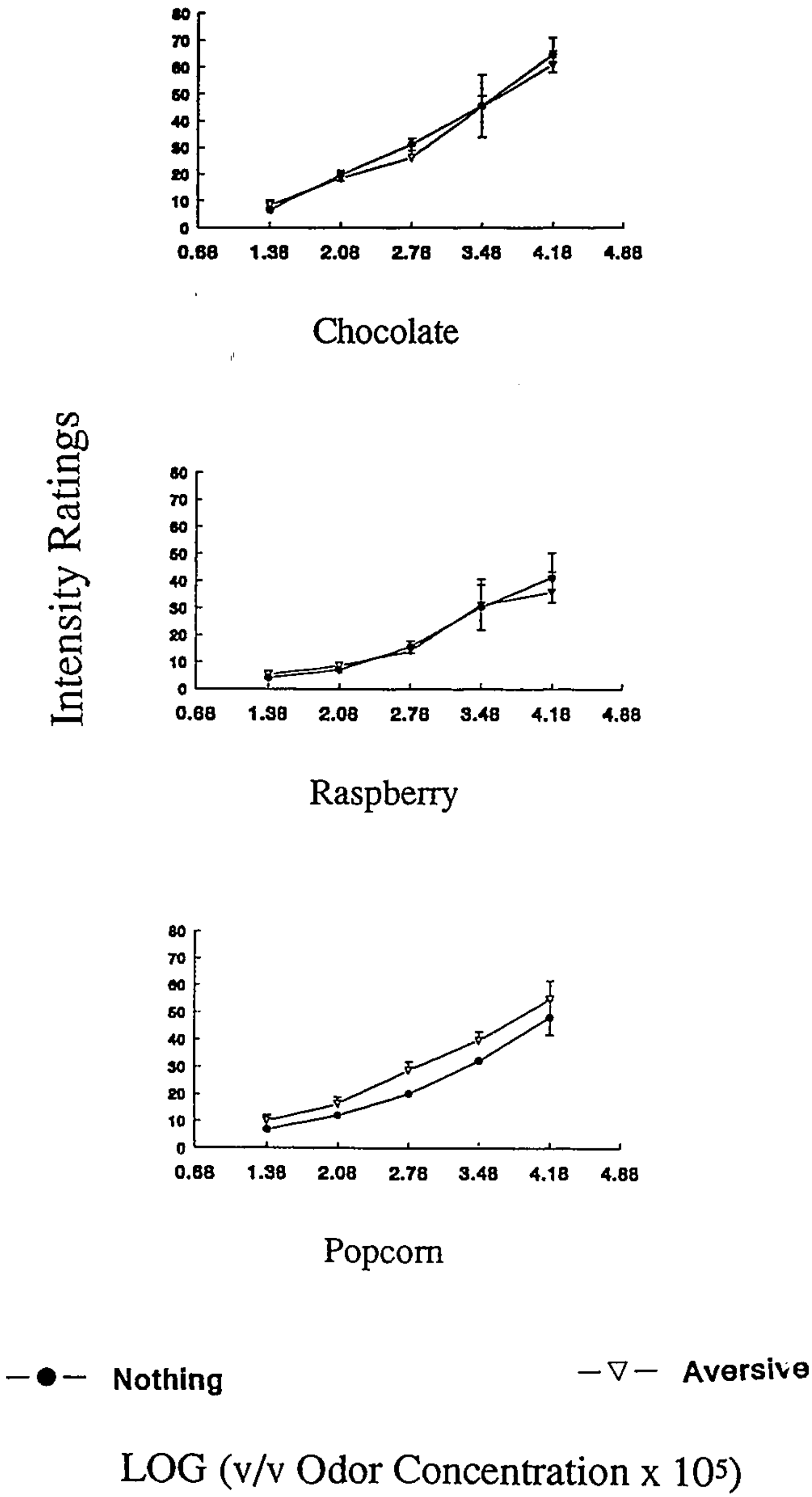
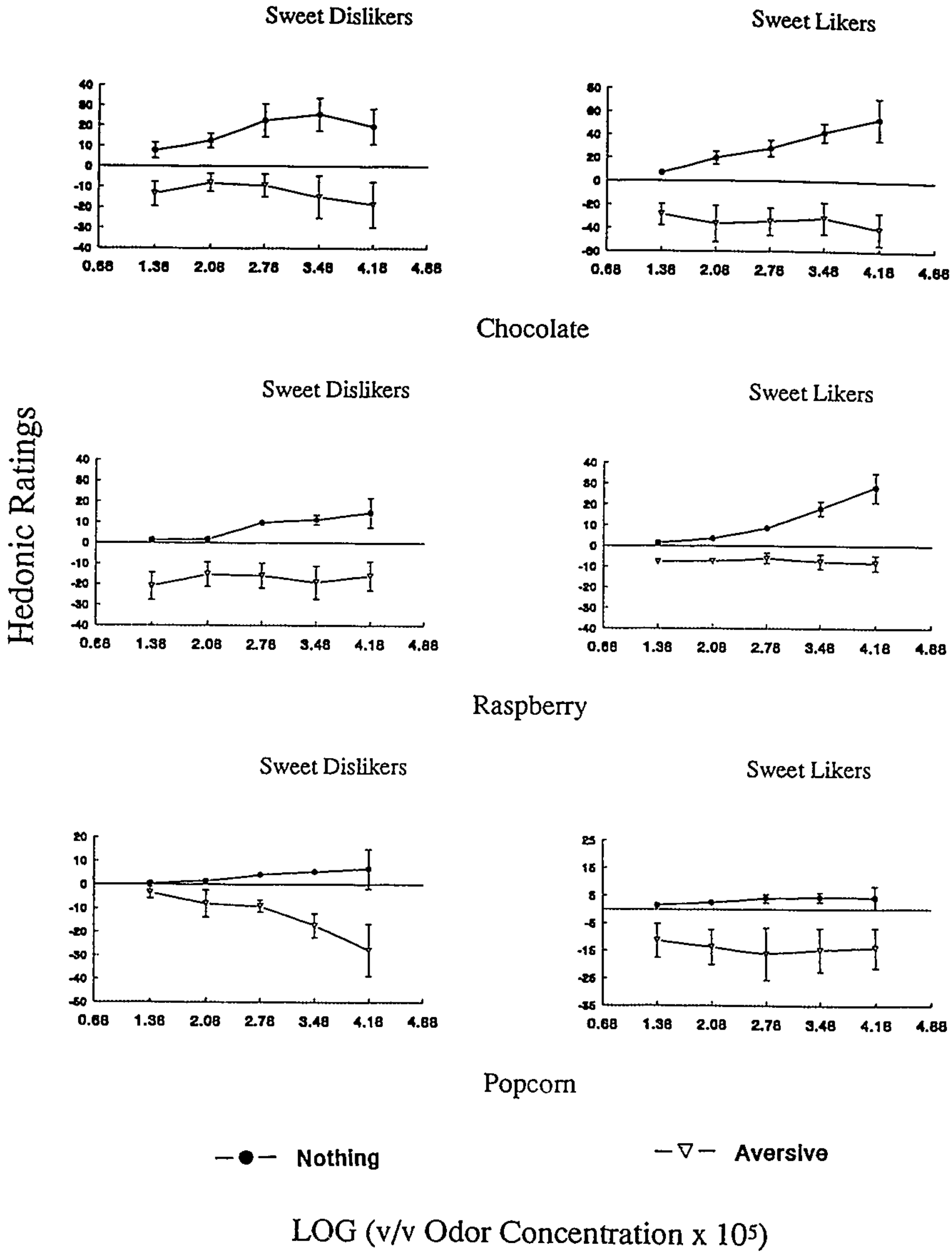

80
70
60
50
40
30
20
10
0
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
Intensity Ratings
Raspberry
Popcorn
Nothing
Aversive
LOG (v/v Odor Concentration x 10^5)

Figure 6: Mean (± SEM) hedonic ratings of odor across five ascending concentrations in the presence of nothing or an aversive taste in the mouth for sweet dislikers (left) and sweet likers (right), for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol).


Sweet Dislikers
Sweet Likers
Chocolate
Sweet Dislikers
Sweet Likers
Raspberry
Sweet Dislikers
Sweet Likers
Popcorn
Hedonic Ratings
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Nothing
Aversive
LOG (v/v Odor Concentration x 10^5)

Chapter Six

Experiment 4

AN AVERSIVE NON-GUSTATORY STIMULUS DOES NOT AFFECT ODOR PERCEPTION

The last two experiments have shown that the concomitant presence of a taste perceived as hedonically negative can reduce reported hedonic ratings of odors. There are two explanations for this result. Due to physiological proximity and frequent perceptual coupling in food, taste and smell may have a "privileged" relationship. That is, taste and smell may have a special tendency to influence one another along the hedonic dimension. Another explanation involves the effect of a negative mood on odor hedonics. It is possible that experiencing an aversive taste induces a general negative affective state and that the negative affect from a taste perceived as unpleasant transfers to the odor. This raises the possibility that any aversive stimulus presented with an odor would reduce reported hedonic ratings.

Link Between Odor, Emotion, and Mood

In the last two experiments, we have shown that subjects give lower hedonic ratings to an odor when they have an aversive taste in their mouth. The extent to which this effect is due to a general negative affective state is unknown. It has been proposed that odor, emotion, and mood are strongly linked (Schiffman, 1991; Ehrlichman & Bastone, 1992). There is some evidence that odor influences mood (see Ehrlichman & Bastone, 1992 for a review), but the converse has not been examined.

There is some evidence that negative affect induced by one stimulus may transfer to another stimulus. Zillman (1971) first described the "excitation transfer effect."

The emotions induced by an arousing experience subsequently affected a second event (Zillman, 1971). Zillman's (1971) interpretation was that arousal from the first event is misattributed to the second event, resulting in affective "transfer." If an excitation transfer interpretation is applied to Experiments 1 and 2 of this dissertation, the negative arousal induced by an unpleasant taste might transfer to the odor, thereby reducing reported hedonic ratings. A brief review of the effects of aversive stimuli on chemosensory hedonics may reveal whether excitation transfer explains the results presented earlier.

Effect of Non-Gustatory Aversive Stimuli on the Chemical Senses

There have been a few studies examining the ability of other modalities to alter hedonic ratings of chemosensory stimuli. The effect of aversive noise and equally loud music on hedonic ratings of sweet and salty tastes has been examined (Ferber & Cabanac, 1987). Despite the equal intensity of the acoustic stimulation, subjects showed increased physiological stress to noise, but not music. In this study, hedonic ratings of taste *increased* in the presence of both noise and music. Such results indicate that a negative affective state (inferred from an increase in physiological indices of stress) induced by aversive acoustic stimulation may not transfer to hedonic ratings of taste substances.

A different aversive stimulation, high ambient temperature (40° C), has been found to reduce hedonic tone of food odors (Russek, Fantino, & Cabanac, 1979). While the authors discussed this finding in terms of the subjects' metabolic state, it could be that the aversiveness of high heat transferred to the hedonic rating of odor. However, this study also showed that the hedonic tone of sweet and salty tastes were unaffected by the same aversive temperature (Russek, Fantino, & Cabanac, 1979).

The effect of aversive stimulation on hedonic perception of chemosensory stimuli is unclear. Different effects of an aversive stimulus on taste and odor hedonic ratings have been reported (Russek, Fantino, & Cabanac, 1979). Further, there may be different effects on chemosensory hedonics depending on what type of aversive stimuli is used (Russek, Fantino, & Cabanac, 1979; Ferber & Cabanac, 1987). Additionally, aversive stimuli have been shown to both elevate and decrease reported hedonic ratings of chemosensory stimuli. Thus, it is not clear that negative affect from an aversive stimulus transfers to chemosensory stimuli, causing a decrease in reported hedonic ratings.

The current experiment examines the effect of a negative non-gustatory stimulus on odor perception, especially odor hedonics. If an aversive non-gustatory stimulus causes a reduction in hedonic ratings of odor, then the results of Experiments 2 and 3 may result from a general effect of negative stimuli on odor pleasantness. If an aversive non-gustatory stimulus does not cause a reduction in hedonic ratings of odor, then the hedonic transfer observed in Experiments 2 and 3 may reflect a privileged relationship between the two chemical senses of taste and smell.

Method

Subjects: Subjects were 28 undergraduate students who participated for credit in the study. There were 5 males and 23 females with an average age of 19.54 ± 0.88 (SD) years in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, popcorn and raspberry. Five concentrations 1.38, 2.08, 2.78, 3.48, and 4.18 (LOG [] x 10^5) of each odor was presented three times in random order throughout the experiment. Each odorant was judged with no sound, while the subject listened to a musical tape of their choice, or with an aversive (loud and high pitched) tone.

<u>Procedure</u>:

Stimulus Delivery: The Two-Module Delivery system was used to present olfactory stimuli (General Method). Since this experiment utilized no tastant, the straw was removed and subjects simply sniffed the cotton ball in the upper portion of the apparatus.

Verification of Hedonic Tone of Acoustic Stimulation: Subjects were instructed to come to the experiment with a musical cassette of their choice. Prior to the experiment, each subject verified that they liked the musical cassette selected and found the volume level acceptable. They were also asked to describe the tone presented as pleasant, aversive, or neutral. All subjects reported that the tone was aversive. It is known that humans find loud, high pitched tones to be hedonically negative (Flora, Schieferecke, & Bremenkamp, 1992). Furthermore, such stimuli are known to increase heart rate and other physiological signs of stress or discomfort (Ferber & Cabanac, 1987).

Ratings: Ratings of odor intensity and hedonics were obtained using the magnitude estimation procedure described in General Method. Subjects rated intensity and hedonics at separate times during the experiment. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated only one odor.

Results

Intensity Ratings

A multifactor within-subjects ANOVA was used to examine the effect of odor concentration and acoustic stimulation on odor intensity ratings. Different ANOVAs were conducted for each odor.

As expected, odor intensity ratings increased with concentration for chocolate ($F(4,36)=21.3$, $p=.0000$), raspberry ($F(4,28)=42.5$, $p=.0000$), and popcorn odor ($F(4,32)=40.2$, $p=.0000$). For all three odors, intensity ratings were unaffected by the different acoustic conditions (Figure 7).

Hedonic Ratings

A multifactor within-subjects ANOVA was used to examine the effect of odor concentration and acoustic stimulation on odor hedonic ratings. Different ANOVAs were conducted for each odor.

The same hedonic functions found in Experiment 1 were maintained in the presence of all acoustic stimulation. Most importantly though, for all odors, hedonic ratings were unaffected by the aversive noise or the hedonically pleasant music (Figure 8).

Discussion

This experiment demonstrates that a negative non-gustatory stimulus does not alter odor perception, particularly hedonic ratings of odor. Therefore, it seems unlikely that the decreased hedonic ratings found in Experiments 2 and 3 occurred because an aversive stimulus induced a negative affective state. Thus, under the experimental conditions used here, the ability of a negative stimulus to reduce hedonic ratings of food odors appears to be specific to the modality of taste, reinforcing the suggestion of others (Bartoshuk, 1991a) that taste and smell may have a privileged relationship.

The experiments that have been presented so far indicate that the presence of a taste perceived as hedonically negative reduces the reported hedonic ratings of odor. However, it could be the case that subjects are reporting the overall hedonics of the mixture rather than odor hedonics *per se*. The question of whether subjects can separate out their hedonic response to taste, odor, and mixture reveals more about taste-smell confusion and the privileged relationship between taste and smell. This question is addressed in the next chapter.

Figure 7: Mean (± SEM) intensity ratings of odor across five ascending concentrations in the presence of nothing, pleasant, or aversive acoustic stimulation, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol).

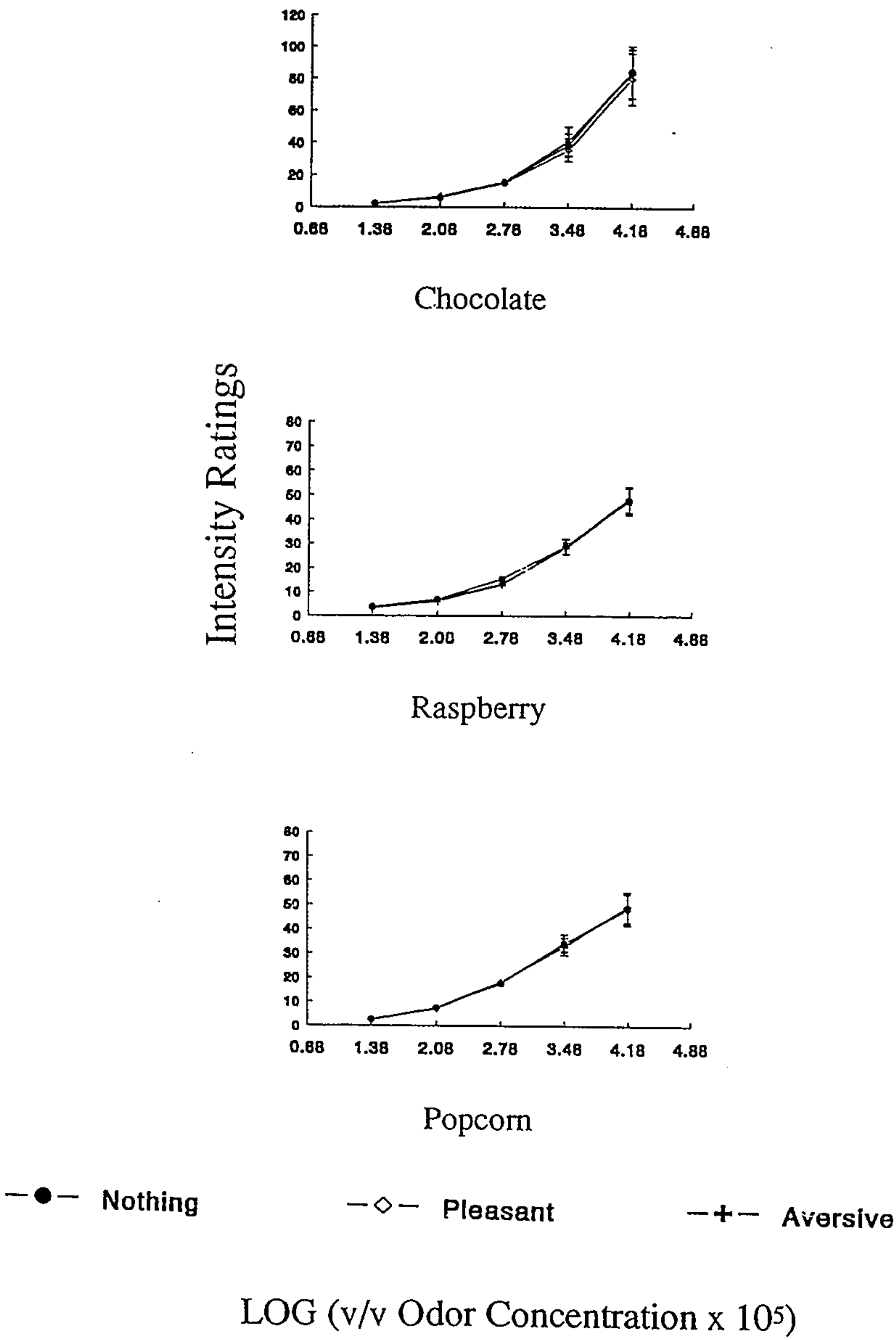
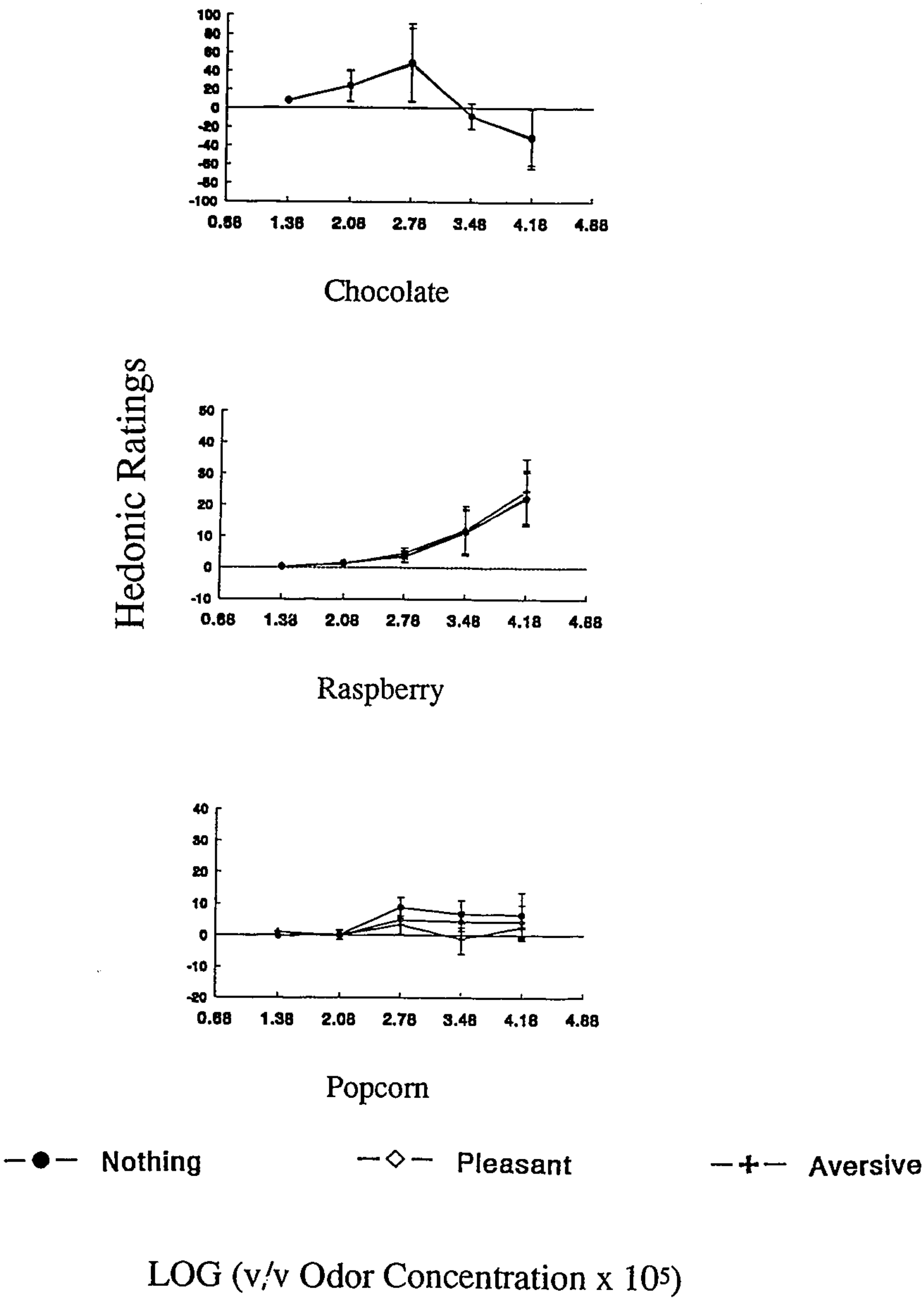

Intensity Ratings
120
100
80
60
40
20
0
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Chocolate
80
70
60
50
40
30
20
10
0
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Raspberry
80
70
60
50
40
30
20
10
0
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Popcorn
Nothing
Pleasant
Aversive
LOG (v/v Odor Concentration x 10^5)

Figure 8: Mean (± SEM) hedonic ratings of odor across five ascending concentrations in the presence of nothing, pleasant, or aversive acoustic stimulation, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol).



Hedonic Ratings
100
80
60
40
20
0
-20
-40
-60
-80
-100
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
50
40
30
20
10
0
-10
Raspberry
40
30
20
10
0
-10
-20
Popcorn
Nothing
Pleasant
Aversive
LOG (v/v Odor Concentration x 10^5)

Chapter Seven

Experiment 5

A STUDY OF SUBJECTS' ABILITY TO BE ANALYTIC ABOUT TASTE AND SMELL MIXTURES

Thus far, the studies in this thesis have utilized the method of modality-specific judgments. As discussed previously, the method is termed *modality specific judgments* since the experimenter asks for ratings of one modality only (e.g. odor) as opposed to both component and mixture ratings. The modality-specific rating method has been used to explore taste-smell confusions. For example, olfactory referral underlies increased taste intensity ratings in the presence of odor (Frank, Ducheny, & Mize, 1989). Experiments 2 and 3 showed that for all odors used, the concomitant presence of a negatively perceived taste significantly reduced reported ratings of odor hedonics. This "hedonic referral" of a negative taste to odor is robust, demonstrated by all subjects, and is not due to a negative affective state.

An issue that has emerged from studies utilizing modality specific judgments is the question of whether subjects are rating the modality specified by the experimenter or rating the mixture. Frank and colleagues (1991) found that subjects presented with a taste-odor mixture will tend to report the overall intensity when asked for only one judgment. Thus, taste intensity ratings in the presence of odor were not different from intensity ratings of taste alone when subjects were asked to break down overall intensity into component intensities (Frank, Wessel, & Shaffer, 1991). However, when subjects are asked for one rating to describe a taste-smell mixture, taste intensity ratings in the presence of odor were higher than intensity ratings of taste alone. In the present experiment, subjects are required to partition their perception of taste-odor mixtures in order to determine whether subjects are rating the modality specified (odor), the taste component, or the mixture.

Methods

Subjects: Subjects were 28 (17 females and 11 males) undergraduate and graduate who were paid $5 / hour for their participation. There were 17 females and 11 males with an average age of 21.57 • 2.44 (SD) in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, popcorn and raspberry. Three concentrations 1.38, 2.78, & 4.18 (LOG [] x 10^5) of each odor were presented. Sucrose at a concentration of 0.8 M was presented as a tastant.

Stimulus Blocks: Each concentration of odor with no taste in the mouth was presented three times in random order. Each concentration of odor with 0.8 M sucrose in the mouth was presented three times in random order. Order of stimulus blocks was counterbalanced across subjects. Subjects rinsed with distilled water in between each stimulus.

Procedure:

Stimulus Delivery: The Two-Module Delivery system was used to present gustatory and olfactory stimuli simultaneously, but independently (General Method).

Hedonic Profile Determination: Prior to the experiment each subject was classified as either a "liker" or "disliker" of concentrated sucrose according to the procedure described in the General Method.

Ratings: When odor was presented alone, subjects rated intensity and hedonics of odor. For taste-odor mixtures, subjects rated the intensity and hedonics of taste ("What you are sipping through the straw"), odor ("What you are smelling on the cotton ball"), and overall sensation ("The combination of the taste and smell") using the magnitude estimation procedure (General Method). Subjects rated intensity and hedonics in separate stimulus blocks. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated only one odor.

Results

Intensity Ratings

A between-within subjects ANOVA was used to examine the effect of odor concentration, component (what subjects were asked to rate), and hedonic profile to sweet on intensity ratings. Different ANOVAs were conducted for each odor.

The ratings obtained in this experiment will be labeled with the following acronyms: odor rated when only odor was presented (O / O); odor rated when odor was presented with taste (O / O+T); taste rated when odor was presented with taste (T / O+T); overall combination rated when odor was presented with taste (O+T / O+T).

As shown in Figure 9, intensity ratings in the (O / O) and (O / O+T) conditions were lower than the (T / O+T) and (O+T / O+T) conditions for chocolate ($F(3,24)=8.17$, $p=.00006$) and popcorn ($F(3,24)=4.83$, $p=.009$) odors. This comparison approached statistical significance for raspberry ($F(3,18)=2.85$, $p=.06$). There was no difference between (O / O) and (O / O+T) ratings, indicating that subjects do not increase their ratings of odor intensity in the presence of taste if they are instructed to be analytical about their judgments. There was no difference between (T / O+T) and (O+T / O+T) ratings, indicating that intensity ratings of the overall mixture (the combination of the taste and smell) are mostly captured by the intensity of the taste.

Hedonic Ratings

A between-within subjects ANOVA was used to examine the effect of odor concentration, component (what subjects were asked to rate), and hedonic profile to sweet on hedonic ratings. Different ANOVAs were conducted for each odor.

The acronyms used to label intensity ratings in the section above will be used to designate hedonic ratings obtained in this experiment: odor rated when only odor was presented (O / O); odor rated when odor was presented with taste (O / O+T); taste rated when odor was presented with taste (T / O+T); overall combination rated when odor was presented with taste (O+T / O+T).

As shown in Figure 10, hedonic ratings in the (O / O) and (O / O+T) conditions were higher than the (T / O+T) and (O+T / O+T) conditions for chocolate ($F(3,24)=4.05$, $p=.018$) and raspberry ($F(3,18)=4.07$, $p=.022$). There was no difference between (O / O) and (O / O+T) ratings, indicating that subjects do not significantly decrease their ratings of odor intensity in the presence of taste if they are instructed to be analytical about their judgments. There was no difference between (T / O+T) and (O+T / O+T) ratings, indicating hedonic ratings of the overall mixture (the combination of the taste and smell) are mostly captured by the hedonic tone of the taste.

Hedonic ratings were significantly affected by hedonic profile to sweet for chocolate ($F(3,24)=5.5$, $p=.005$), raspberry ($F(3,18)=4.0$, $p=.024$), and popcorn ($F(3,24)=13.7$, $p=.00002$) odors. Figure 11 shows that for both sweet likers and dislikers, hedonic perception of the combination of taste and odor is mostly captured by the hedonic tone of the taste, as there is no difference between (T / O+T) and (O+T / O+T) hedonic ratings.

Discussion

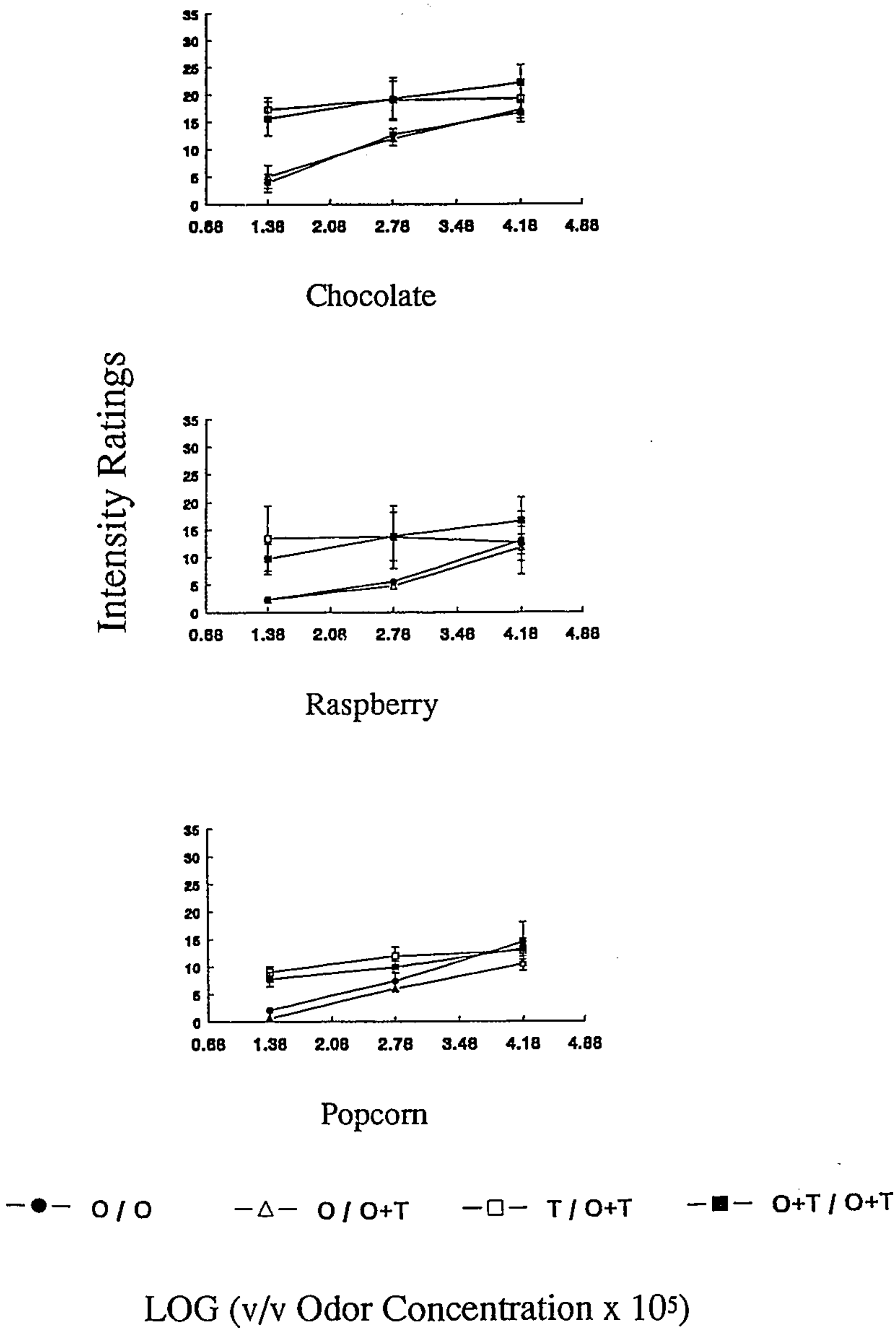
If instructed, subjects can clearly distinguish between how much they like a taste and how much they like an odor when they experience the two modalities concomitantly. Odor hedonic ratings in the odor alone and odor with sucrose conditions were remarkably similar. The hedonic tone of the overall sensation is dominated by the taste component for likers and dislikers.

The results of the present experiment allow for better interpretation of the previous findings described in this dissertation. When subjects are presented with a taste-odor mixture consisting of a taste they perceive as negative and a pleasant or neutral odor, they are capable of differentiating their hedonic response to the components. However, if only asked for one rating, they will tend to report hedonic response to the mixture. Hedonic perception of the taste component tends to dominate the mixture, regardless of the affective direction since sweet likers and dislikers (T / O+T) ratings were not different from (O+T / O+T) ratings. However, perception of the taste as hedonically negative is especially salient and results in a greater shift than a hedonically positive perception of the taste. Previous studies have found that disliking seems to be the more salient direction of affective response to simple stimuli (Moskowitz, 1977; Cabanac, 1979) and food (Rozin & Vollmecke, 1986).

In the experiments reported here, the taste component of a taste-odor mixture predicts the hedonic tone of the overall sensation. But that does not mean that taste is always the most hedonically salient component of a taste-odor mixture. It may be that taste dominated the overall percept in these experiments because it was the more intense component. One study has shown that the overall intensity of taste-odor mixtures is determined by the most intense component. Commetto-Muniz (1981) utilized complex stimuli (e.g. almond or vanilla extract) that stimulates olfaction and gustation. Subjects were then asked to rate odor intensity when stimuli were presented in sniff bottles, taste intensity when stimuli were presented orally and the nose was pinched, and overall intensity when stimuli were presented orally and the nose was open. Odor functions grew less rapidly than taste functions for all stimuli. At high concentrations of taste, flavor intensity functions were very similar to taste intensity functions. However, at low concentrations of taste, odor is more salient to flavor intensity functions. Cometto-Muniz (1981) did not obtain hedonic ratings, but the results suggest that the more intense component of a taste odor combination dominates the mixture.

Another explanation is that the component with the greater absolute hedonic value dominates the hedonic tone of the mixture. Enns and Hornung (1987) asked subjects to rate the pleasantness of the taste, smell and overall pleasantness of the two together. If one component was negative and the other positive, the flavor followed the component with the greater absolute hedonic value (Enns & Hornung, 1987). Given the relationship between intensity and hedonics in chemosensory perception, these two explanations are not mutually exclusive and both are consistent with the findings presented here.

Figure 9: Mean (± SEM) odor intensity ratings when odor was presented alone (O / O) across three ascending odor concentrations; mean (± SEM) odor intensity ratings when odor was presented with 0.8 M sucrose across three odor concentrations (O / O+T); mean (± SEM) taste intensity ratings when odor was presented with 0.8 M sucrose across three odor concentrations (T / O+T); mean (± SEM) overall stimulus intensity ratings when odor was presented with 0.8 M sucrose across three odor concentrations (O+T / O+T), for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). No distinction is made between sweet likers and dislikers. (SEMs not visible fall within the symbol.)



Intensity Ratings
35
30
25
20
15
10
5
0
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
Raspberry
Popcorn
O / O
O / O+T
T / O+T
O+T / O+T
LOG (v/v Odor Concentration x 10^5)

Figure 10: Mean (± SEM) odor hedonic ratings when odor was presented alone (O / O) across three ascending odor concentrations; mean (± SEM) odor hedonic ratings when odor was presented with 0.8 M sucrose across three odor concentrations (O / O+T); mean (± SEM) taste hedonic ratings when odor was presented with 0.8 M sucrose across three odor concentrations (T / O+T); mean (± SEM) overall stimulus hedonic ratings when odor was presented with 0.8 M sucrose across three odor concentrations (O+T / O+T), for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). No distinction is made between sweet likers and dislikers. (SEMs not visible fall within the symbol.)

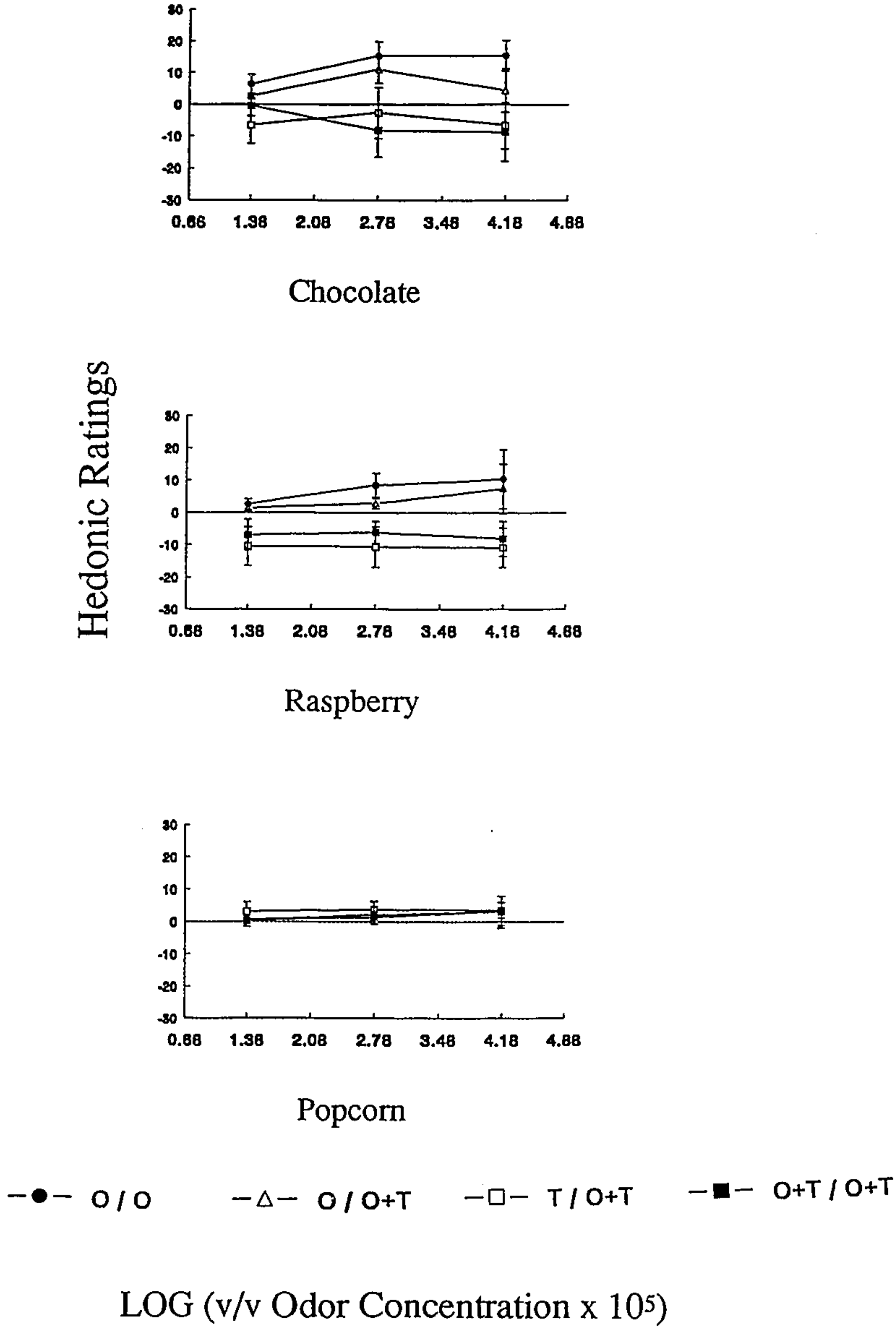
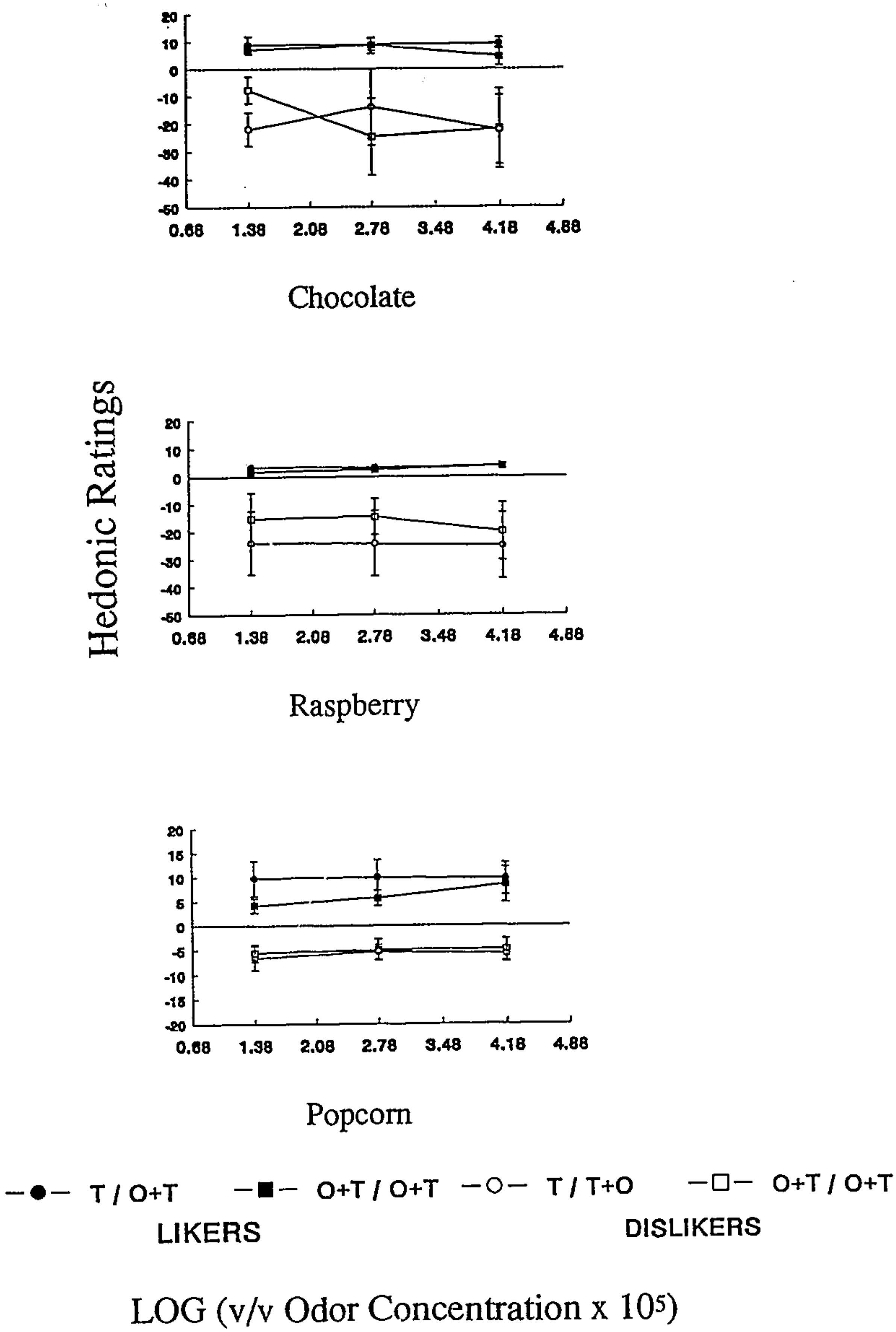

Hedonic Ratings
30
20
10
0
-10
-20
-30
0.66
1.36
2.06
2.76
3.46
4.16
4.86
Chocolate
Raspberry
Popcorn
O / O
O / O+T
T / O+T
O+T / O+T
LOG (v/v Odor Concentration x 10^5)

Figure 11: Mean (± SEM) hedonic ratings of taste when odor was presented with 0.8 M sucrose across three odor concentrations (T / O+T); mean (± SEM) overall stimulus hedonic ratings when odor was presented with 0.8 M sucrose across three odor concentrations (O+T / O+T), for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). Sweet likers and sweet dislikers are compared. (SEMs not visible fall within the symbol.)


Hedonic Ratings
20
10
0
-10
-20
-30
-40
-50
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
20
10
0
-10
-20
-30
-40
-50
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Raspberry
20
15
10
5
0
-5
-10
-15
-20
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Popcorn
T / O+T
O+T / O+T
LIKERS
T / T+O
O+T / O+T
DISLIKERS
LOG (v/v Odor Concentration x 10⁵)

Chapter Eight

Experiment 6

ALLIESTHESIA IN THREE TASTANTS AND THREE FOOD ODORS

Alliesthesia

The pleasantness of sensory stimuli is influenced by internal state, a phenomenon called alliesthesia (Cabanac, 1971). Alliesthesia is bi-directional. In positive alliesthesia, the stimulus becomes more pleasant with a change in internal state. In negative alliesthesia, a pleasant stimulus becomes indifferent or unpleasant (Cabanac, 1979). It has been argued that such affective changes have the larger function of motivating behaviors that contribute to the regulation of vital biological systems (Cabanac, 1979).

Chemosensory Alliesthesia

In the specific case of chemosensory stimuli, pleasantness is affected by whether the subject is hungry or sated. The pleasantness of sweet taste (DuClaux & Cabanac, 1970; Cabanac, 1971) decreases after a meal or glucose load in normal weight non-fasted subjects. Shifts in pleasantness due to changes in internal state are independent of sensory magnitude, as perceived intensity is not altered by hunger or satiety (Cabanac, 1971).

The evidence for odor alliesthesia is not as clear as the evidence for taste alliesthesia. An early demonstration of alliesthesia showed that hedonic ratings of the smell of orange syrup were lower when subjects were sated compared to hungry (Cabanac, 1971). Cabanac and colleagues (DuClaux, Feisthauer & Cabanac, 1973) later expanded the range of odor stimuli and examined the effect of internal state on food and non-food odors. Subjects reported lower hedonic ratings in response to food odors only after a glucose load relative to a hungry state (DuClaux, Feisthauer & Cabanac, 1973). As with taste, the changes in odor pleasantness that accompany satiety are not due to shifts in perceived intensity.

However, another study did not find clear evidence for food odor alliesthesia. Engen and colleagues (Mower, Mair, & Engen, 1977) had subjects rate the pleasantness and intensity of chocolate, orange, maple, and licorice odors while hungry and sated. No changes in intensity ratings accompanied the change in internal state as would be expected according to Cabanac's (1979) view that hedonic perception is involved in motivation. All subjects demonstrated negative alliesthesia for at least one odor, but did not shift consistently for all food odors. Internal state did not affect hedonic ratings of licorice odor for any subject (Mower, Mair, & Engen, 1977). It is not clear if the varied results of odor alliesthesia studies are due to methodological differences, differences in odor stimuli used, or lack of a robust effect.

Alliesthesia and Ingestive Behavior

Alliesthesia, especially negative alliesthesia, is an important phenomenon in understanding the relationship between sensory input (particularly the hedonic aspect of perception) and food intake and food choice. Within a meal, negative alliesthesia is the sensory correlate of meal termination (Weingarten & Gowans, 1991 but see Mook & Votaw, 1992). Alliesthesia for sweet taste is a robust finding (Cabanac, 1971). But results on pure odor alliesthesia are mixed. In the context of flavor perception, the question of which component changes due to internal state remains unexplored. However, before alliesthesia in taste-odor mixtures can be examined, alliesthesia in simple stimuli, particularly food odors, must be demonstrated.

Method

Subjects: Subjects were 20 undergraduates who participated for credit in an Introductory Psychology class. There were 16 females and 4 males with an average age of 22.9 • 1.71 (SD) in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, raspberry, and popcorn. Odors were arranged in independent blocks (odors were not mixed) of five concentrations (1.38, 2.08, 2.78, 3.48, and 4.18 LOG [] x 10^5) presented two times in random order. Taste stimuli consisted of a prototypical sweet (sucrose at five concentrations: 0.0, 0.1, 0.2, 0.4, 0.8 M), bitter (sucrose octaacetate at five concentrations: 0, 2, 8, 16, 32 x 10^{-6} M), and salty (sodium chloride at five concentrations: 0.0, .0068, .0137, .0517, .106 M). Taste stimuli were also arranged in independent blocks of five concentrations presented twice in random order. Whether a subject judged tastes or odors first was counterbalanced across subjects. The presentation order for the different tastants and odorants was random.

Procedure:

Subjects participated in two sessions, each separated by a seven-day interval. Half the subjects were tested first in the deprived condition (after an 18-hour fast), the other half in the sated condition (30 minutes after a satiating meal). Both deprived and sated sessions were conducted at the same time of day.

The sip-and-spit procedure, described in the General Method section, was followed for both sessions. In both sessions, subjects evaluated the same stimuli and made the same ratings of stimulus intensity and hedonics.

Stimulus Delivery: Odors were presented in the Two-Module Delivery system, but with no taste component. Tastes were delivered in medicine cups with approximately 15 ml of solution in each cup. Subjects rinsed with distilled water in between each taste sample.

Hedonic Profile Determination: Prior to the experiment each subject was classified as either a "liker" or "disliker" of concentrated sucrose according to the procedure described in the General Method.

Ratings: Ratings of odor intensity and hedonics were obtained using the magnitude estimation procedure described in the General Method. Ratings of taste intensity and hedonics were also obtained using the magnitude estimation procedure described in the General Method. Subjects rated intensity and hedonics at separate times during the experiment. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated all odors and tastes, for a total of sixty stimuli.

Verification of Subjects' Internal State: To ensure that subjects were truly in a physiological state of satiation or deprivation, hunger ratings were obtained from all participants. Hunger ratings were obtained at three times during each session: prior to rating the first stimulus, at the mid-point of the session (in between the intensity and hedonic ratings), and at the end of the session. Subjects used a 200 mm visual analog scale with anchors labeled "not hungry at all" (20 mm) and "extremely hungry" (180 mm) to rate how hungry they felt. The hunger scale was reproduced on a single sheet of paper, but a separate sheet was provided for each rating. Subjects were asked to describe "How hungry are you right now?" by placing a mark on the scale ranging from "not hungry at all" to "extremely hungry." The data obtained from a visual analog scale are the distances from one end of the line to the subject's mark. The visual analog scale technique is assumed to produce ratio-scale data (Price, McGrath, Rafii & Buckingham, 1983) and can therefore be analyzed using parametric tests such as analysis of variance.

The purpose of obtaining subjective measures of hunger for each participant was two-fold: First, subjective hunger ratings confirm that subjects actually were responsive to the deprivation and satiation manipulations. Second, experiencing chemosensory stimuli might actually alter subjects' internal state. Most people have had the experience of suddenly feeling hungry upon smelling food. If smelling food odors and tasting sapid substances increase subjects' feelings of hunger as the experimental session progresses, then data analysis would have to take stimulus presentation time into account. If hunger ratings remain the same throughout the course of the session, then it is proper to group stimuli from one session together.

Data Normalization Across Sessions: Because this experiment consisted of two sessions, an additional step in the data normalization procedure was conducted. "Normalizing the data across sessions" eliminates the possibility that subjects arbitrarily decide to use totally different numbers during the two sessions. If this happened, one could not compare the ratings given during the two sessions. An obvious way to ensure that subjects are consistent in their use of numbers in both sessions would be to remind them of the numbers they used in the first session and ask them to use similar numbers in the second session. However, Marks (1974) has argued that for the purposes of studying sensory processes, the magnitude estimation procedure is most accurate when minimal constraint is put on the subject. This is the rationale for not imposing a prescribed modulus at the beginning of the experiment.

So as to minimally constrain subjects, no further instruction was given beyond the standard directions for magnitude estimation (General Method). To ensure that subjects are using consistent numbers across sessions, a normalization procedure described by Murphy, Cain, and Bartoshuk (1977) was used. A subject's ratings for a subset of stimuli common to both sessions was used to derive a ratio to correct for differences in numbers used in different sessions. In this case, the arithmetic mean of ratings for stimulus concentrations in the middle of the range served as the subset of common stimuli. The average of the middle range stimuli for a subject was calculated. A ratio of the overall average of the middle stimuli to the average of the middle range stimuli for a particular session was derived. This ratio was then multiplied by the average of all a subject's judgments to produce a rating that is "normalized across sessions." A subject's "normalized across sessions" ratings were then compiled so a subject median could be determined. Data normalization across subjects (to eliminate differences in the numbers used by individual subjects) was then done according to the procedure described in the General Method.

Results

Hunger Ratings

Hunger ratings were examined using repeated measures ANOVA. Session and time within each session were the two within-subjects factors. Subjects gave different hunger ratings in the sated and hungry testing conditions ($F(1,19)=629.9$, $p=.000000$). Within each session, hunger ratings were not different at the beginning, mid-point, or end of the session. Therefore, sampling taste-odor stimuli did not alter subjects' perceived level of hunger. Additionally, there was no difference between the hunger ratings of sweet likers and dislikers. Hunger ratings were taken to verify subject compliance with the internal state manipulation and to ensure that the data are not confounded by hunger changes within a session. It is apparent that our subjects complied with the internal state manipulations and that the data are not confounded by changes in hunger within a session or by differences between sweet likers and dislikers in internal state.

Odor Intensity Ratings

Odor intensity ratings were examined using a between-within subjects ANOVA. Underlying hedonic profile to sweet and whether the subject experienced the sated or fasted condition first were the two between subjects factors. Internal state and stimulus concentration were the two within subjects factors. Odor intensity ratings were significantly higher with increasing concentration for chocolate ($F(4,64)=56.0$, $p=.00000$), raspberry ($F(4,64)=74.81$, $p=.000000$) and popcorn ($F(4,64)=51.06$, $p=.000000$) odors. Figure 12 shows that odor intensity was significantly affected by internal state for popcorn odor ($F(1,16)=7.25$, $p=.016$), but not chocolate and raspberry odors. Order of session, whether a subject participated in the fasted or sated session first, did not influence odor intensity ratings.

Taste Intensity Ratings

Taste intensity ratings were examined using a between-within subjects ANOVA. Underlying hedonic profile to sweet and whether the subject experienced the sated or fasted condition first were the two between subjects factors. Internal state and stimulus concentration were the two within subjects factors. Taste intensity ratings were significantly higher with increasing concentration for sucrose ($F(4,64)=337.6$, $p=.000000$), SOA ($F(4,64)=244.1$, $p=.000000$) and sodium chloride ($F(4,64)=416.4$, $p=.000000$). Taste intensity ratings were significantly affected by internal state for sucrose ($F(1,16)=9.67$, $p=.0067$) and sodium chloride ($F(1,16)=5.16$, $p=.03$). Figure 13 shows that taste intensity ratings were lower in the sated condition than in the hungry condition for sucrose and sodium chloride stimuli. Order of session, whether a subject participated in the fasted or sated session first, did not influence taste intensity ratings.

Odor Hedonic Ratings

Odor hedonic ratings were examined using a between-within subjects ANOVA. Underlying hedonic profile to sweet and whether the subject experienced the sated or fasted condition first were the two between subjects factors. Internal state and stimulus concentration were the two within subjects factors. Hedonic ratings were significantly affected by concentration for chocolate ($F(4,64)=7.13$, $p=.000082$) and raspberry ($F(4,64)=11.99$, $p=.000000$) odors. Internal state significantly affected hedonic ratings of chocolate ($F1,16)=16.53$, $p=.000899$), raspberry ($F(1,16)=102.8$, $p=.000000$), and popcorn ($F(1,16)=16.25$, $p=.000967$) odors. Figure 14 shows that hedonic ratings of all these odors were lower in the sated condition. For all odors, the extent to which odor hedonic ratings were reduced in the sated condition depends on odor concentration. The Internal State x Concentration interaction was significant for chocolate ($F(4,64)=5.4$, $p=.000816$), raspberry ($F(4,64)=20.5$, $p=.000000$), and popcorn ($F(4,64)=11.18$, $p=.000001$). When subjects are sated, hedonic ratings became more negative with increasing odor concentration. Order of session, whether a subject participated in the fasted or sated session first, did not influence odor hedonic ratings.

Figure 12: Mean (± SEM) intensity ratings of odor across five ascending concentrations while subjects were sated and deprived, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol.)

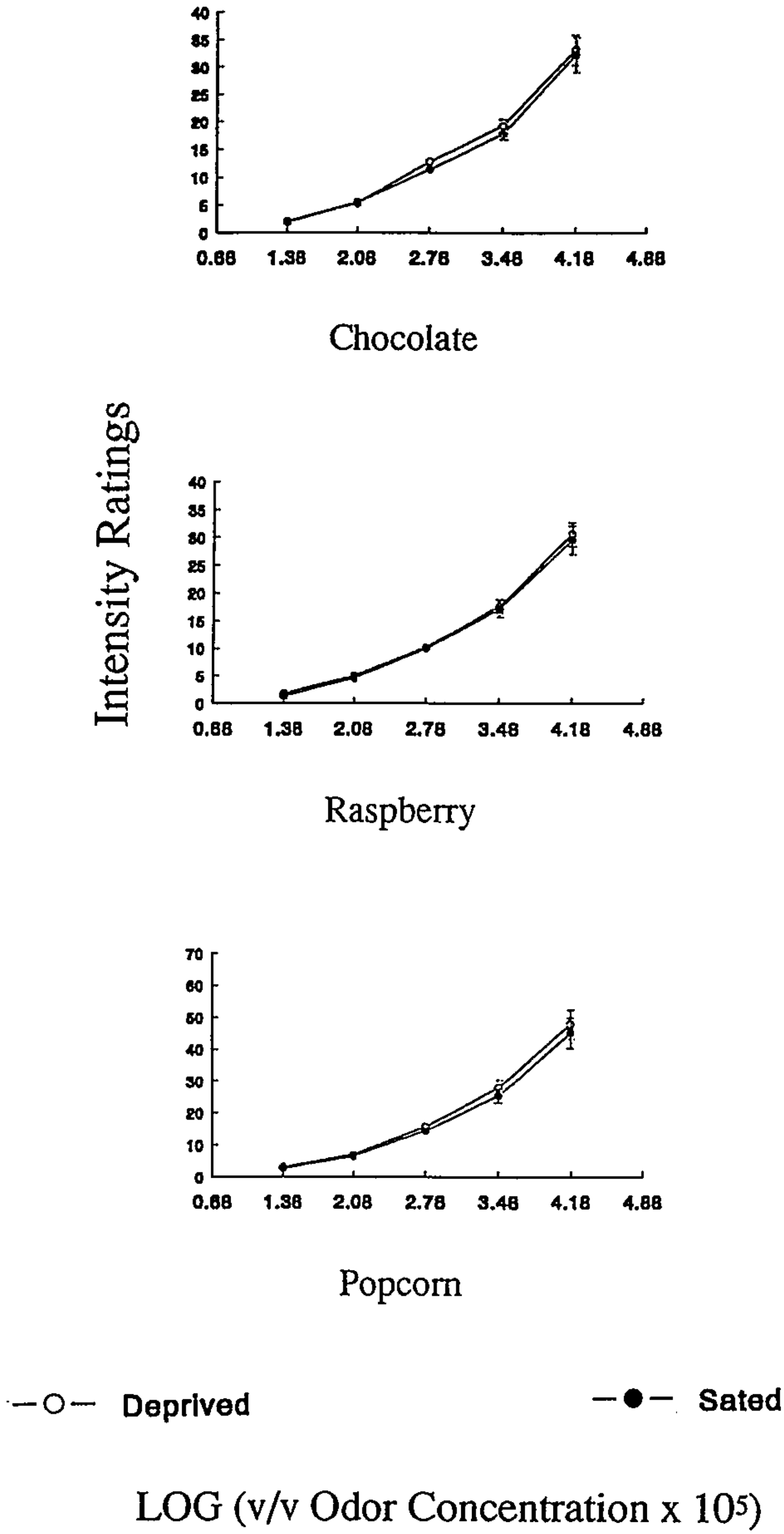

40
35
30
25
20
15
10
5
0
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
Intensity Ratings
40
35
30
25
20
15
10
5
0
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Raspberry
70
60
50
40
30
20
10
0
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Popcorn
Deprived
Sated
LOG (v/v Odor Concentration x 10^5)

Figure 13: Mean (± SEM) intensity ratings of taste across five ascending concentrations while subjects were sated and deprived, for sucrose (top panel), SOA (middle panel), and sodium chloride (bottom panel). (SEMs not visible fall within the symbol.)

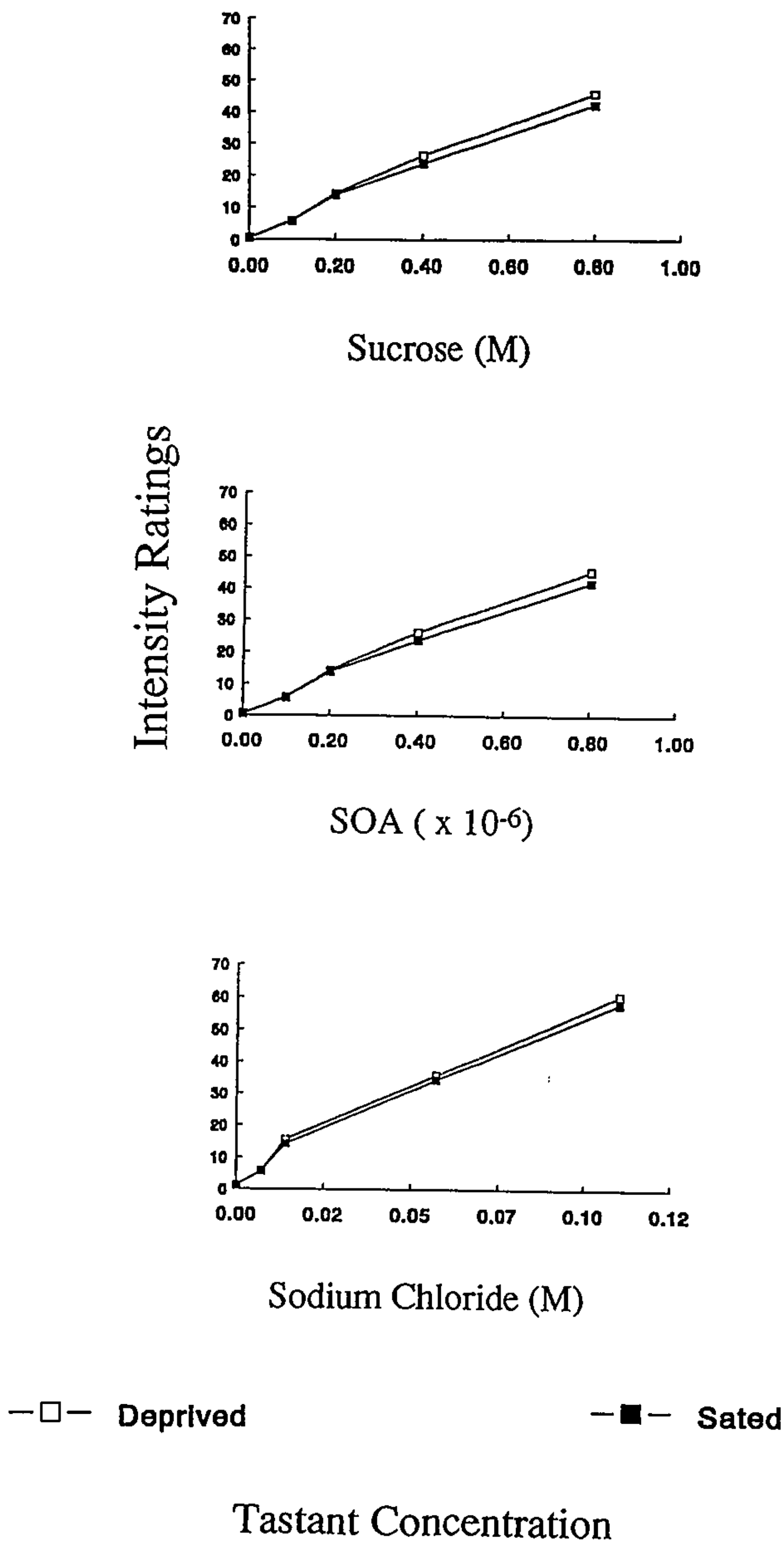
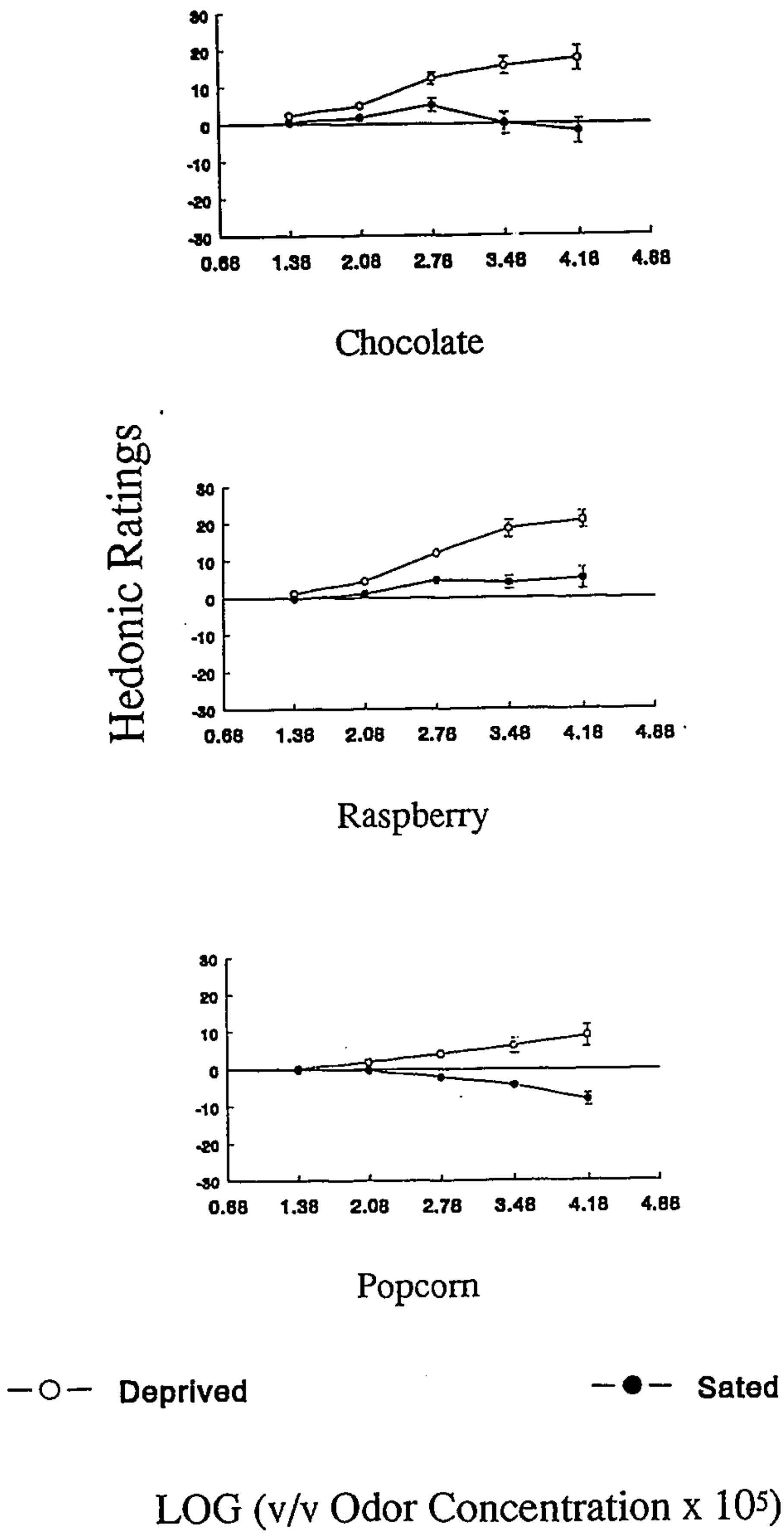
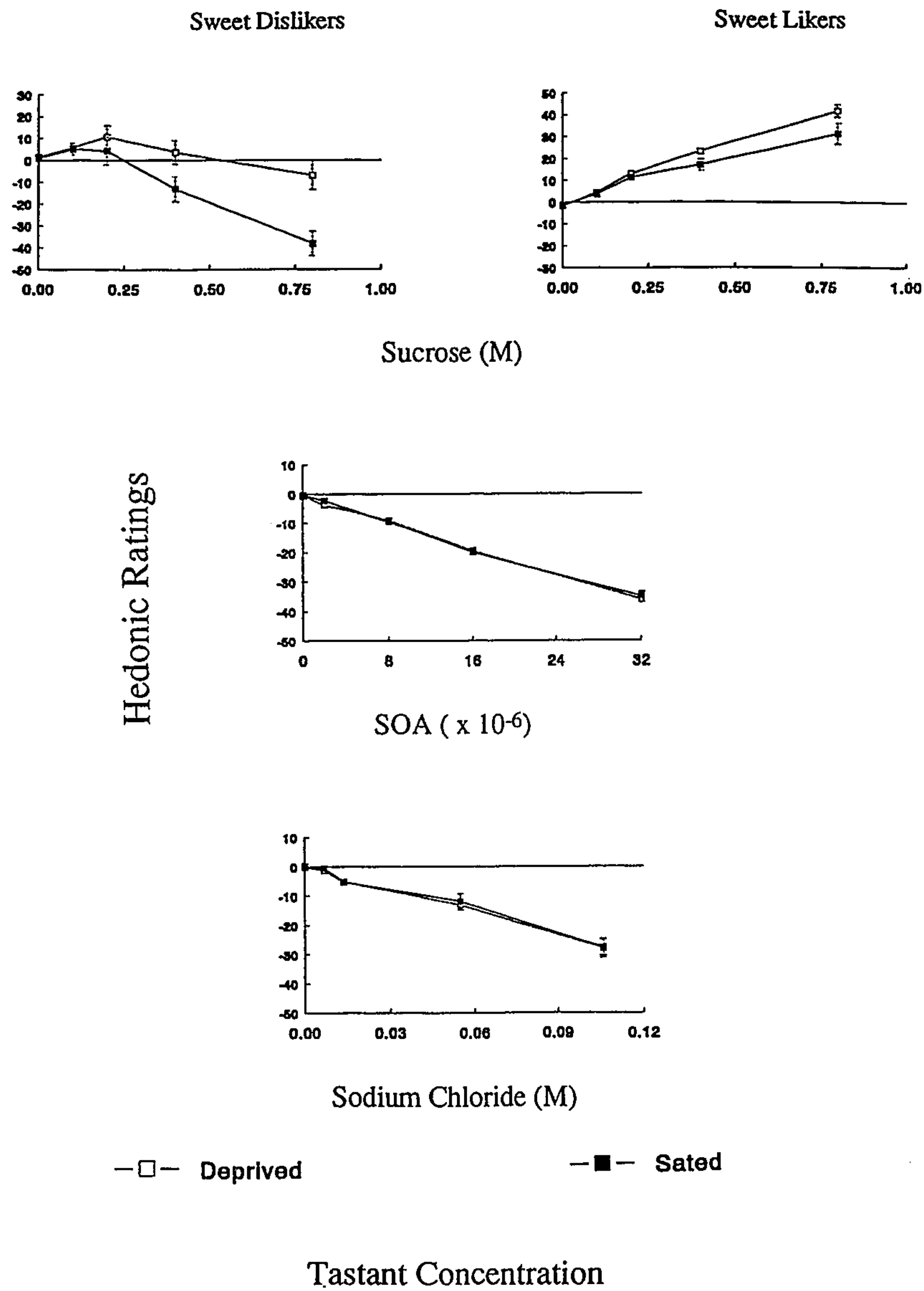

Intensity Ratings
70
60
50
40
30
20
10
0
0.00
0.20
0.40
0.60
0.80
1.00
Sucrose (M)
SOA (x 10-6)
0.00
0.02
0.05
0.07
0.10
0.12
Sodium Chloride (M)
Deprived
Sated
Tastant Concentration

Figure 14: Mean (± SEM) hedonic ratings of odor across five ascending concentrations while subjects were sated and deprived, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol.)



Hedonic Ratings
30
20
10
0
-10
-20
-30
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
Raspberry
Popcorn
Deprived
Sated
LOG (v/v Odor Concentration x 10^5)

Figure 15: Mean (± SEM) hedonic ratings of taste across five ascending concentrations while subjects were sated and deprived, for sucrose (top panel), SOA (middle panel), and sodium chloride (bottom panel). Hedonic ratings of sucrose are compared for sweet dislikers (left) and likers (right) in the top panel. (SEMs not visible fall within the symbol.)


Sweet Dislikers
Sweet Likers
30 20 10 0 -10 -20 -30 -40 -50
0.00 0.25 0.50 0.75 1.00
50 40 30 20 10 0 -10 -20 -30
0.00 0.25 0.50 0.75 1.00
Sucrose (M)
Hedonic Ratings
10 0 -10 -20 -30 -40 -50
0 8 16 24 32
SOA (x 10-6)
10 0 -10 -20 -30 -40 -50
0.00 0.03 0.06 0.09 0.12
Sodium Chloride (M)
Deprived
Sated
Tastant Concentration

<u>Taste Hedonic Ratings</u>

Taste hedonic ratings were examined using a between-within subjects ANOVA. Underlying hedonic profile to sweet and whether the subject experienced the sated or fasted condition first were the two between subjects factors. Internal state and stimulus concentration were the two within subjects factors. Taste hedonic ratings were significantly affected by stimulus concentration for sucrose ($F(4,64)=3.46$, $p=.0126$), SOA ($F(4,64)=267.44$, $p=.000000$) and sodium chloride ($F(4,64)=49.3$, $p=.000000$). Figure 15 shows that internal state significantly influenced taste intensity ratings for sucrose ($F(1,16)=32.5$, $p=.000033$), but not for SOA and sodium chloride. Hedonic ratings of sucrose were lower when subjects were sated compared to the hungry condition. The effect of internal state on hedonic ratings of sucrose depends on a subject's underlying hedonic profile to sweet ($F(1,16)=9.28$, $p=.00769$). The top panel of Figure 15 (top panel) shows that dislikers show a greater shift due to internal state than likers.

Discussion

This experiment replicates sweet taste alliesthesia demonstrated by others (Cabanac, 1971). Hedonic ratings of sucrose were elevated in the hungry state relative to the sated state. Furthermore, the interaction of alliesthesia with the underlying hedonic profile to sweet and internal state found previously (Looy & Weingarten, 1991) was also replicated. More importantly, this experiment demonstrated clear odor alliesthesia whereas prior studies had been equivocal (DuClaux, Feisthauer, & Cabanac, 1973; Mower, Mair, & Engen, 1977). Under the experimental conditions used here, reported hedonic ratings of odor were higher in a hungry state relative to a state of satiety.

It is possible that shifts in chemosensory hedonics due to changes in internal state might be involved in meal termination, food choice, and intake. For example, hunger may elevate the sensory hedonics of food resulting in an increased willingness to eat. In contrast, satiety may decrease the sensory hedonics of a particular food resulting in a decreased willingness to eat that food. While the hedonics of a food's taste and smell are tightly coupled with subsequent ingestion in laboratory studies (Rolls, Rolls, Rowe, & Sweeney, 1981) and survey reports (Shepherd, 1989), it is unknown whether taste or odor is more salient in the motivation of ingestive behavior. The extent to which the components of flavor are modified by internal state may indicate whether taste or odor has the larger role in driving food choice and intake. This issue is examined in the next experiment.

Chapter Nine

Experiment 7

AN EXAMINATION OF ALLIESTHESIA IN TASTE-ODOR MIXTURES

The previous experiment replicated previous work demonstrating sweet taste alliesthesia (Cabanac, 1971; Looy & Weingarten, 1991) and in contrast to previous literature (Mower, Mair, & Engen, 1977), also showed a clear and robust odor alliesthesia effect. In the current alliesthesia literature, taste and smell have been treated as separate sensations. Since the flavor of food is a combination of taste and odor, it is disappointing that alliesthesia in taste-odor mixtures has not been explored. An examination of alliesthesia in taste-odor mixtures may further our understanding of two issues. First, a direct comparison of the extent to which odor and taste drive ingestive behavior has not been done. It may be that the component more modifiable by internal state in a taste-odor mixture might be more salient in the motivation of ingestive behavior. Second, it has been suggested that odor hedonics are more labile than taste hedonics. A comparison of the extent to which odor and taste-odor mixtures are modifiable by internal state may provide support for greater hedonic lability of odor.

Method

Subjects: Subjects were 29 undergraduates who participated for course credit. There were 19 females and 10 males with an average age of 26.97 • 1.97 (SD) years in the study.

Stimuli: The test stimuli consisted of three different food odors (supplied by IFF): chocolate, popcorn and raspberry. Three concentrations 1.38, 2.78, and 4.18 (LOG v/v concentration x 10^5) of each odor was presented three times in random order throughout the experiment. Each concentration was judged with nothing in the mouth or in the presence of 0.8 M sucrose. Subjects rinsed with distilled water in between each stimulus.

Procedure:

Subjects participated in two sessions, sated and deprived, each separated by a seven-day interval. Half the subjects were tested first in the deprived condition (after an 18-hour fast), the other half in sated condition (30 minutes after a satiating meal). Both deprived and sated sessions were conducted at the same time of day.

The sip-and-spit procedure, described in the General Method section, was followed for both sessions. In both sessions, subjects evaluated the same stimuli and made the same ratings.

Stimulus Delivery: The two-module delivery system (described in the General Method) was used to present gustatory and olfactory stimuli simultaneously, but independently.

Hedonic Profile Determination: Prior to the experiment each subject was classified as either a liker or disliker of concentrated sucrose (Looy & Weingarten, 1992) according to the procedure described in the General Method.

Ratings: In the previous experiment subjects rated taste and smell in isolation. In the present experiment subjects rate taste and smell together. Subjects rated intensity and hedonics of odor (described as "what you are smelling on the cotton ball") and overall sensation (described as "the combination of the taste and smell") according to the magnitude estimation procedure given in the General Method. For clarity, these will be labeled by the acronyms (O / O) and (O+T / O+T) respectively. Note that the ratings required of subjects in the present experiment reflect the conditions of specific interest. Order of rating the components was counterbalanced across subjects. Subjects rated intensity and hedonics at separate times during the experiment. Order of rating intensity and hedonics was counterbalanced across subjects. There was a 3-5 minute break between rating of intensity and hedonics. Each subject rated only one odor.

Verification of Subjects' Internal State: To index whether subjects were in a physiological state of satiation or deprivation, hunger ratings were obtained from all participants. The method for measuring subjects' hunger perception is described in Chapter Eight.

Data Normalization Across Sessions: Because this experiment consisted of two sessions, an additional step in the data normalization procedure was conducted. The procedure for normalizing data across sessions is described in Chapter Eight.

Results

Hunger Ratings

Hunger ratings were examined using repeated measures ANOVA. Session and time within each session were the two within-subjects factors. Subjects gave different hunger ratings in the sated and hungry testing conditions ($F(1,28)=274.9$, $p=.000000$). Within each session, hunger ratings were not different at the beginning, mid-point, or end of the session. Additionally, there was no difference between the hunger ratings of sweet likers and dislikers.

Intensity Ratings

Intensity ratings of chocolate and popcorn odors were examined using a between-within subjects ANOVA. Underlying hedonic profile to sweet was the single between factor and internal state , presence of taste, and odor concentration were the three within factors. Raspberry odor intensity ratings were examined by a repeated measures ANOVA, since all subjects who rated raspberry (n=4) were sweet dislikers. Internal state, presence of taste, and odor concentration were the three within factors.

Intensity ratings significantly increased with odor concentration for chocolate ($F(2,30)=66.6$, $p=.000000$), raspberry ($F(2,6)=12.6$, $p=.007$) and popcorn ($F(2,12)=112.9$, $p=.000000$). As expected, and as can been seen in Figure 16, (O+T / O+T) intensity ratings were higher than (O / O) intensity ratings for chocolate ($F(1,15)=21.75$, p.0003), raspberry ($F(1,3)=10.4$, $p=.04$), and popcorn ($F(1,6)=10.83$, $p=.016$) odors. Both (O / O) and (O+T / O+T) intensity ratings were unaffected by internal state for chocolate and raspberry odors. Intensity ratings in the (O+T / O+T) condition were significantly higher in the sated condition for popcorn odor ($F(1,6)=10.89$, $p=.0164$). Intensity ratings in the (O+T / O+T) condition were unaffected by underlying hedonic profile to sweet.

Hedonic Ratings

Hedonic ratings of chocolate and popcorn were examined using a between-within subjects ANOVA, with liker / disliker status as the single between factor and internal state, presence of taste, and odor concentration as the three within factors. Raspberry hedonic ratings were examined by a repeated measures ANOVA, since all subjects who rated raspberry (n=4) were sweet dislikers. Internal state, presence of taste, and odor concentration were the three within factors.

As expected, and as can been seen in Figure 17, (O+T / O+T) hedonics ratings were lower than (O / O) hedonics ratings for chocolate ($F(1,15)=21.03$, p.0003), raspberry ($F(1,3)=15.08$, $p=.03$). As seen in previous experiments, the reduced hedonic ratings in the (O+T / O+T) condition is accounted for by the ratings of sweet dislikers for chocolate ($F(1,15)=15.08$, $p=.001$) and popcorn ($F(1,6)=46.3$, $p=.0004$) odors. Since there were no sweet likers in the group that rated raspberry odor, the comparison between likers and dislikers could not be made, but recall that there was an overall reduction in (O+T / O+T) hedonic ratings for raspberry odor.

Both (O / O) and (O+T / O+T) hedonics ratings were lower in a state of satiety compared to the hungry state for raspberry ($F(1,3)=15.08$, $p=.03$) and popcorn ($F(1,6)=12.36$, $p=.01$). Therefore, a general reduction in hedonic ratings accompanied satiety, but no distinction could be made between hedonic ratings of odor alone and hedonic ratings of a taste-odor mixture.

Discussion

The purpose of the current experiment was to examine perception of odor alone and taste-odor mixtures while subjects were hungry and stated. Intensity was generally unaffected by internal state, both for odor alone and for taste-odor mixtures. Hedonic ratings were generally lower when subjects were sated relative to hungry. However, no distinction could be made in the extent to which hedonic ratings of odor alone were reduced compared to hedonic ratings of taste-odor mixtures. For raspberry odor, taste-odor mixtures in the sated condition were significantly lower than all other conditions. However, one must be cautious about interpreting this result because the sample size was quite small (n=4) and all subjects were sweet dislikers.

Prior work on chemosensory alliesthesia has utilized simple stimuli. Taste and odor alliesthesia have been examined in separate experiments. The results of the present experiment demonstrate alliesthesia in taste-odor mixtures. That is, subjects report lower hedonic ratings of a taste-odor mixture when sated compared to hungry.

However, the effect of internal state on hedonics was not different among odor alone and taste-odor mixtures. Thus, under these experimental conditions, the degree of hedonic shift due to internal state was not different for odor alone and taste-odor mixtures.

This experiment attempted to address two issues. The first issue is centered around the hedonic salience of taste and odor in the motivation of eating. It may be that if one component of flavor is influenced more by internal state, greater hedonic salience and perhaps a greater role in motivating ingestion might be suggested. Hedonic perception of taste and odor, both in isolation and mixture, is influenced by internal state. However, the experiment presented here could make no distinction between degree of taste and odor hedonic shift due to changes in internal state. The second issue centered around the relative hedonic lability of taste and odor. While differences may exist in the hedonic lability of odor and taste, none were found under this experimental preparation.

Figure 16: Mean (± SEM) odor intensity ratings when odor was presented alone across three odor concentrations (O / O) while subjects were sated and deprived; mean (± SEM) overall intensity ratings when odor was presented with 0.8 M sucrose (O+T / O+T) while subjects were sated and deprived, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol.)

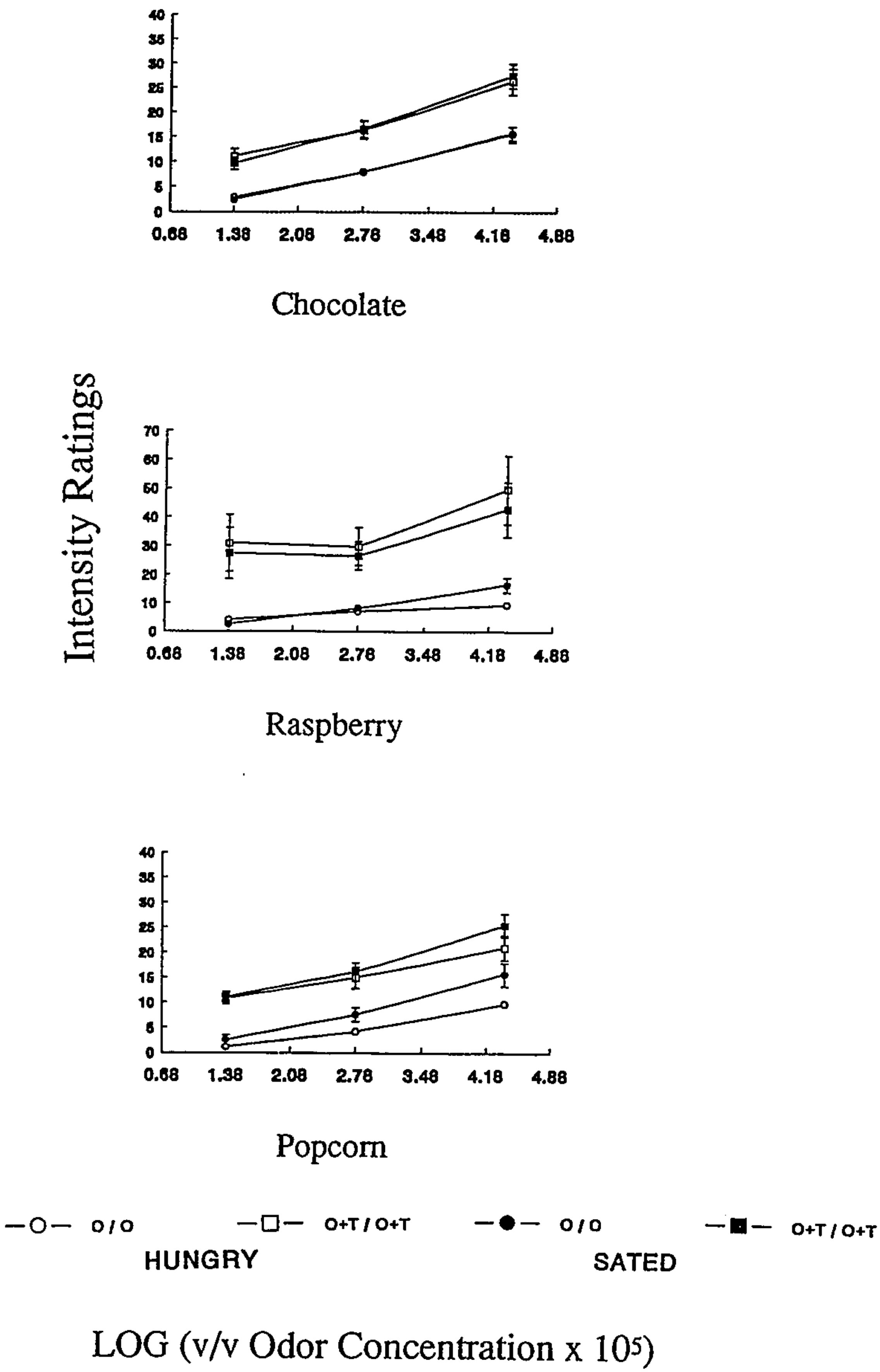
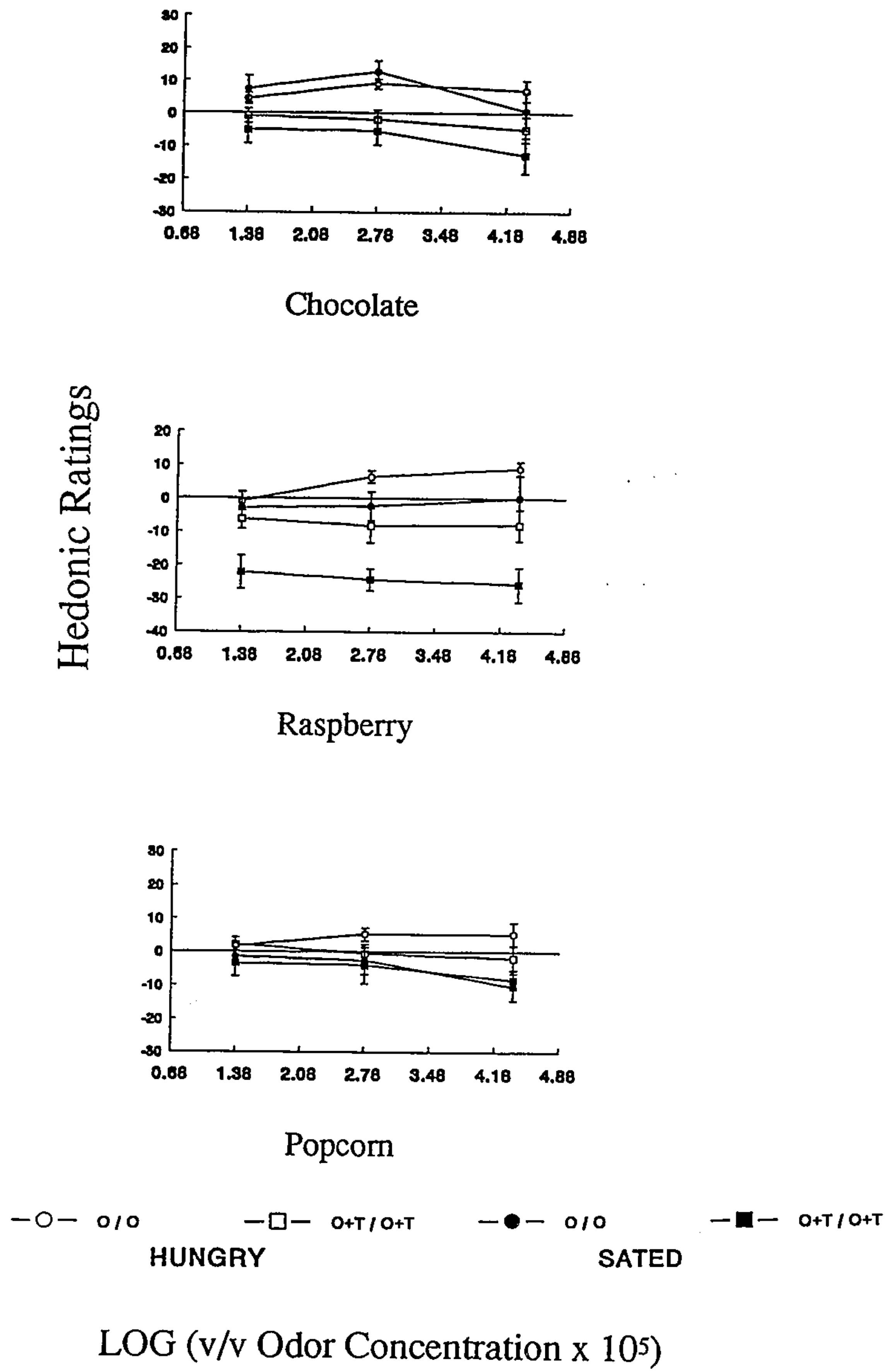

Intensity Ratings
0 5 10 15 20 25 30 35 40
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Chocolate
0 10 20 30 40 50 60 70
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Raspberry
0 5 10 15 20 25 30 35 40
0.68 1.38 2.08 2.78 3.48 4.18 4.88
Popcorn
O / O
O+T / O+T
HUNGRY
O / O
O+T / O+T
SATED
LOG (v/v Odor Concentration x 10^5)

Figure 17: Mean (± SEM) odor hedonic ratings when odor was presented alone across three odor concentrations (O / O) while subjects were sated and deprived; mean (± SEM) overall hedonic ratings when odor was presented with 0.8 M sucrose (O+T / O+T) while subjects were sated and deprived, for chocolate (top panel), raspberry (middle panel), and popcorn (bottom panel). (SEMs not visible fall within the symbol.)



Hedonic Ratings
30
20
10
0
-10
-20
-30
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Chocolate
20
10
0
-10
-20
-30
-40
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Raspberry
30
20
10
0
-10
-20
-30
0.68
1.38
2.08
2.78
3.48
4.18
4.88
Popcorn
O/O
O+T/O+T
O/O
O+T/O+T
HUNGRY
SATED
LOG (v/v Odor Concentration x 10^5)

CHAPTER 10

GENERAL DISCUSSION

This thesis examined the effect of taste on odor perception. First, the basic relationships among concentration, perceived intensity, and perceived hedonics were described for the three food odors selected for study (Experiment 1). Next, the question of whether taste refers to odor was addressed. Odor intensity ratings increased in the presence of a taste and this taste-induced enhancement of odor intensity is observed regardless of whether the taste is perceived as hedonically negative or positive. More importantly, odor hedonic ratings were significantly lower in the presence of a taste, but only when the taste is perceived as hedonically negative. Thus, taste does refer to odor, particularly in the hedonic realm, and this effect was termed "hedonic referral." Subsequent experiments examined the properties of hedonic referral and these are discussed below.

Some Properties of Hedonic Referral

1. Hedonic Referral in a Negative Direction: Hedonic referral is demonstrated by all subjects and generalizes to all taste qualities perceived as hedonically negative (Experiment 3). Pairing with negative experience can alter the hedonic value of chemosensory stimuli. Association of a flavor with nausea produces aversion in humans (Bernstein & Webster, 1980). Other negative experiences can change hedonic tone of odor. For example, pairing an olfactory stimulus with negative visual images lowers pleasantness ratings of the odor (Hvastja & Zanattini, 1989). Thus, hedonic shift of odor in a negative direction due to simultaneous presentation with an aversive taste was not completely surprising. However, pairing with positive experiences will also influence subsequent preference of chemosensory stimuli (Booth et al., 1982; Zellner et al., 1983). While increased odor hedonics were observed for subjects who found the taste hedonically positive (Figure 4), these results were not statistically significant. Why was hedonic referral of taste to odor observed in a negative direction only? One explanation is that positive hedonic shifts are more difficult to establish than negative hedonic shifts. This interpretation has been applied to the food preference literature, which indicates that food likes are more difficult to establish than dislikes (Zellner & Rozin, 1985; Zellner, 1991).

2. Hedonic Referral Does Not Reflect A Negative Mood State: It has been suggested that odor and mood are closely related (Ehrlichman & Bastone, 1992) and that negative affect from one event can transfer to a subsequent event (Zillman, 1971). The results of one study suggest that pairing a negative event with an odor can reduce reports of mood upon subsequent presentation of that odor (Kirk-Smith, Van Toller, & Dodd, 1983). Thus, one possible explanation of the hedonic referral of taste to odor is that the taste induces a negative mood state which is transferred to hedonic ratings of the odor. If hedonic referral reflects a negative mood state induced by an aversive taste, then other aversive stimuli would be expected to shift odor hedonic ratings. Results presented here demonstrate that hedonically positive or negative acoustic stimulation has no effect on odor hedonics (Experiment 4), suggesting that hedonic referral does not reflect a negative affective state.

3. A Privileged Relationship Between Taste and Smell? A third property of hedonic referral to odor is that it may be limited to the taste modality. That is, taste may have a special impact on the hedonic perception of odor. A brief digression to subject reactions in Experiment 4 may illustrate this property of hedonic referral. When asked for hedonic ratings of the odor in the presence of an aversive tone, subjects in this experiment often commented that the two stimuli "had nothing to do with each other." It is possible that acoustic stimulation did not hedonically refer to odor because subjects could easily separate the two stimuli. Since the gustatory and olfactory systems are physiologically proximal and taste-odor mixtures are regularly experienced in flavor, these modalities may be more difficult to psychologically separate.

4. What Are Subjects Rating? A major issue in the literature on taste-odor mixtures has been the degree to which increased ratings of taste in the presence of odor compared to taste alone represents "true" enhancement. That is, some have questioned whether subjects are reporting mixture perception rather than the specified component simply because the experimenter only asks for one rating. Previous literature has shown that when instructed to rate taste in the presence of an odor, subjects will add the intensity of odor to the taste. Olfactory referral produces an "enhancement" of taste intensity by odor. However, when instructed to partition overall intensity into taste and odor contributions, it is clear that odor adds to the overall intensity rather than enhances the taste (Frank, Wessel, & Shaffer, 1990).

Experiment 5 represented an attempt to extend the current literature by applying the above analysis to taste referral rather than olfactory referral and by examining hedonic rather than intensity perception. That experiment demonstrated that subjects can be analytical about their *hedonic* perception of taste-odor mixtures if instructed to partition the overall hedonics into taste and odor components (Experiment 5). However, if asked for a single modality-specific rating, subjects will tend to report a rating that reflects their hedonic perception of the mixture which tends to reflect hedonic perception of the more intense component. If the results of Experiments 2 and 3 are interpreted in light of the analytic experiment, then subjects were most likely reporting their hedonic response to the more intense component, in this case, the taste.

Generalization To Ingestive Behavior

The General Introduction reviewed factors that influence food choice and intake. Among these were the sensory properties of food, particularly hedonic perception of taste and odor. Survey studies indicate that the sensory aspects of food are important in food choice and intake (Spitzer & Rodin, 1981; Shepherd, 1989). Furthermore, laboratory studies have demonstrated that the hedonic perception of a food's taste and odor are highly correlated with subsequent ingestion (Rolls, Rowe, & Rolls, 1982). Hedonic perception of taste is strongly related to acceptance or rejection from the oral cavity (Steiner, 1977). Willingness to ingest a food is dependent on the pleasantness of its odor (Pelchat, 1993). These findings support the view that chemosensory hedonic perception influences ingestive behavior. However, support for the connection between sensory hedonics and ingestive behavior is stronger if an organism's need state affects sensory hedonics.

If the sensory properties of food do drive ingestive behavior, then some aspect of sensory perception should be modified by physiological need, just as motivation is modified by need. Demonstrations of alliesthesia, changes in hedonic perception due to changes in metabolic state, strongly support the view that hedonic perception motivates ingestive behavior for several reasons. First, while changes in internal state do not affect perceived intensity, the effect of internal state on hedonics is robust. Thus, changes in hedonics due to metabolic state may be attributed to motivational state rather than general perceptual alterations. Second, alliesthesia shows intersensory specificity. For example, gastric loads do not alter the pleasantness of thermal sensations just as core temperature changes do not alter chemosensory hedonics (Cabanac, 1979). Such specificity would be expected if sensory hedonics drives behaviors vital to physiological regulation. Third, alliesthesia is quantitative rather than all or nothing. Once again, it makes sense that a motivational system would be sensitive to amount of physiological need. Thus, metabolic signals relating to hunger and satiety may be interpreted by the chemical senses. Hedonic perception of the chemical senses may then motivate ingestive behavior.

The final two experiments presented in this dissertation represent attempts to generalize the examination of taste-odor mixture perception closer to ingestive behavior through an investigation of chemosensory alliesthesia. Demonstrations of pure odor alliesthesia have been equivocal. Additionally, studies of chemosensory alliesthesia have been limited to simple stimuli rather than taste-odor mixtures. Results presented here extend the literature with a clear demonstration of reduced odor hedonics when subjects are sated compared to hungry (Experiment 6) and by demonstrating that hedonic ratings of taste-odor mixtures are generally increased in the hungry state relative to the sated state (Experiment 7).

Issues For Future Research

1. Mechanisms of Taste-Odor Interaction: Taste-smell confusions have been recognized for over a century (Cain, 1978). However, the mechanisms of taste-smell confusion, be they physiological or psychological are not completely understood. Future work should examine the mechanisms underlying taste-smell confusions.

Some have suggested that taste-smell confusions may partially originate at the cognitive level (Hornung & Enns, 1987). But several physiological mechanisms have been proposed to account for olfactory referral, a type of taste-smell confusion. One possibility is that olfactory information is sent to the brain differently depending on whether the input originates from the mouth or at the nostrils. Such differential gating could lead to qualitatively different sensations (Engen, 1982). Another possibility is that olfactory input fuses when combined with a taste. There is some evidence that olfactory, gustatory, and cutaneous inputs from the oral cavity converge on a neural substrate located in the nucleus of the solitary tract (Van Buskirk & Erickson, 1977), suggesting central integration of all sensory stimulation present in the mouth. A third possibility is that the sensation evoked at the olfactory mucosa is different depending on the route of olfaction (Rozin, 1982). An investigation of the mechanisms underlying taste-smell confusions may further our understanding of flavor perception.

2. Hedonic Lability of Taste and Odor: Hedonic perception of chemosensory stimuli is modifiable by experience, or labile. A comparison of taste and odor lability has led some to suggest that odor is more hedonically labile than taste (Bartoshuk, 1991a). It has been proposed that taste hedonics are relatively fixed according to the gustatory function of nutritive selection toward calories and away from toxins (Bartoshuk, 1989a). Odor complements taste as the more hedonically modifiable component of flavor and functions as a "label" for specific foods (Bartoshuk, 1989a). It has been argued that odor is more modifiable than taste so that organisms can adjust hedonic perception of food based on post-ingestive consequences (Bartoshuk, 1991a). One factor that modifies hedonic perception of taste and odor is metabolic state. While the final experiment presented in this dissertation did not reveal any difference in the hedonic lability of taste compared to odor, future experiments should continue to investigate this issue.

3. Generalization of Hedonic Perception to Ingestive Behavior: As mentioned previously, most of the research on taste and smell has tended to focus on perceived intensity rather than hedonics. This is surprising since some have suggested that hedonic perception of chemosensory stimuli drives intake (Young, 1966). Hedonic response to one component of flavor may be a better predictor of eating behavior. It may be that the smell, the taste, the most intense component, or the component with the greater hedonic value may account for willingness to eat a food. Attempts should be made to study the relationship between hedonic perception of taste-odor mixtures in the laboratory and food choice and intake under more realistic conditions.

4. Specificity of Alliesthesia: There is some evidence that alliesthesia is characterized by *intersensory* specificity. That is, changes in one physiological system do not modulate sensory hedonics of an unrelated system. For example, a gastric load does not change hedonic perception of thermal sensations (Cabanac, 1979). The assertion that alliesthesia is characterized by *intrasensory* specificity has less empirical support. Intrasensory specificity restricts metabolic alliesthesia to alimentary stimuli. Thus, it has been proposed and demonstrated that only food odors are affected by satiety (DuClaux, Feisthauer, & Cabanac, 1973). However, this study may be confounded by overt identification of the odors as food related. Results of another study suggest that a food odor not perceived as food related is not affected by internal state (Mower, Mair, & Engen, 1977). An odor alliesthesia study that directly manipulates subject perception of odors as food related may reveal whether intraspecificity characterizes the modulation of odor hedonics by internal state. Such a study may also provide support for the suggestion that odor hedonics is mostly equivalent to a subject's interpretation of the odor (Cain, 1984).

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APPENDIX

The odorants, concentrations, and rating procedures used in this thesis were not chosen haphazardly. Rather, choices were made based on an extensive series of pilot experiments summarized in this section.

Choice of Odorants and Concentration Range

Odorants: Early work employed low quality flavors that could be delivered into the mouth (e.g. strawberry flavoring, almond extract). However, these stimuli did not evoke a strong hedonic response and were confounded by the taste of an alcohol solvent. Therefore, thirteen odors were obtained from International Flavors and Fragrances: almond, baked bread, cherry, chocolate, cinnamon, jasmine, leather, mint, musk, pine, popcorn, raspberry, and rose. Because of the interest in flavor, it was decided that only food odors would be used. Seven food odors were sampled by the experimenter. Baked bread odor was eliminated as a potential stimulus because it was quite unpleasant and not readily identified as a food odor. Cherry and almond odors are very similar (benzaldehyde is their common chemical base), so only one of those odors was tested further. A pilot experiment measured intensity and hedonic perception of the remaining food odors (chocolate, popcorn, cinnamon, almond, and raspberry) over four concentration ranges. Cinnamon odor was eliminated because it tended to make subjects sneeze, probably due to some trigeminal component. Almond odor was eliminated because it generated flat hedonic functions within the concentration range tested. Chocolate, popcorn, and raspberry were found to produce known psychophysical functions over the concentrations used and were therefore chosen as odor stimuli.

Concentration Ranges: Different subjects experienced the four concentration ranges. Subjects rated intensity and hedonics of two odorants at five concentrations. Odorants were rated in separate blocks. Each concentration was repeated five times (random order) for a total of twenty-five stimuli per odorant. As described below (Choice of Rating Procedure), subjects sampled a stimulus and then gave an intensity and hedonic rating using two Visual Analog Scales.

In the first concentration range, 5 ml of the pure odorant was added to 95 ml of heavy mineral oil (Big V Pharmacies Company, Ltd.) for a total volume of 100 ml. From this "stock" solution, a 1/5 dilution series was done. Five concentrations of each odor were made (1/20, 3/100, 3/500, 3/2500, & 3/12500 vol. / vol.). For ease of graphing perceived intensity and hedonic functions across concentrations, the vol. / vol. concentrations were converted. Each vol. / vol. concentration was multiplied by 10^5, then the LOG of this number was taken. Therefore, notation for the five concentrations of odor used in this set of stimuli was, from lowest to highest, 0.9, 1.6, 2.3, 3.0, and 3.7 (LOG [] x 10^5).

Upon visual inspection of perceived odor intensity and hedonic response functions, it was clear that these concentrations were too low. Most subjects did not perceive an odor until the third concentration. Therefore, a second concentration range was made.

In the second concentration range, five concentrations of each odor were made (1/20, 1/40, 1/100, 1/1000 vol. / vol., a mineral oil "blank"). For ease of graphing perceived intensity and hedonic functions across concentrations, the vol. / vol. concentrations were converted. Each vol. / vol. concentration was multiplied by 10^5, then the LOG of this number was taken. Therefore, notation for the five concentrations of odor used in this set of stimuli was, from lowest to highest, 0.0, 2.0, 3.0, 3.4, and 3.7 (LOG [] x 10^5).

Upon visual inspection of perceived odor intensity and hedonic response functions, it was observed that the concentrations were not spaced far enough apart. A mineral oil blank was utilized to see if subjects reported "false positives" (report of odor when there was none). "False positives" were rare and slight when they did occur. Therefore, a third concentration range was made.

In the third concentration range, 5 ml of the pure odorant was the highest concentration. From this "stock" solution, a 1/5 dilution series was done. Five concentrations of each odor were made (20/20, 1/5, 1/25, 1/125, 1/625 vol. / vol.). For ease of graphing perceived intensity and hedonic functions across concentrations, the vol. / vol. concentrations were converted. Each vol. / vol. concentration was multiplied by 10^5, then the LOG of this number was taken. Therefore, notation for the five concentrations of odor used in this set of stimuli was, from lowest to highest, 2.2, 2.9, 3.6, 4.3, and 5.0 (LOG [] x 10^5).

Upon visual inspection of perceived odor intensity and hedonic response functions, it was observed that the concentrations were too strong at the upper end of the range. Subjects could not differentiate between the three highest concentrations. Therefore, a fourth concentration range was made.

In the fourth concentration range, 15 ml of the pure odorant was added to 85 ml of heavy mineral oil (Big V Pharmacies Company, Ltd.) for a total volume of 100 ml. From this "stock" solution, a 1/5 dilution series was done. Five concentrations of each odor were made (3/20, 3/100, 3/500, 3/2500, & 3/12500 vol. / vol.). For ease of graphing perceived intensity and hedonic functions across concentrations, the vol. / vol. concentrations were converted. Each vol. / vol. concentration was multiplied by

10^5, then the LOG of this number was taken. Therefore, notation for the five concentrations of odor used in this set of stimuli was, from highest to lowest, 1.38, 2.08, 2.78, 3.48, and 4.18 (LOG [] x 10^5).

Upon visual inspection of perceived odor intensity and hedonic response functions, the stimuli in this concentration range appeared to be well spaced. Furthermore, the concentrations were generally discriminable. Therefore, this concentration range was chosen for further work.

Rating Procedure

Visual Analog Scale Rating System: The Visual Analog Scale (VAS) method was initially utilized for stimulus rating. VAS was chosen because various reports in the literature used this method for intensity and hedonic ratings of taste (Looy & Weingarten, 1991; Murphy, 1982) and is easily automated by computer. Odor intensity and hedonic value were rated on two separate visual analog scales. For odor intensity rating, subjects were asked: "How strong was the odor?" Subjects were instructed to place a mark on a 200 mm visual analog scale ranging from zero intensity (labeled "not strong at all") to maximum intensity (labeled "very strong") to describe their perception of odorant intensity.

Subjects' hedonic (affective) response to odor stimuli was measured in the same way. Subjects were asked: "How did you like the odor?" Subjects were instructed to respond on a continuum of affective response ranging from extreme liking to extreme disliking. The midpoint of the line represents a neutral reaction.

The data obtained from the visual analog scales are the distances from one end of the line to the subject's mark. As long as subjects are instructed that they may extend the line to match the magnitude of their perception, the visual analog scale technique is assumed to produce ratio-scale data and can therefore be analyzed using parametric tests (Price, McGrath, Rafii, & Buckingham, 1983).

Problem With VAS: Examination of pilot data revealed a problem with the VAS rating technique for our stimuli. Subjects tended to "overuse" anchors on the VAS so that concentrations were not discriminated very well. An experiment was conducted to compare perceived intensity and hedonic functions obtained by the Visual Analog Scale and Magnitude Estimation (described in General Method) procedures. The VAS intensity ratings we had obtained were artificially limited by the small range the subject could move the line across the computer screen. A necessary part of the VAS procedure is that subjects must be able to extend the line scale to reflect their perception, however, our computer setup obviously limited subjects' ratings. Magnitude Estimation does not have this problem. Ratings from Magnitude Estimation differentiated concentrations better than the VAS procedure. Therefore, Magnitude Estimation was chosen for use in future experiments.

Problem With Simultaneous Rating of Stimulus Attributions: Another problematic observation was addressed in a second experiment. Recall that subjects initially sampled a stimulus, then rated odor intensity and hedonics. Rating was done in this way to reduce sensory fatigue over a large number of stimulus repetitions (five). However, examination of pilot data revealed that subjects tended to give hedonic ratings that reflected intensity. For example, a subject might give an intensity rating of 10 and a hedonic rating of 5 and continue this pattern across concentrations. While odor hedonics is often directly related to perceived intensity (Doty, 1975; Moskowitz, Dravnieks, & Klarman, 1976), some odors would be expected to produce hedonic functions distinct from their intensity functions (Moskowitz, 1977). Parallel ratings of intensity and hedonics might reflect perception, but the experimenter wanted to be certain that hedonic response functions were not due to rating procedure.. An experiment was conducted to examine perceived intensity and hedonic functions when those attributes were rated concurrently or separately. Graphs of simultaneous judgments were compared to separate judgments. Visual inspection of these graphs indicated that separate judgments yield hedonic functions that do not parallel intensity as closely as simultaneous judgments. Odor concentration, perceived intensity, and hedonic tone are often closely related (Doty, 1975; Moskowitz, Dravnieks, & Klarman, 1976), so parallel functions are to be expected to some degree. However, we did not want to risk the possibility that the rating process itself was producing the intensity-hedonic functions obtained. Therefore, we decided to continue using separate judgments of odor intensity and hedonics.

Reduction of Stimulus Repetitions: Using separate judgments of odor intensity and hedonics eliminates the above problem. However, separate judgments of intensity and hedonics effective doubles the amount of stimuli sampled. Instead of producing sensory fatigue, we decided to reduce the number of stimulus repetitions from five to three.

The preceding section summarizes a series of pilot experiments that served as a basis for choice of odorants, concentrations, and rating procedures used in this thesis. Initially, we used low quality flavors, a narrow concentration range, a computer form of VAS, and a simultaneous attribute rating procedure. Intensity and hedonic functions were relatively flat and experimental findings were not robust. Multiple pilot experiments revealed that stimuli lacked volatility and that the rating procedure lacked sensitivity and constricted subject response. High quality stimuli were obtained and a subset of food odors was selected after pilot testing. Further testing enabled the selection of a concentration range that produces differential intensity ratings. More pilot studies demonstrated that Magnitude Estimation is a reliable and non-constricting stimulus rating procedure for odor intensity and hedonics. Furthermore, rating odor intensity and hedonics separately rather than simultaneously reduces subjects' tendency to report parallel ratings and allows for more reliable psychophysical functions.

The work described in this section informed the methodological choices of this thesis. Once high quality odorants, a reasonable stimulus range, and a reliable rating procedure were employed, then taste-odor mixture hedonics could be explored with confidence.