HUMAN SWEET TASTE REACTIVITY:

DETERMINANTS OF HEDONIC RESPONSE

By

HEATHER ANN LOOY

A Thesis

Submitted to the School of Graduate Studies

in Partial Fulfillment of the Requirements

for the Degree

Doctor of Philosophy

McMaster University

DETERMINANTS OF HEDONIC RESPONSE TO SWEET

DOCTOR OF PHILOSOPHY (1991)
(Psychology)

MCMASTER UNIVERSITY
Hamilton, Ontario

TITLE: Human Sweet Taste Reactivity: Determinants of Hedonic Response

AUTHOR: Heather Ann Looy
B.A.(Honours) (Queen's University)
M.A. (Queen's University)

SUPERVISOR: Dr. Harvey P. Weingarten

NUMBER OF PAGES: xi, 168

ABSTRACT

This series of experiments explored aspects of sweet taste reactivity in humans, primarily focusing on individual differences which may be relevant for understanding the interactions between taste and food intake.

The effect of metabolic state on sweet reactivity depends upon the subjects' underlying hedonic response to sweet (Experiment 1). Subjects can be classified into two major categories: sweet likers (i.e., increased liking with increasing concentration) and sweet dislikers (i.e., decreased liking with increasing concentration). Only the sweet dislikers show an attenuated dislike for concentrated sucrose when deprived; as well, they sip less solution when sated than deprived.

Experiment 2 establishes the predictive validity of the hedonic response measures by demonstrating that another known index of hedonic response, facial expressions, can be used to predict sweet liker/disliker status.

The sweet liker/disliker distinction correlates strongly with the genetically-determined ability to taste 6-n-propylthiouracil (PROP): PROP nontasters are almost always sweet likers, while sweet dislikers are almost always PROP tasters. This relationship also holds for 7-to-10 year old

children, as Experiment 3 shows.

Sensory differences may underlie the hedonic differences in taste response, since sweet dislikers perceive a purer sweet sensation than likers, who report nonsweet (bitter, salty or sour) components in pure sucrose solutions (Experiment 4).

The sweet liker/disliker distinction transfers almost perfectly to red, strawberry-flavoured solutions (Experiment 5). However, sweet dislikers show an attenuated dislike for concentrated sweet tastes with the addition of the odour and colour, suggesting that other sensory dimensions of the taste stimulus, such as smell and vision, have an impact on the hedonic value of the taste.

These experiments suggest that the sweet liker/disliker distinction reflects an individual difference in taste reactivity which should be accounted for in future explorations of both gustatory encoding, and of the role of taste in eating. Further studies should explore the generality of the sweet liker/disliker distinction to other gustatory stimuli, its predictive value for "real food" preferences and intake, and identify the specific sensory differences which underlie these hedonic response patterns.

DEDICATION

This thesis is dedicated to my mother, Elske, who taught me never to sell myself short, and, through the grace of God, gave me wings.

ACKNOWLEDGEMENTS

To Dr. Harvey P. Weingarten: You are a supervisor par excellence. I have benefited greatly by your knowledge, insight, and ability, and your contagious enthusiasm taught me how exciting and satisfying research can be. Thank you also for your patience, availability, and encouragement. Without all these, I would never have made it through.

To the "Weingarten Feeding Lab" gang--Dawn Elston, Sue Gowans, Anh Duong, Fiona Ghosh, Kevin McHugh, Whit Whitten and Siobhan Callaghan--thanks for making the lab such a happy, crazy place. Your laughter, conversation, and encouragement made being at school a pleasure.

My sincere thanks also go to my committee members: to Dr. Lorraine Allan, for her insightful comments and questions throughout; and to Dr. Grant Smith, for his quiet support, encouragement and feedback from the first day I arrived at McMaster.

To my husband, Anthony: this thesis is a product of both our efforts. As we once promised each other, you have served me with tenderness and respect, and encouraged me to develop my God-given gifts. I am humbly grateful for your steadfast faith in me, your love and companionship. Thank you for being the wind beneath my wings.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Chapter One

GENERAL INTRODUCTION

Historically, the study of eating behaviour has focused on internal signals, tied to energy depletion or repletion, which trigger meal initiation and termination (Weingarten, 1985). However, more recently scientists have acknowledged that eating is also driven by factors which are not directly related to the current physiological needs of the body (Warwick, 1990). Such "external" factors in the control of food intake include the sensory qualities of food, learning, and experience (Warwick, 1990; Weingarten, 1989).

The sensory qualities of food (taste, smell, texture, temperature, and colour) constitute one set of external factors which are powerful determinants of eating behaviour (Rolls, 1986). Under normal circumstances, the oral cavity acts as a "gateway" through which all food stimuli must initially pass. Therefore, the sense of taste (and smell) lies at the interface between the internal and external environment of the organism, and allows the organism to evaluate, accept or reject a food stimulus at the first stage of ingestion (Scott, 1991). Considerable research has focussed on the impact of this sensory evaluation of food stimuli on food preferences and intake (Cowart, 1981; Weingarten & Bédard, 1991). Many basic questions about this relationship remain unanswered, partly due to a lack of understanding of the mechanics of the gustatory system, and the enormous complexity inherent in the behaviours and stimuli related to food intake. Despite these difficulties, however, we do know something about the relationship between the sense of taste and eating, and this knowledge will be reviewed in the remainder of this chapter.

Anatomy of the Taste System

The term "taste" is used in different contexts to refer to either the flavour of a stimulus, a concept which includes smell as well as taste, or more narrowly to the sensations arising from stimulation of receptors in the mouth. While olfactory sensations play an important role in the experience of flavour, this thesis primarily focusses on taste in the narrow sense.

The physical structure of the taste system (Bartoshuk, 1988) begins with the papillae on the tongue and elsewhere in the oral cavity. There are four kinds of papillae--fungiform, foliate, circumvallate, and filiform--which are located in different regions of the tongue. All but the filiform papillae contain varying numbers of taste buds. These taste buds in turn contain receptor cells which synapse with nerve fibres, although the precise mechanisms by which the cell is stimulated are not understood. The neuron which innervates one taste receptor may also innervate other receptors, either within the same papilla, or across many papillae. As well, any one receptor may be innervated by more than one fibre (Travers, Travers & Norgren, 1987). This multiple innervation allows for the possibility of peripheral integration or lateral inhibition of neural responses.

Neural signals from the taste receptors travel along one of three nerves: the chorda tympani and greater superficial petrosal (branches of cranial nerve VII), the glossopharyngeal (cranial nerve IX), and the vagus (cranial nerve X). Each of these nerves innervates a different type of papilla and therefore a different region of the tongue or oral cavity. These nerves project to the nucleus tractus solitarius (NTS) in the medulla, and then to the pontine taste area (PTA). From here, neurons project to the thalamus and/or the amygdala, and ultimately to cortical taste areas. Very little crossing over occurs in the taste system before the cortical level, and even in the cortex representation is mainly ipsilateral (Bartoshuk, 1988; Pfaffman, Frank & Norgren, 1979).

The function of the taste system is the transduction of a chemical stimulus into a neural signal, which ultimately, after modification and integration with other signals, results in a particular taste sensation.

Encoding of Taste Qualities

Studies involving the taste system are difficult for two major reasons. First, the physical dimensions of tastants which constitute the relevant stimuli for taste quality have not been reliably identified (Kuznicki & Ashbaugh, 1982). Second, it is unclear whether taste stimuli are perceived continuously (i.e., every stimulus giving rise to a unique sensation) or categorically (i.e., grouped into sweet, salty, sour, bitter). And, if taste perception is categorical, the dimensions and characteristics of these categories are unknown (Erickson, 1985).

A comparison with the visual system may clarify the importance of these issues. The stimulus for vision is a particular range of electromagnetic radiation. The relevant physical dimension of this stimulus for the perception of colour is wavelength. Wavelength of light varies continuously; however, the visual system is structured to perceive this continuous variation in a categorical manner. For example, a person will perceive blue for a given range of wavelengths, but when wavelength is increased slightly beyond this range, they will quite abruptly begin perceiving green.

In contrast, all that is known about the physical stimulus for taste is that it is embodied in a bewildering variety of chemical substances. Some effort has been directed toward finding chemical or structural similarities among taste stimuli which evoke similar sensations (for example, among all stimuli which are perceived as sweet). Acids evoke the sensation of sourness, and the degree of sourness perceived seems to be related to the strength of the dissociation between the anion (e.g., Cl^-) and the cation (H^+). The picture is less clear for substances which taste salty. Originally, saltiness was attributed to the anion (e.g., Cl^-), but later research suggested that the cations (e.g., Na^+) also play a role (Schiffman, McElroy & Erickson, 1980). No common physical or chemical property has been found for molecules which taste sweet or bitter, although some elaborate schemes have been proposed (Bartoshuk, 1988). In general, there is no physical or chemical dimension of gustatory stimuli which has been identified as directly relevant for the encoding of taste quality.

Whether the variety of gustatory stimuli is perceived in a categorical manner is a hotly-debated question: some argue that the qualities of sweet, sour, salty and bitter constitute true categories of taste sensation, and indeed psychologically are experienced as separate sensory modalities (McBurney, 1979; McBurney & Gent, 1979; Öhrwall, cited in Erickson, 1985). Others believe that the qualities of sweet, sour, salty, and bitter simply define the boundaries of possible taste sensations, and that each stimulus evokes a unique, unitary sensation within the limits of these boundaries (Erickson, 1982; 1985; Henning, 1916; Schiffman & Erickson, 1971).

Considerable psychophysical and electrophysiological research has been directed towards resolving this debate; however, no clear answers have emerged from the data so far.

Chemical stimulation of single taste papillae, using stimuli which evoke one of the four "basic" tastes--sweet, sour, salty and bitter--reveals that each papilla can mediate more than one taste quality (Arvidson & Friberg, 1980; Bealer & Smith, 1975). As well, an identical gustatory stimulus can be experienced as having a different taste quality depending upon which type of papilla it stimulates (Sandick & Cardello, 1981). Therefore the three types of papillae which contain taste buds--circumvallate, fungiform and foliate--cannot be functionally discriminated in terms of the taste quality they encode.

However, it is possible that individual taste buds contain chemically-specific receptors which mediate separate taste qualities. Arvidson & Friberg (1980) reported that the number of taste buds found within a fungiform papilla was correlated with the number of taste qualities evoked by stimulation of that papilla (r=.80). Tonosaki and Funakoshi (1988) measured receptor potential in the taste buds of the mouse in response to sucrose and NaCl stimuli. They found that membrane resistance increased with sucrose stimulation, and decreased with NaCl stimulation, evidence for differential responses to gustatory stimuli at the level of the taste receptor.

At the neural level, two models describe possible ways in which different taste stimuli could be neurally encoded: the "across-fibre pattern" and the "labelled-line" theories (Bartoshuk, 1988; Pfaffman, 1951; Pfaffman, Frank & Norgren, 1979). The across-fibre pattern theory argues that taste quality is encoded in a pattern of activation across a number of fibres, rather than the all-or-none response of one particular fibre or fibre type alone. In contrast, the labelled-line theory says that specific taste qualities are mediated by specific nerve fibre types. Thus, sweetness is perceived when one fibre type is activated, while sourness would be perceived if the information is carried by another type of fibre.

Pfaffman (1941) was the first to directly examine neural responses to taste stimulation by taking electrophysiological recordings from single nerve fibres in the chorda tympani and glossopharyngeal nerves of the cat. He found three fibre types: those that responded to acid only, acid and NaCl, and acid and quinine. Pfaffman argued that his results supported an across-fibre pattern theory of quality encoding: saltiness is perceived when one set (acid-NaCl) of fibres fires, bitter when acid-quinine fibres are activated, and sour when all the fibres, acid-only, acid-salt, and acid-quinine, are activated. Further support for this theory was evidence that indeed the pattern of activity across neurons in the rat in response to stimuli which evoke a particular taste quality differed from the pattern observed with stimuli which evoke a different quality (Erickson, 1963).

However, a classic experiment by Frank (1974) suggested that there are indeed fibre types, or "labelled lines". She demonstrated that hamster chorda tympani fibres could be classified on the basis of the stimulus to which they maximally responded. Knowledge of a fibre's best stimulus allowed accurate prediction of its response to stimuli which evoke different taste qualities. Frank argued that there were four fibre types, each maximally responsive to stimuli which evoke one of the four presumed basic taste qualities.

Replications and extensions of this work have continued to support the concept of "broadly-tuned" taste neurons which are maximally and specifically sensitive to a given stimulus or class of stimuli (Boudreau, 1974; Boudreau, Sivakumar, Do, White, Oravec & Hoang, 1985). While generally neurons further from the periphery appear to be more broadly tuned than those of the chorda tympani, the fibre types Frank (1974) reported have been observed in the NTS and the parabrachial nucleus of the hamster (Smith, VanBuskirk, Travers & Bieber, 1983a; b).

The modern version of the labelled-line theory of taste quality encoding does not imply that a given gustatory stimulus will activate one and only one fibre type. Rather, a number of fibre types may be activated, yielding a complex taste sensation which is dominated by one quality but not to the exclusion of all others. Even very simple chemical stimuli can produce rather complex taste sensations (Bartoshuk, 1988; Erickson & Covey, 1980).

However, the studies of neuron types have not always classified neurons into four categories, and even when they do, these categories do not necessarily correspond to the four basic taste qualities as Frank's (1974) study suggested. This may be due to cross-species differences: hamsters, cats and rats may not encode taste qualities in the same manner as humans. Recent preliminary recordings from single nerve fibres in chimpanzees have in fact found narrowly-tuned neurons responsive to one of the four taste qualities humans perceive: sweet, sour, salty, and bitter (Hellekant, Ninomiya & Dubois, 1991). Nevertheless, the neural recording studies have not clearly established what information the neurons are in fact encoding and how that is 9ultimately translated into the experience of taste quality. Further, the neuron classes defined in these studies do not have clear-cut boundaries. Indeed, within a class, even the response of narrowly-tuned neurons does not always discriminate between a midrange concentration of that neuron's best stimulus and a high concentration of a qualitatively-different stimulus (DiLorenzo & Schwartzbaum, 1982a; b). It would appear that some combination of labelled-lines and across-fibre patterns may be required to account for the unambiguous encoding of a particular taste quality. However, until we know which aspects of the neural response are relevant for encoding taste quality, and how the elements of this response can be interpreted in terms of the organism's taste experience, the mechanics of taste quality encoding will remain somewhat of a mystery.

A major critique of experiments designed to address the question of taste quality encoding is based on the lack of understanding of the physical dimension(s) underlying taste quality. In the absence of this information, taste stimuli are usually defined in terms of the <u>sensations</u> they produce--that is, in terms of their taste quality. This implies that taste quality is a characteristic of the stimulus, not the person doing the tasting. That is, within a species, a particular chemical should always evoke the same quality, regardless which individual is doing the tasting. Further, this method of defining the stimulus forces researchers to make important assumptions about the number and type of possible taste qualities to enable them to appropriately select and group stimuli. Therefore, attempts to determine whether, and how, taste stimuli are categorized during the process of transduction are often based on a circular argument: stimuli are selected on the basis of predetermined categories of evoked taste quality, and when the subjects (or neurons) respond differentially to stimuli belonging to these different preselected categories, this is taken as evidence for categorical perception of gustatory stimuli!

Schiffman and Erickson (1971) have attempted to avoid this problem by using multidimensional scaling, a technique which reveals relationships among stimuli, and can also suggest something about the dimensions which underlie those relationships, without imposing preselected categories on the stimuli. Using a large number of stimuli, selected to provide both a range of subjective taste quality and chemical composition, they had subjects rate the similarity of the taste of every possible pair combination, as well as repeatedly rating each stimulus on a number of semantic differential scales. Primarily on the basis of the similarity judgements, Schiffman and Erickson (1971) concluded that the dimensions on which taste stimuli are best described and perceived are: molecular weight, pH, and hedonic value (relative pleasantness or unpleasantness). While there was some grouping of stimuli into the quality categories of sweet, sour, salty, bitter and alkaline, the two stimulus dimensions, pH and molecular weight, and the hedonic dimension accounted for the variance in sensations more adequately. Unfortunately, there appear to be no replications or extensions of this method (although see Schiffman, McElroy & Erickson, 1980, for an application of this procedure to the class of sodium salts) and therefore the intriguing possibilities regarding taste quality encoding which emerged from this original study have not been developed further.

In contrast with Schiffman and Erickson's (1971) conclusions, psychophysical cross-adaptation studies suggest that the four basic taste qualities function independently of one another, implying that gustatory stimuli are indeed encoded into these quality categories. Although there are some exceptions, in general adaptation of the tongue to a stimulus evoking one quality reduces sensitivity to other stimuli which evoke the same quality, but does not significantly affect sensitivity to other qualities (McBurney, 1972; McBurney & Bartoshuk, 1973; McBurney, Smith & Schick, 1972; Schiffman, Cahn & Lindley, 1981; Smith & McBurney, 1969). Taste modifiers, such as Gymnema sylvestre and a class of compounds called the ziziphins, selectively reduce or remove the sensation of sweetness without affecting the other taste qualities (Bartoshuk, 1974; 1988; McBurney & Gent, 1981; Smith & Halpern, 1983). Measurement of neural activity in the chorda tympani of humans treated with Gymnema sylvestre reveals a decreased rate of firing in response to sweet stimuli, but no change in the neural responses to sour, salty, and bitter stimuli (Diamant, Oakley, Strom, Wells & Zotterman, 1965; Oakley, 1985).

At present, the strongest statement that can be made regarding taste quality encoding is that the taste system is not easily described or defined in terms of current models or analogies with other sensory systems. A simple system based on four categories of taste quality (sweet, sour, salty and bitter) and their combinations seems inadequate to explain both the neural data and the diversity of people's taste experiences. Yet the facts that we can and do use a limited number of terms to categorize our taste experiences (whether or not that captures the richness of those sensations), and that these categories appear to operate fairly independently, suggests that certain basic or primary tastes constitute an important and fundamental aspect of taste perception at some level. Certainly nearly all the literature which deals with taste uses the notion of basic taste quality categories as a useful heuristic. Whether or not we understand the mechanisms whereby these taste qualities are encoded, assuming the existence of quality categories of sweetness, saltiness, sourness and bitterness has helped us effectively probe a number of questions regarding taste perception as well as its role in eating behaviour.

Taste Perception and Eating Behaviour

Given the dearth of knowledge regarding the encoding of taste quality, connections between taste perception and eating behaviour have been based on the assumptions that (1) certain broad categories of taste quality are perceived as pleasant (e.g., sweet and perhaps salty) or unpleasant (e.g., bitter and sometimes sour), and (2) that pleasant-tasting foods will be preferred and consumed in large quantities, while unpleasant-tasting foods will generally be avoided (Blundell, Rogers & Hill, 1988; Zellner, Berridge, Grill & Ternes, 1985). Thus the literature on the role of taste in eating behaviour has focussed primarily on the impact of general food palatability on eating. The relationship between specific aspects of taste perception, such as perceived quality categories and intensity, has not been extensively examined.

"Palatability" refers to the pleasantness of the sensory properties, primarily the taste, of a stimulus. It can be inferred indirectly through measures of food preference or intake, or directly, in human subjects, by asking them to evaluate the pleasantness of a stimulus. Manipulations of the palatability of food can affect consumption; however, palatability is not itself a stable characteristic of the external stimulus, the food. Identical food stimuli will be evaluated as more or less palatable by different individuals, and also by the same individual under different conditions (Weingarten & Bédard, 1991). The effects of palatability on food preferences and intake have been studied extensively in animals and humans.

Animal Studies of Palatability

Since animals cannot be asked to evaluate and report directly on the pleasantness of a taste stimulus, indirect behavioral measures must be used from which the animals' hedonic evaluations are inferred. This results in a rather circular definition of palatability: An animal is assumed to behave more positively toward a palatable relative to an unpalatable stimulus; therefore any stimulus toward which the animal responds in a relatively more positive manner is defined as palatable.

Intake measures are one method for assessing the palatability of stimuli. The procedure most commonly used involves giving an animal a choice of stimuli and recording the relative intake of each (Young and Greene, 1953). The assumption is that the animal will consume more of the substance it finds most palatable. However, it is equally possible that the animal preferentially ingests the substance which is associated with more positive postingestive consequences (Weingarten & Bédard, 1991). In fact, food preferences can be created in rats by associating one flavour with a positive, and a second flavour with a neutral, postingestive consequence (Sclafani, 1988). In such a situation it seems unlikely that the preference is based on an increase in the relative palatability, or hedonic experience, of the flavour.

A more valid approach to determining the relative palatability of stimuli for an animal is to isolate sensory factors from postingestive consequences. One strategy involves response measures taken during the first few minutes of contact with the food stimulus (Weingarten & Bédard, 1991). These measures include: initial choice from a selection, short-term intake, and lick rate (Davis & Smith, 1988). The data resulting from such techniques do not always coincide with those obtained from intake measures, providing some confirmation that intake and "brief exposure" methods do in fact measure different aspects of an animal's response to a food stimulus (Weingarten & Bédard, 1991). However, even very brief exposures to a food stimulus (i.e., less than three minutes) may not completely isolate palatability responses from the contribution of (unidentified) postingestional events, some of which may be triggered extremely rapidly after oral stimulation (Davis, 1973; Weingarten & Bédard, 1991).

A second strategy for isolating the effects of oral stimulation from postingestive and postabsorptive consequences is sham-feeding (Weingarten & Watson, 1982). In this procedure, an indwelling cannula is surgically implanted into the stomach of a rat. When the cannula is closed, any food the rat consumes passes normally through the digestive system. However, if the cannula is opened, ingested solutions drain out of the fistula, thereby preventing gastric distension and the passage of nutrients into the duodenum and small intestine. The advantage of sham feeding over brief exposure techniques is that intake can be measured over a much longer period of time, since the possibility of postingestive consequences has been greatly minimized.

Both sham feeding and brief exposure techniques have shown that rats' intake of sugar solutions increases with increasing concentration (Weingarten & Watson, 1982; Young & Greene, 1953). The inference, therefore, is that higher concentrations of sugar are more palatable to the rat. Changes in metabolic state also affect sham feeding. Rats sham-feed more of a sucrose solution when they are food-deprived than when sated, implying that sucrose becomes more palatable when the organism is in a state of depletion (Weingarten, Duong, Gowans & Elston, 1990). Hyperglycemia reduces sham feeding intake of sweet solutions (Bédard & Weingarten, 1989), suggesting that elevations in plasma glucose suppress the palatability of sweet-tasting substances. However, it is unclear whether the hyperglycemia-induced change in palatability is a reflection of a change in the hedonic value (pleasantness) of glucose, or a change in perceived intensity. Giza and Scott (1987a) trained rats to avoid a particular glucose concentration by way of a conditioned taste aversion. They used degree of generalization of the aversion to other glucose concentrations to demonstrate that experimentally-induced hyperglycemia caused the rats to behave as if the concentrations of the glucose solutions were weaker than they in fact were--that is, they tasted less intensely sweet after glucose adminstration. (This interpretation of the data is of course based on the assumption that rats always consume more of a glucose solution the sweeter--more concentrated--it is.) The change in perceived intensity was specific to glucose--hyperglycemia did not affect response to quinine. These behavioural data are consistent with electrophysiological recordings measured under similar experimental conditions (Giza & Scott, 1987b).

There are further problems with the interpretation of intake measures. As noted earlier, intake measures of palatability are indirect and circular. It is not clear whether changes in intake are perfectly positively correlated with changes in palatability. Intake may change for a number of alternate reasons: (1) postingestive consequences (even with sham feeding, there is a significant rise in plasma glucose (Sclafani & Nissenbaum, 1985)); (2) the intensity, rather than the hedonic value, of the solutions may have changed; and (3) the manipulations performed which result in changed intake may have their effects on intake through mechanisms which do no involve palatability at all.

To avoid these problems of interpretation, what is needed is a method by which the palatability, or hedonic value, of a stimulus can be assessed directly. This is extremely difficult to do in animals. Grill and Norgren (1978) have developed a procedure which appears to provide a rough measure of "pure" taste reactivity in animals.

Solutions are infused into the mouth (with little or no actual ingestion) and the facial expressions elicited by this stimulation are recorded. These facial responses can be divided into two categories: ingestive and aversive. It is clear that such responses are solely to the taste of the substance, since there is no possibility of any contribution by postingestive consequences. Cabanac and LaFrance (1990) have used this technique to demonstrate that, after a gastric load of glucose, rats showed a change from the ingestive facial responses to sucrose on the tongue seen prior to the load to aversive responses to sucrose after the load. These data were interpreted to reflect a change in the palatability of a sweet-tasting gustatory stimulus in response to a change in internal metabolic/nutritional state.

However, even this technique does not permit unambiguous interpretation in terms of the pleasantness or unpleasantness of the taste of a stimulus. Again, an animal may show ingestive or aversive facial expressions because it has associated the taste with positive or negative consequences, and indeed might be willing to ingest a substance which tastes unpleasant simply because it was associated with a positive consequence (Sclafani, 1988).

In summary, animal studies do not permit the direct measurement of the palatability, or hedonic value, of a substance. Rather, palatability must be inferred indirectly from behavioural measures. However, these behavioural responses can be interpreted in a number of alternate ways, changes in palatability being only one of a number of possibilities.

Human Studies of Palatability

The issue of isolating hedonic response to a taste stimulus is simpler when using human subjects, since they can be asked to give direct assessments of palatability. Although palatability may be affected by postingestive factors in experiments where subjects actually ingest the substances they are evaluating, the fact that humans can assess palatability directly means that the cumulative effects of such postingestive factors on palatability can also be evaluated. This was not possible in animal studies, except with the use of special techniques like sham feeding, since changes in preference or rate of ingestion over time could be interpreted as reflecting changes in palatability, the effects of satiety signals independent of palatability, or both.

When ingestion is not a factor, as when subjects taste and expectorate the substance (a procedure known as "sip and spit"), palatability can be assessed somewhat independently from other aspects of taste perception, such as the quality of the taste or its intensity (Moskowitz, Kluter, Westerling & Jacobs, 1974; but see McBride, 1985 for arguments against this conclusion). Moskowitz et al. (1974) had subjects rate the intensity of sweetness and the pleasantness of different concentrations of sucrose solutions and other sweet stimuli (pudding, cake, cherry drink). They found that the relationship of perceived intensity to sucrose concentration was represented by a mathematical function unique from the function which represented the relationship of pleasantness to concentration. That is, while ratings of intensity increased monotonically with concentration, pleasantness increased at a slower rate, and flattened out or decreased beyond a certain concentration.

Another study further supports the conclusion that humans can independently assess taste intensity and hedonic value (Lundgren, Jonsson, Pangborn, Sontag, Barylko-Pikielna, Pietrzak, dos Santos Garruti, Moraes & Yoshida, 1978). Subjects were divided into subgroups based on their pattern of hedonic response to a range of concentrations of sweet stimuli. If there were an absolute relationship between taste intensity and hedonic value, then the intensity ratings should differ in shape or level for each subgroup. In fact, the intensity functions were similar for all subjects, regardless of their pattern of hedonic response.

A number of interesting questions can be addressed regarding the relationships between palatability, internal states of depletion and repletion, and eating behaviour. For example, how does metabolic state affect taste reactivity? Do inter- and intra-individual differences in taste reactivity have any effect on food preference and intake? Do changes in palatability reflect physical changes in taste perception (i.e., perceived intensity or even quality of a stimulus), changes in the hedonic evaluation of a stimulus whose physical encoding by the gustatory system is unchanged, or some combination of these two possibilities?

In humans, these issues are primarily addressed within the taste quality category of sweetness. While palatability can be manipulated by changing a number of dimensions, such as the texture, temperature, or taste quality of a stimulus (see Drewnowski, Sande, Brunzell, Iverius & Greenwood, 1985), the dimension of sweetness is a very powerful taste cue (Blundell et al., 1988) and as such has received the most attention.

However, prior to reviewing this literature, methods of measuring taste reactivity in humans will be briefly addressed.

Measurement of Taste Intensity: The relationships between the perceived intensity of a taste and its hedonic value are of special interest both to researchers in the food industry, and also to those who wish to compare animal and human studies. In animal studies, palatability within a taste quality category (i.e, sweetness) is usually manipulated by changing the concentration, and therefore the intensity of the taste, of the stimulus. Human studies can tell us how changes in hedonic value are related to these changes in concentration/intensity, although caution must be exercised in assuming that these relationships apply across species.

Perceived intensity increases with increasing concentration of the relevant gustatory stimulus (Stevens, 1961). The method of magnitude estimation is usually used to measure perceived intensity of gustatory stimuli. The stimuli vary only in concentration, and are presented in a random order. There are two basic techniques. In one, the subject is given a standard stimulus of moderate intensity, and assigns a value to that stimulus (for example, 10 or 100). The subject then assigns a number to each of the test stimuli that represents their intensity relative to the standard. Thus, a stimulus which tastes twice as strong as the standard would be assigned a number twice as large (e.g., 20 or 200). A stimulus which is one-quarter as strong as the standard would be given a number one-quarter as large (e.g., 2.5 or 25). In the second type of magnitude estimation procedure, no standard stimulus is provided. The subject assigns a number to the first stimulus which seems to them to reasonably represent its intensity. The second stimulus is then given a number which reflects how much stronger or weaker it was relative to the first, and so on through the entire set of stimuli.

Data obtained using either technique are assumed to approximate a ratio scale (Bartoshuk, 1978). Therefore, in analyzing such data, the ratios between the numbers are of interest, and not their absolute size. However, individual subjects may use numbers which differ in absolute size by several orders of magnitude (e.g., 10's and 1000's). As a result, prior to averaging across subjects, magnitude estimates must be converted to a common scale. There are several techniques available for this (Marks, 1974). It should be noted, however, that there is some debate about the assumption that magnitude estimation does in fact produce ratio-scale data (Westermann, 1982; Zwislocki & Goodman, 1980). Nevertheless, it remains a standard procedure employed to study the relationship between physical and perceived intensity.

Another technique to measure perceived intensity involves the use of a visual analogue scale. Rather than asking subjects to assign numbers to stimuli in proportion to their intensity, they are asked to make a mark along a line which represents a continuum from zero intensity (the absence of the target sensation) to maximum intensity. The more intense the stimulus, the further along the line toward the "maximum intensity" end the mark is placed. Again, subjects are asked to place their marks in a manner which represents the relative intensity of the taste. Thus, if stimulus #2 is twice as intense as stimulus #1, the subject marks the line twice as far along from the zero point for #2 than they did for #1. To allow for the possibility that subjects may place a mark in such a manner that they have insufficient space left to indicate the true relationship between two stimuli in perceived intensity (e.g., a stimulus may taste three times stronger than the previous one, but there is no room on the line to place a mark three times further along), Bartoshuk (personal communication) suggests that the "anchors" of "zero intensity" and "maximum intensity" be placed some distance within the extreme limits of the line. This usually ensures that subjects will place their marks within these boundaries, but gives space should a particular stimulus demand a placement beyond them. Once all the stimuli are evaluated, the experimenter then assigns numerical values to the marks on the visual analogue scales by measuring the distance from one end of the line to the mark.

The advantage of the visual analogue scale over the classical magnitude estimation procedure is that subjects are given a limited range (i.e., the length of the line) within which to evaluate stimulus intensity. Therefore, data from individual subjects do not need to be converted to a common scale prior to averaging. Intensity data obtained using visual analogue scales is comparable, though not always identical, to that obtained using magnitude estimation (Price, McGrath, Rafii & Buckingham, 1983). It is generally assumed that the visual analogue technique produces ratio-scale data (Price et al., 1983), and is usually analyzed using parametric techniques such as analysis of variance. Apart from the question of the validity of this assumption, the visual analogue technique at least provides a good descriptive account of subjects' responses to gustatory stimuli, and allows confirmation that subjects can discriminate among concentrations of a stimulus on the basis of taste intensity (Duncan, Bushnell, & Lavigne, 1989; Hill, Magson & Blundell, 1984; Mattes & Mela, 1986). As well, at present the best statistical technique available for analyzing visual analogue data is analysis of variance.

Another method for measuring perceived intensity is the category scale. Usually a 5 to 9 point scale is used, with each number corresponding to a subjective description of intensity. For example 1=very weak, 3=moderate, and 5=very strong. Such scales are easier for subjects to use; however, the more conservative, less powerful nonparametric statistics must be used to analyze the data (Stone & Sidel, 1985). Although some differences emerge when comparing data obtained using category versus visual analogue scales or magnitude estimation (Duncan et al., 1989; Piggott & Harper, 1975), at a descriptive level, category scales appear to be comparable to magnitude estimation or visual analogue scales (Jensen, Karoly & Braver, 1986; Mattes & Mela, 1986; Moskowitz et al., 1974).

Measurement of Hedonic Value: The hedonic value of a taste stimulus (the degree of "liking") is probably the most direct representation of what is meant by the construct of "palatability". In humans, the hedonic value of a substance is an extremely important aspect of the taste experience. Indeed, pleasantness-unpleasantness appears to be a dimension upon which people naturally assign or group gustatory stimuli (Schiffman & Erickson, 1971).

The hedonic value of a set of gustatory stimuli can be measured in a number of ways. Subjects can be asked to give numerical magnitude estimates of the pleasantness of the taste in the same manner as was described above for intensity (Moskowitz et al., 1974). Or, a visual analogue scale can be employed (e.g., Mattes & Mela, 1986; Rolls, Rolls & Rowe, 1983). Another standard procedure is to provide a 5-, 7-, or 9-point category scale, where 1=dislike extremely, 3(4 or 5)=neutral, and 5(7 or 9)=like extremely (Cabanac, 1971; Stone & Sidel, 1985). Subjects simply circle or otherwise indicate in which category they would place a given stimulus.

Hedonic value can also be measured relatively; that is, as a preference. Subjects are presented with pairs of stimuli, and asked to indicate which of the two they prefer, or like better. By having the subject evaluate all possible pair combinations of a set of stimuli, the experimenter can rank order the stimuli in terms of preference (Stone & Sidel, 1985). At a theoretical level, it is unclear whether preference tests measure the same aspect or construct of hedonic value as the direct measures described above. Indeed, there is some evidence that preference tests do not produce completely comparable data to the other hedonic measures, and in fact, preference tests <u>may</u> more accurately predict behaviours such as food choice or amount consumed (Lucas & Bellisle, 1987; Mattes & Mela, 1986).

Taste Reactivity in Response to Short-term Metabolic Changes: Since taste lies at the interface of the internal and external environment (Scott, 1991), it is important to explore whether and how internal physiological changes can affect taste reactivity, on the assumption that changes in taste reactivity will affect food choice and intake in such a manner to help moderate and regulate these internal changes.

The early literature on this subject focussed on taste thresholds, and examined the effects of short-term deprivation (i.e., testing subjects prior to a meal) and satiation (i.e., testing immediately after a meal) on the quality detection thresholds for sweet (sucrose or glucose). Sometimes salt and bitter thresholds were also tested. Some studies reported systematic changes in the threshold for sweet, with a decreased threshold immediately prior to, and an increased threshold following, a meal (Goetzl, Ahokas & Payne, 1950; Yensen, 1959). Others found no such relationship (Janowitz & Grossman, 1949; Meyer, 1952). It is not clear which results should be taken more seriously, as neither set has been consistently replicated. The question of whether threshold changes for sweet accompany metabolic changes has not been pursued in recent years, probably because in the "real world" people tend to consume foods which have taste intensities well above threshold values.

Examinations of metabolic effects on taste responsiveness to above-threshold stimuli have been more fruitful. Cabanac (1971; 1979) had subjects fast prior to testing. He then gave them the same sucrose solution at regular time intervals. In one session, the subject sipped the solution, spit it out, and then evaluated its pleasantness on a 5-point scale (-2, -1, 0, 1, 2; 0=neutral). In the other session, the subject sipped and swallowed the solution each time. Cabanac found that subjects continued to rate the solution as pleasant-tasting as long as they did not swallow it. If they ingested the solution however, pleasantness was reported to decrease, and by the end of the session, subjects found the solution to be quite unpleasant. Cabanac called this phenomenon _alliesthesia_, to refer to the change in the pleasantness of a sensation as a result of changed internal signals. This alliesthesia hypothesis would predict that an individual should evaluate a sweet taste more positively when deprived than when sated, due to the changing signals from their gut. In other words, things should taste better when one is hungry.

Cabanac and Fantino (1977) suggested a mechanism for the alliesthesia effect by demonstrating that the greatest decrement in pleasantness of sweet stimuli (maximal alliesthesia) occurred with the most _concentrated_ (smallest volume) glucose load. They concluded that taste responsiveness is affected by signals from the duodenum regarding the concentration, not the volume, of nutrient present.

Scherr and King (1982) used "real foods" rather than sucrose solutions to test the alliesthesia hypothesis. Subjects rated the intensity and hedonic value of sweet vanilla pudding and nonsweet mashed potatoes. They were then given a small preload of some common liquid or solid food (e.g., cake), and then rated the intensity and pleasantness of the pudding or mashed potatoes four times at 15-minute intervals, using Cabanac's 5-point scale. Subjects did swallow the test stimuli; however, the amounts were very small (about 2 ml). Scherr and King found that intensity ratings did not change after the preload, but pleasantness ratings decreased, and decreased maximally when the preload was high in calories. This decrease in pleasantness was quite small at the first 15-minute rating, but became more pronounced at subsequent intervals. This gradual development of alliesthesia suggests that taste responsiveness could be modified by postabsorptive cues from the gut, signals which take some time to accumulate or trigger.

While Scherr and King (1982) observed decreased pleasantness ratings for <u>all</u> tested foods regardless of the type of preload given (solid or liquid), Rolls, Rolls and

Rowe (1983) demonstrated changes in taste responsiveness which were specific to the category of substance (food or water) consumed. Five-hour fasted subjects rated the intensity and the pleasantness of a variety of foods and water on 100 mm visual analogue scales. They were then instructed to eat one of the foods, or to drink the water, to satiety, after which they rated all the foods and water again. Results showed that perceived intensity of the tastes did not vary significantly. However, pleasantness decreased for all the foods when one food was consumed, and for water when water was consumed. Pleasantness ratings for stimuli in the unconsumed category (food or water) remained unchanged. The authors argue that these results imply a motivation-specific satiety--if one is hungry and thirsty, and eats food to satiety, then the hunger motivation has been reduced, but the thirst motivation remains. Taste responsiveness is adjusted accordingly--a decrease in pleasantness for the substance one no longer needs, but no decrease for substances which would fulfill the unmet need.

Palatability of foods is not only modified in a category-specific manner, but can also be affected much more specifically, that is, <u>within</u> the category of solid food. In the study just described (Rolls et al., 1983), while the pleasantness of all the foods decreased significantly after consumption of any one food, the pleasantness of the food consumed decreased significantly more than the pleasantness of the other foods. In another study, Rolls, Rolls, Rowe and Sweeney (1981) had subjects rate the pleasantness (on Cabanac's 5-point scale) of eight foods (which were not swallowed), after which they ate one of the foods to satiety. They then rated the pleasantness of all eight foods again, both two and twenty minutes after the meal. Even at two minutes postmeal, the pleasantness of the eaten food had decreased significantly more than that of the other seven foods. This effect was still present, although less strongly, twenty minutes postmeal. These results suggest that the hedonic value of a specific food (and therefore a specific taste) is sensitive to the food type ingested immediately prior to testing.

However, it is unclear whether this change in palatability is due to postabsorptive signals regarding changes in the individual's internal nutritional status, or to some kind of relati ly short-term adaptation to the sensory qualities of the food. One test of this would be to examine whether the decrease in pleasantness for a specific food generalized to other foods which were similar to the target food in nutrient content but differed in sensory qualities (taste, texture, temperature, odour), or to foods which differed in nutrient content but shared similar sensory attributes. A second experiment by Rolls et al.

(1981) suggested that there was some generalization of the decrease in palatability to foods in the same nutrient category (e.g., meats, or desserts), although this result is difficult to interpret since each of these categories not only share nutrient contents but a number of sensory attributes (e.g., meats are salty/savoury, desserts are sweet).

Rolls et al. (1981) also found that the pleasantness ratings predicted the amount consumed in an unexpected "second course", given immediately after the two-minute postmeal ratings. Foods which were eaten in the first course, and therefore rated as less pleasant-tasting after that meal, were consumed in smaller quantities in the second course. Foods which were not eaten in the first course, and which therefore did not show a decrement in hedonic value, were consumed in quantities (measured in terms of calories) similar to the caloric intake of the first course. Again, however, eating less of a food in a second course which one has just consumed substantial quantities of in a first course may have less to do with internal signals than with sensory adaptation. Indeed, Rolls, Rowe and Rolls (1982) refer to this phenomenon as "sensory-specific satiety", and they argue that subjects are showing changes in taste reactivity which are due to immediately previous sensory experiences rather than to internal physiological changes.

The sensory qualities of the food that subjects respond to include: colour, shape, and flavour (Rolls et al., 1982).

These experiments demonstrate that taste reactivity is sensitive to the sensory qualities of the foods being ingested, and that these changes in the hedonic value of particular foods will affect food choice and intake at least in the latter part of the same meal. This conclusion implies that previous studies (see above) which have related short-term metabolic changes--almost always induced by having subjects ingest something--to changes in taste reactivity may instead be further demonstrations of the phenomenon of sensory-specific satiety. However, the fact that Rolls et al. (1981) found some generalization of changes in palatability across food categories (e.g., meats), and the observation that sensory-specific satiety takes a few minutes to emerge and lasts for at least twenty minutes, suggests that even here, metabolic or nutritional status may play a significant role. This would be consistent with Cabanac's (1979) argument that changes in palatability are governed by internal signals from the gut (see also Cabanac and Fantino, 1977).

All the above studies reported changes in taste reactivity, specifically in hedonic response, which corresponded to ingestion or changes in short-term metabolic state. Moskowitz, Kumraiah, Sharma, Jacobs and Sharma

(1976) obtained somewhat contrasting results. In their study, subjects were tested either after a 14-hour fast, immediately after breakfast, after lunch, or shortly after an oral glucose load. Each subject tasted a series of randomly-ordered glucose solutions varying in concentration from 0.06 to 2.0 M, using a sip-and-spit procedure. They rated the intensity and pleasantness of each solution on a 6-point category scale. Intensity ratings, as expected, increased with increasing concentration, and did not differ across groups. Average hedonic ratings increased monotonically with increasing concentration up to 1.0 M, then decreased for 2.0 M glucose. These ratings did not differ across the fasted and sated groups, but subjects who received the oral glucose load rated the glucose concentrations as increasingly pleasant with concentration, all the way to 2.0 M glucose. That is, after an oral glucose load, they showed no decrement in the palatability of glucose at concentrations above 1.0 M. The explanation for these findings is not clear. Metabolic state in general did not appear to affect either the intensity or the hedonic value of the glucose solutions. The authors suggest that the unexpected effect of the oral glucose load on palatability may reflect a loss of ability to make hedonic evaluations as a result of a sudden and artificial satiety. The subjects in this state therefore simply "guessed" at the hedonic value based on the perceived intensity of the stimulus. An alternative explanation is simply that, because of the "between subjects" design of this study, variance across groups was such that an average decrement in palatability for 2.0 M glucose was not observed in the "glucose load" group. Since changes in palatability were not large in any of the groups, and since the decrement in palatability for the fasted and sated groups only occurred between the two highest glucose concentrations, this alternative explanation seems very reasonable.

In summary, the question of whether short-term changes in metabolic state affect taste reactivity has not been clearly answered. In studies where metabolic state manipulations have had an effect, this effect has been on suprathreshold taste stimuli, and was due to changes in the hedonic evaluation (palatability) of the taste, not to changes in perceived taste intensity. This is consistent with by Cabanac's (1979) alliesthesia hypothesis. However, the work by Rolls and colleagues (Rolls et al., 1981; 1982; 1983) on sensory-specific satiety sheds some doubt on whether changes in internal signals, based on metabolic state, affect sweet taste reactivity, or whether the changes in taste reactivity are primarily due to the sensory qualities of the ingested food. Further research is needed to clarify whether states of energy depletion and repletion do in fact have an effect on taste reactivity, and if so, the magnitude and direction of this effect.

Can Changes in Taste Reactivity Predict Intake?: Although the reasons for changes in taste reactivity are as yet unclear, the fact remains that taste reactivity can change. The question then arises: Do changes in the hedonic value of (sweet) tastes affect when, what or how much food a person eats?

If calories are uncoupled from sweetness in experimental manipulations, it appears that sweetness, not calories, predicts intake, at least over the short term (Blundell, Rogers & Hill, 1988; Rolls, Hetherington & Laster, 1988). If sweetness is generally related to food intake, then are variations in the evaluation of sweetness related to variations in food intake? Three studies which addressed this specific question have not provided a clear answer. Brala and Hagen (1983) designed a complex experiment in which they manipulated sweetness intensity and calories. Hedonic ratings of sucrose and artificial sweeteners, dissolved in cherry Koolaid, were obtained prior to and after a preload. The ratings were made on 15-point (for hedonic ratings) and 25-point (for intensity ratings) category scales. While, as Cabanac (1979) would predict, subjects reported a decrease in the pleasantness of the taste of sucrose after the preload, these ratings did not predict absolute amount ingested, number of calories consumed, nor type of food chosen (sweet/nonsweet) in a test meal given one hour after the preload. Mattes and Mela (1986) had subjects rate their hedonic responses to written food lists and actual sweet-tasting foods using category, visual analogue, and adjustment scales, and compared these ratings with various measures of food preference and intake. While the hedonic ratings taken individually predicted food preferences, only a combination of the various types of hedonic rating (a "preference profile") significantly predicted actual food intake.

Lucas and Bellisle (1987) reported that hedonic ratings of various sucrose concentrations in yogurt, using the standard sip-and-spit procedure, predicted the preferred sucrose concentration in a food that was actually swallowed, and the amount eaten, only for those subjects who indicated a decrease in palatability at high sucrose concentrations. Subjects who preferred high sucrose concentrations (until they reached 30% sucrose) showed no relationship between hedonic ratings and intake.

Thus the relationship between taste responsiveness and intake is ambiguous. Differences <u>between</u> subjects in hedonic ratings of sweet may not be good predictors of differences in intake. However, in none of the studies discussed above were changes in intake and changes in taste reactivity measured within subjects. The more sensitive within-subjects design would control for numerous other factors which may affect food intake across individuals, isolating the role of changes in taste reactivity. This question, of whether within an individual changes in palatability affect intake, has not yet been addressed. The data presented by Lucas and Bellisle (1987) suggest the possibility that differences between subjects in the hedonic assessment of sweet taste stimuli are relevant in determining for which individuals hedonic ratings do in fact predict intake.

Individual Differences in Hedonic Response to Sweet: An issue which emerged in our discussion of the Lucas and Bellisle (1987) study (see above), and which repeatedly recurs in the human taste reactivity literature is the question of individual differences in the hedonic response to sweet tastes.

Investigators looking for differences in taste reactivity between obese and normal-weight individuals have occasionally reported that inter-subject variation in hedonic response patterns across concentrations of sucrose solutions was much greater than any inter-group variation (Thompson, Moskowitz & Campbell, 1977; Witherly, Pangborn &

Stern, 1980). Two, three, and sometimes four patterns of hedonic response have been reported for individual subjects in various studies (Akey, Chen, Rosen, Palson, Travers & Travers, 1991; Brala & Hagen, 1983; Cabanac, 1979; Enns, VanItallie & Grinker, 1979; Lucas & Bellisle, 1987; Lundgren et al., 1978; Pangborn, 1970). Across similar concentration ranges, some individuals report increasing palatability with increasing sweetness, while others report decreasing palatability. As well, some show an inverted U-shaped function, with a peak in hedonic value at some intermediate concentration, while the occasional individual shows little affective response to all levels of sweetness. The proportion of each type of response in any given subject sample (where this information is provided) appears to be quite inconsistent.

At least two studies have also reported sex differences in hedonic response patterns, with females in one case rating higher concentrations of sucrose as more pleasant (Weizenbaum, Benson, Solomon & Brehony, 1980), and in the other study as less pleasant, than males (Enns et al., 1979). However, these differences were not large, especially among young adults.

While these individual and gender differences in hedonic response to sweetness have been reported and acknowledged, few investigators have suggested that these differences might in themselves be worth exploring. Some simply delete subjects that show, in the context of that particular sample, unusual patterns of response. Others collapse the data into means across subjects despite the variability. In fact, it is not known how many individual patterns have been "hidden" by averaging, especially in those studies which do not mention different patterns. However, knowing that these patterns exist makes it difficult to interpret the findings of studies which measure taste reactivity, and particularly palatability. Recall that Lucas and Bellisle (1987) observed that for subjects who disliked concentrated sucrose in yogurt it was possible to predict subsequent intake from their hedonic response, while for subjects who generally liked concentrated sucrose such a prediction of intake was not possible. This suggests that in fact individual differences in hedonic response to sweet may be an important dimension in evaluating the relationships between taste perception and eating behaviour.

Taste Preferences: The question of individual differences in hedonic response to relatively simple taste stimuli leads to the larger question of the origin and acquisition of taste preferences in general. It is usually assumed that preferences for simple tastes which belong to the presumed basic taste quality categories (sweet, sour, salty and bitter) are at least an underlying factor in preferences for the much more complex stimuli which comprise the human diet.

In humans, taste preferences can be attributed to three sources: innate predispositions, early feeding experiences, and social modelling (Warwick, 1990). Evidence for each of these will be discussed briefly.

There is strong evidence for the existence of innate predispositions to like or dislike certain taste qualities. Tests of taste preferences in newborns utilize similar methods, with a similar rationale, as have been used in animals (see above). These include: intake measures, facial responses, and sucking patterns (Cowart, 1981). Intake measures reveal that infants prefer sweet tasting substances to unsweetened ones. Preferences or aversions for sour, salty and bitter substances have not been clearly demonstrated using intake measures (Cowart, 1981). However, recordings of sucking patterns do show differential responding of infants to sweet tastes and salty tastes, relative to sucking for water (Crook, 1978). Because the changes in sucking pattern to sweet and salty tastes are in opposite directions, Crook (1978) has suggested that sweet tastes are hedonically positive, while salty tastes are aversive, to newborns.

Steiner (1979) has explored the taste preferences of newborns by observing their facial responses to gustatory stimulation. He has identified three types of facial response patterns, each of which corresponds to a taste quality category. Reactions to sweet tastes include sucking, licking of the lips, and an expression of satisfaction (i.e., a smile). Sour tastes elicit pursing the lips, blinking, increased salivation, flushing, and wrinkling the nose. Bitter tastes evoke a pulling back of the lips, turning down the corners of the mouth, tongue protrusions, spitting, vomiting, grimacing, and general expressions of anger and dislike. These responses can be evoked immediately after birth, prior to any dietary experiences. Steiner (1979) suggests that they therefore represent reflexive, innate hedonic reactions to gustatory stimuli. Further support for this conclusion is found in the work of Grill and Norgren (1978), who found similar "fixed action patterns" in the facial responses of rats to gustatory stimulation (see above).

Based on this evidence, and that of other researchers (Beauchamp & Cowart, 1985; Beauchamp & Moran, 1982), the notion that there is an innate preference for sweet tasting substances over neutral or nonsweetened stimuli has gained wide acceptance. While less widely accepted, it is also generally believed that newborns are indifferent to salty tastes, and find sour and bitter tastes aversive (Warwick, 1990; but see Crook, 1978).

Such innate taste preferences may have a genetic basis. A twin study suggested that heritability of taste preferences for sucrose (sweet) and sodium chloride (salty) is very low (Greene, Desor & Maller, 1975). However, there is one well-established genetically-based aspect of taste perception which may be related to taste preferences--the presence or absence of a sensitivity to the bitter taste of phenylthiocarbamide (PTC) or 6-n-propylthiouracil (PROP) and related compounds (Fischer, 1967; Whissell-Buechy, 1990a). Inheritance studies suggest that high sensitivity to the bitter taste of PROP is encoded on a single dominant gene; those most sensitive to PROP ("tasters") are either homozygous or heterozygous for the dominant allele, while those least sensitive ("nontasters") are homozygous for the recessive allele (Whissell-Beuchy, 1990a).

The genetically-determined sensitivity to PROP predicts an individual's perception of a number of other taste stimuli. For example, PROP tasters find other bitter-tasting compounds more intensely bitter than do nontasters (Bartoshuk, 1979; Marks, Stevens, Bartoshuk, Gent, Rifkin & Stone, 1988). Also, sucrose and saccharin taste more intensely sweet to tasters than to nontasters (Gent & Bartoshuk, 1983; Marks et al., 1988).

Differences between tasters and nontasters in the quality or intensity of their taste experiences may result in differences in food preferences (Drewnowski, 1990). Several studies suggest that PROP sensitivity can predict food likes and dislikes, particularly for those foods containing bitter- or sharp-tasting components, such as milk products, dark green vegetables, cheeses, and grapefruit (Fischer, Griffin, England et al., 1961; Glanville & Kaplan, 1965; Krondl, Coleman, Wade & Milner, 1983; Marino, Bartoshuk, Monaco, Anliker, Reed & Desnoyers, 1991).

While PROP sensitivity seems to be related to the perceived intensity of simple substances, and to preferences for some "real" foods, it is unclear whether these food preferences are related to differences in hedonic evaluation of <u>simple</u> taste stimuli. The question of whether, and how, the gene which encodes PROP sensitivity results in a taste system which predisposes an individual toward particular taste preferences has not been clearly answered. The possibility that there might be a genetic aspect to the hedonic evaluation of taste stimuli is intriguing.

Early feeding experiences also affect taste preferences. Beauchamp and colleagues (Beauchamp & Cowart, 1985; Beauchamp & Moran, 1982; 1984) have demonstrated that infants who were fed sweetened water during the first two years of life maintained their inborn preference for sucrose solutions (as measured by intake relative to water), while infants not fed sweetened water showed a decrease in intake of sucrose solutions. This differential effect of dietary experience was evident at six months of age, and still present at two years. However, the effect did not generalize to other sweetened substances, such as fruit drinks, suggesting that the children may have responded to the familiarity of the stimulus, rather than to its sweetness per se. Although some children showed a preference for higher salt concentrations in their food than did others, previous dietary experience did not appear to be related to these preferences. Beauchamp and Cowart (1985) conclude that preferences for sweet tastes are innate and present at birth, while preferences for salty tastes reflect maturational processes. Dietary experience does not actually change these preferences, but rather teaches the child associations between particular foods and sweet or salty tastes.

The preference for sweet tastes, which appears to be innate, may nevertheless be subject to modification over time. Over the lifespan, sweet tastes may generally be preferred over sour, salty, or bitter tastes, but the strength of the hedonic response to sweet may decrease in magnitude. Measurement of preferred concentration of sucrose for 9-15 year old and adult humans revealed that the younger subjects preferred a higher sucrose concentration than did the adults (Desor, Greene & Maller, 1975). A follow-up study nine to ten years later of the original 9-15 year old subjects further confirmed the decrease in preferred level of sweetness over time (Desor & Beauchamp, 1987). In contrast, Enns, VanItallie and Grinker (1979) found no significant differences in hedonic ratings of sweet tastes when comparing fifth graders, university undergraduates, and elderly persons.

Any modifications in taste preferences which occur over the lifespan may be due to maturational changes, but are more likely the result of social influences. Examination of food preferences and attitudes in North American teenagers reveals that while food preferences are related to taste, they are also strongly related to perceived healthfulness of the food, body image, and perceptions of the socially-desirable body image (large and muscular for boys, slim for girls) (George & Krondl, 1983; Krondl & Coleman, 1986).

Issues for Further Research

Despite a great deal of literature exploring this topic, the role of taste perception in eating behaviour is far from being understood. We know that, from birth, humans can discriminate some simple tastes, such as sweet, bitter and sour, and that a preference for sweet tastes and an aversion to bitter or sour tastes is evident at this time also. We also know that a genetically-determined taste trait, sensitivity to PROP/PTC, is related to more general differences in the perception of the intensity, at least, of other bitter and salty substances, and of sweet. But how the perception of simple taste qualities might be related to preferences for the much more complex stimuli which comprise the human diet, and how such preferences might affect intake, are still unclear. The evidence for the effect of differences across subjects, or changes within subjects, in the hedonic value of sweet tastes in particular on food preferences and intake is equivocal.

There are a number of questions which need to be addressed further. They include: Is taste perception indeed responsive to internal cues, such as changes in metabolic state? Are there individual differences in this responsiveness? That is, does taste reactivity differ for different individuals? If so, are these differences innate or learned? And finally, would any differences in taste reactivity generalize beyond simple substances to "real" foods? The experiments which follow represent an exploration into these issues, with a particular focus on the perception and evaluation of sweet tastes. While they do not provide final answers, they contribute to a more complete understanding of taste reactivity in humans, particularly with regard to individual differences.

Chapter Two

GENERAL METHOD

The procedures described in detail in this chapter were employed repeatedly throughout the experiments which follow. Only modifications specific to individual experiments will be outlined in the appropriate Methods sections.

Subjects: Subjects were primarily university undergraduates, both males and females, registered in an introductory psychology course. Some psychology graduate students and psychology department staff also participated. All subjects gave informed consent prior to testing, and the undergraduates received course credit for their participation.

A. METHOD FOR EVALUATING SWEET TASTE REACTIVITY

Sweet Stimuli: Sweet-tasting solutions were made by dissolving sucrose in distilled water at room temperature (22°C). Concentrations ranged from 0.03 M to 0.83 M. The specific range and number of concentrations used varied with experiments, although 0.83 M was always employed as the highest concentration. In each experiment, stimuli were presented in blocks. Each block included all concentrations used. The order of stimuli was randomized within a block and there were five, six, or eight replications of block in a test session.

Rating Scales:

1. Intensity: The rating for taste intensity consisted of a 200 mm visual analogue scale. The line was preceded by the question: "How strong was the sweet taste?". Beneath the line, 20 to 30 mm from either end, were two "anchors" labelled, on the left, "not sweet at all", and on the right, "extremely sweet". Subjects were instructed to make a mark on the line which represented how strong the solution tasted to them. If a given solution tasted twice as sweet as the preceding one, they were to make a mark twice as far along the line. If a solution tasted half as strong as the preceding one, they were to place their mark half as far along, and so forth. To assist subjects in assessing taste intensity, they were asked to taste both the strongest and the weakest concentration in the series prior to rating the test solutions.

2. Hedonic Value: Subjects rated the hedonic value of the sucrose solutions on a second 200 mm visual analogue scale. This scale was preceded by the question: "How much did you like the taste?", and the anchors were labelled "disliked very much" and "liked very much". As well, a

neutral point at 100 mm was labelled "neither liked nor disliked".

The intensity and hedonic value scales were reproduced on one sheet of paper, but a separate sheet was provided for each solution.

Procedure: Each subject was tested alone, seated before a tray of plastic medicine cups, each containing 10 to 15 ml of sucrose solution. The cups were numbered in order. After giving informed consent, the rating scales were explained, and the strongest and weakest concentrations tasted. Subjects were instructed to begin with solution #1, sip some, swish it around their mouth, and spit it out (the "sip and spit" procedure). A sink or a funnel attached to a jug were provided for this purpose. They were then to rate the intensity and hedonic value of the solution, rinse their mouth with distilled water, and proceed to the next solution. They were not permitted to swallow, or to taste any solution more than once.

Data Analysis: The intensity ratings were scored by measuring the distance, from 0 to 200 mm, beginning before the "not sweet at all" end of the scale. Hedonic ratings were measured from the neutral point to the extremes, "liking" ranging from 0 to +100 mm, "disliking" from 0 to -100 mm. Each subject's intensity and hedonic ratings were averaged over the replications of each sucrose concentration. These averaged data were analyzed using analyses of variance (ANOVAs). Although ANOVA assumes that the data being analyzed are ratio-scale and it is not clear that visual analogue data do in fact fit this assumption, nevertheless ANOVA is the best available method to analyze such data, and is used routinely (e.g., Rolls et al., 1983).

All significant F values will be reported for each analysis; nonsignificant values will not be given.

B. METHOD FOR DETERMINING PROP TASTER/NONTASTER STATUS

PROP Solutions: 6-n-propylthiouracil (PROP) solutions were made by dissolving PROP in room temperature (22°C) distilled water. Fifteen concentrations were prepared, ranging from 3.2×10^{-3} M to 1.0×10^{-6} M, in 0.25 log steps.

Procedure: A forced-choice detection procedure developed by Wetherill & Levitt (1965; see also Bartoshuk, 1978; McBurney & Collings, 1984) was used to determine the threshold concentration for detection of the taste of PROP for each subject.

Subjects were tested individually. They were seated behind a barrier which prevented them from seeing the solutions which the experimenter supplied. They were instructed to sip each solution provided, swish it around their mouth, and spit it out without swallowing. Prior to tasting each solution, they were to rinse their mouth with distilled water.

To obtain an initial idea of approximately which PROP concentration each subject could begin to taste, the experimenter began with the weakest concentration. She gave each subject about 10 ml of this solution in a plastic medicine cup, and asked them to indicate whether or not the solution had a taste (even if the quality of that taste could not be identified). This was repeated with every second increasing concentration of PROP until subjects reported the presence of a taste.

Subjects were then provided with two cups of solution. One contained distilled water, the other the PROP solution in which the subject had first reported detecting a taste. Subjects were asked to taste both solutions, and then indicate which one of the two had a taste. They were required to make a choice even when they could not in fact detect a difference--the forced-choice procedure. If the subject chose correctly, the test was repeated with the same concentration. If they were correct again, the next lower concentration was tested. If the subject was incorrect (on either the first or second try), the next higher concentration was tested. Subjects were not given feedback regarding the accuracy of their responses.

This procedure was continued until seven "turn-around" points were obtained. The first was discarded, and the geometric mean (calculated because the PROP concentrations varied in logarithmic steps) of the concentrations at the other six provided the precise concentration which represented the subject's PROP detection threshold.

Subjects with a threshold greater than or equal to 2 x 10^{-4} M were classified as nontasters; those with a threshold at or below 1 x 10^{-4} M were classified as tasters; and those who fell between these two cutpoints were labelled "borderline".

Chapter Three

Experiment 1

THE EFFECT OF METABOLIC STATE ON HUMAN SWEET TASTE REACTIVITY

One aspect of a food stimulus which plays an important role in determining whether that stimulus will be accepted or rejected is its palatability. Palatability is not a stable characteristic of a food (Weingarten & Bédard, 1991). Rather, identical food stimuli will be perceived as more or less palatable by different individuals, and even by the same individual under different conditions. It is this variation in the perceived palatability of foods which suggests that palatability may play an important role in food selection and intake. In fact, it is known that the sweetness of a food--a factor which strongly affects palatability--has a potent influence on the amount of food consumed (Blundell et al., 1988; Rolls et al., 1983; Sclafani, 1987).

However, in spite of the acknowledged correlation between sweetness and food intake, the mechanisms by which sweet taste influences consumption are poorly understood. Animal studies suggest that metabolic state may be one condition which influences perception of and reaction to sweet. For example, Bédard and Weingarten (1989) showed that, in rats, hyperglycemia suppressed sham feeding of sweet solutions, suggesting that elevated plasma glucose suppresses the palatability of sweet. This conclusion is reinforced by electrophysiological studies which show that neural activity in the nucleus tractus solitarius evoked by sweet-tasting, but not bitter-tasting, stimuli is decreased by hyperglycemia (Giza and Scott, 1983).

A major limitation of animal studies, however, is the inability to articulate the mechanisms which mediate palatability shifts. For example, decreased sham intake, which is used to index a lowering of palatability (Weingarten & Watson, 1982) may reflect a change in the intensity or the hedonic value of sucrose, or both. Alternatively, sham intake may change because of processes independent of taste. To illuminate the mechanism underlying a shift of palatability, a preparation is required in which the parameters of taste intensity, taste hedonics, and intake can be assessed independently.

In "sip and spit", a preparation used widely to assess responses to tastes, humans can make somewhat independent assessments of the intensity and hedonic value of sweet tastes (Moskowitz, Kluter, Westerling & Jacobs, 1974). The sip and spit procedure also allows measurement of the amount sipped. This latter measure is important because, in animal studies of taste reactivity, intake in typically the only variable measured. Ironically, while sip and spit is presented as the human analogue of sham-feeding in animals, intake is typically not measured in sip and spit studies. Measurement of intake in the sip and spit procedure permits an examination of the generality of conclusions regarding palatability from animal to human studies.

The present study examines the influence of metabolic state on sweet taste reactivity in humans. Current data on this issue are equivocal, as discussed in detail in the General Introduction. In summary, based on indices of hedonic value, Cabanac (1971, 1979) argued that the pleasantness of tastes decreases with satiety. Other investigators, who measured both taste intensity and hedonics, found that only hedonic ratings, and not intensity, increase with deprivation (Rolls et al., 1983; Scherr & King, 1982). In contrast, Moskowitz, Kumraiah, Sharma, Jacobs & Sharma (1976) found that the hedonic value of glucose did not change with deprivation. In fact, they found that satiety induced by an oral glucose load resulted in an increase in the pleasantness of glucose.

In sum, the strength and direction of hedonic changes to sweet with changes in deprivation are unclear.

The relationship between intake and changes in reactivity to sweets has not been explored. The current experiment uses the sip and spit procedure to compare reactivity to sucrose solutions under conditions of energy depletion or repletion. Depletion was effected by imposing an overnight 18-h fast. Repletion was produced by testing subjects in a postprandial state, 30 min after a satiating meal. Our purpose was to identify whether changes in metabolic state affect sweet intensity, hedonics, or both, and how changes in these variables are related to intake.

Method

Subjects: Subjects were 28 undergraduate and graduate psychology students. There were 16 females and 12 males in the age range 18 to 33 years (mean=20.5 years, SD=3.5).

Solutions: Nine sucrose concentrations were employed: 0.83, 0.62, 0.42, 0.31, 0.21, 0.16, 0.10, 0.05, and 0.03 M. In test sessions, each concentration was presented eight times, for a total of 72 solutions. Precisely 15 ml of solution was measured into each cup for tasting.

Procedure: Subjects participated in two sessions, each approximately one hour long, with no more than a three-day interval between sessions. Half the subjects were tested first in the deprived condition (after an 18-hour overnight fast), the other half in the sated condition (30 minutes after a satiating meal).

The sip and spit procedure for evaluating sweet taste reactivity, described in detail in the General Method (chapter 2), was followed for both sessions. That is, subjects evaluated the intensity and hedonic value of the taste of each solution. They were also asked to rate how hungry they felt, using a 200 mm visual analogue scale similar to that used for intensity, with anchors labelled "not hungry at all" and "extremely hungry". These hunger ratings were made three times: prior to tasting the first solution, halfway through (after solution #36), and at the end of the session.

At the end of the second session, subjects were asked to fill out a questionnaire consisting of demographic and health information, and the Eating Disorders Inventory (EDI; Garner, Polivy & Olmstead, 1983). Height and weight were also measured.

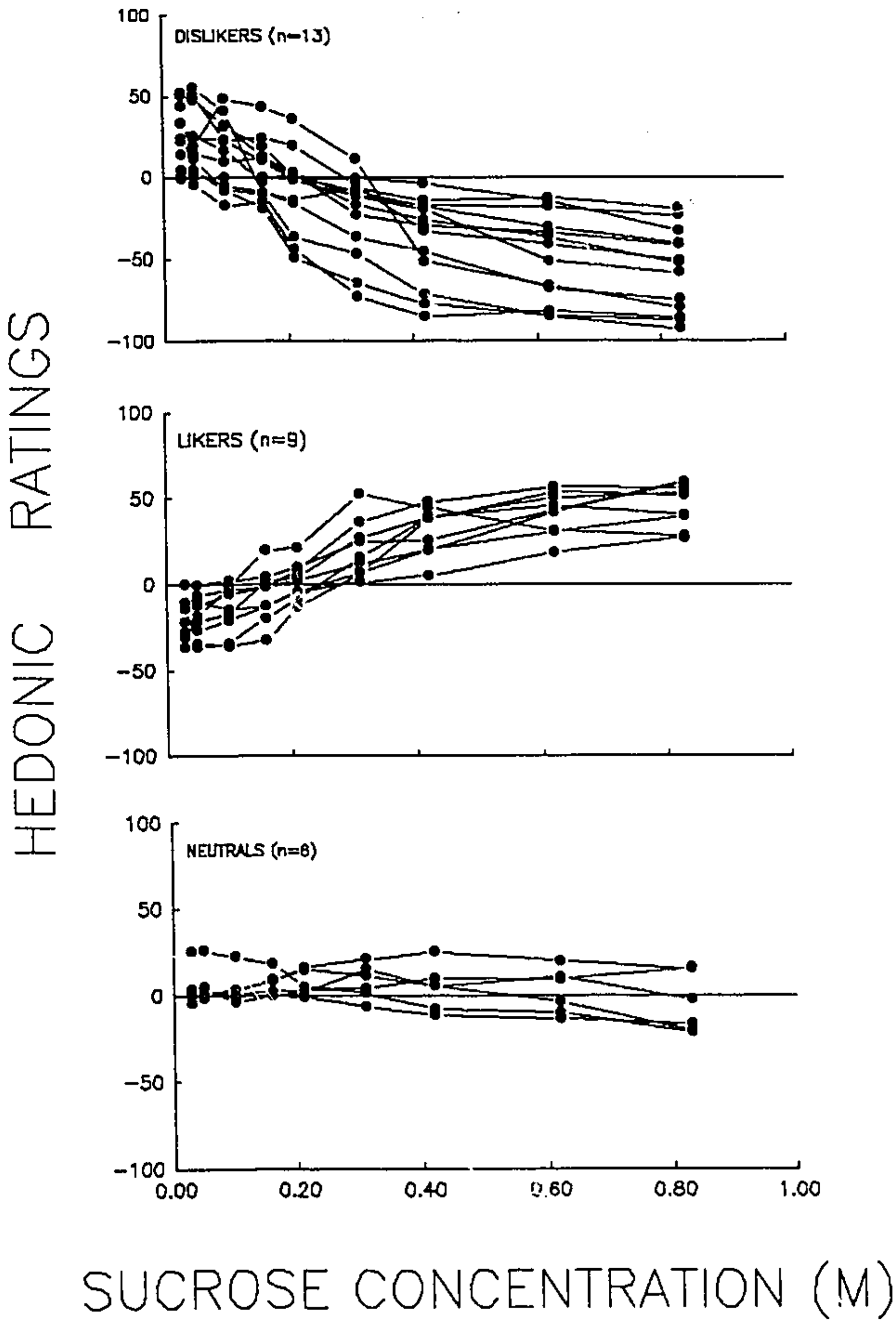
After each session, the amount of each solution the subject sipped was measured by subtracting the amount remaining in the cup from 15 ml. Subjects were unaware of this dependent measure.

Results

Subjects differed in their patterns of hedonic response. Some subjects showed increased liking of a solution the sweeter it was (13/28). Others disliked a solution more with increasing sweetness (9/28). A few subjects (6/28) rated most concentrations as relatively neutral. These three types of hedonic response are graphed in Figure 1. While Figure 1 shows the hedonic response functions for subjects in the sated state, the general pattern of each function was similar for each subject when deprived as well. That is, subjects would be classified in the same category whether this classification was based on their hedonic responses in the sated or the deprived states. This does not imply, however, that subjects showed no change in hedonic response with metabolic state, as will be described below.

In this, and in all subsequent experiments, sweet "likers" and "dislikers" were classified by visual assessment of each function relating hedonic response to sucrose concentration. Sweet likers generally report increasingly positive ratings with increasing concentration; their functions have a positive slope. Sweet dislikers report increasingly negative ratings with increasing concentration; their functions have a negative slope. Only data from those subjects who could be clearly and unambiguously classified as a liker or a disliker were used; if an individual's hedonic response function was relatively flat ("neutral"), erratic, or symmetrically U-shaped, that

Figure 1: Hedonic ratings of sucrose concentrations for each subject. Ratings were averaged across sated and deprived conditions. In all cases, the classification of a subject, based upon the slope of the hedonic curve, as a sweet liker, disliker, or neutral, was the same under both deprived and sated conditions.


DISLIKERS (n=13)
LIKERS (n=9)
NEUTRALS (n=6)
100
50
0
-50
-100
0.00
0.20
0.40
0.60
0.80
1.00
HEDONIC RATINGS
SUCROSE CONCENTRATION (M)

subject was not classified nor their data analyzed.

Manipulation check: Hunger ratings were scored in a manner identical to that for intensity ratings; that is, by measuring the distance in millimetres along the line from 0 (on the left) to the subject's mark. After 18 h deprivation, subjects reported feeling much hungrier (Mean=129.1) than they did 30 min postmeal (Mean=52.6; $F(1,85)=250.2$; $p<.0001$), showing the success of the deprivation manipulation.

Characteristics of sweet likers and dislikers: Seventy-nine percent of females (11/14), but only 25% (2/8) of males, were sweet dislikers. This distribution of gender across hedonic response category is significant (X^2 (with Yates correction)=4.03, $p<.05$). The Body-Mass Index (BMI = weight(kg)/height(m^2)), and the Drive for Thinness, Bulimia, and Body Dissatisfaction subscales of the EDI were calculated for each subject (Garner et al., 1983). On the basis of independent t-tests, sweet likers and dislikers did not significantly differ in BMI or attitudes toward eating and body weight as measured by the EDI (see Table I).

Intensity and hedonic ratings: Intensity and hedonic ratings were analyzed using mixed ANOVAs, with sweet liker/disliker as the between-subjects factor, and state (sated/deprived) and sucrose concentration as the within-subjects factors.

Table I: Subject Characteristics

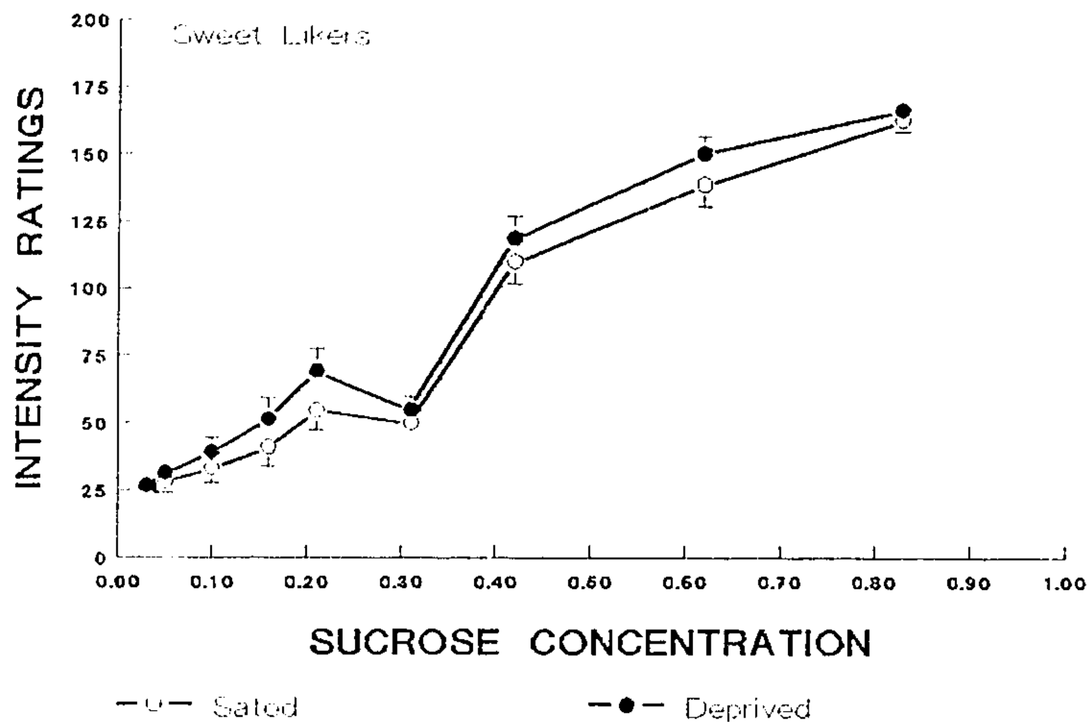
Group	Female:Male Ratio	BMI(kg/m^2) Mean (SEM)	EDI: Mean (SEM) DT	B	BD
SWEET LIKERS	1:3	23.9 (0.9)	1.4 (0.5)	0.9 (0.3)	7.0 (1.7)
SWEET DISLIKERS	5.5:1	23.0 (0.9)	4.9 (1.8)	0.8 (0.3)	10.5 (2.3)

BMI=Body Mass Index; EDI=Eating Disorder Inventory; Subscales: DT=Drive for Thinness; B=Bulimia; BD=Body Dissatisfaction

Mean ratings for sweetness intensity of sucrose solutions under the sated and deprived conditions for sweet likers and dislikers are shown in Figure 2. Intensity ratings increased steadily with increasing sucrose concentration, although there was a small but consistent dip at 0.31 M sucrose. ANOVA revealed significant Group x State ($F(1,340)=11.6$, $p<.01$) and Group x Concentration ($F(8,340)=3.4$, $p<.01$) interactions. Examination of Figure 2 suggests that the Group x State interaction was due to the slightly increased intensity ratings given by sweet likers when they were deprived relative to the sated state, a difference which was less apparent among the sweet dislikers. The Group x Concentration interaction may be due to the consistently higher intensity ratings given by sweet dislikers relative to sweet likers (the overall means were 75.21 for likers, 83.66 for dislikers). There was also a main effect of Concentration ($F(8,340)=559.3$, $p<.0001$), but no main effects of Group or State.

Hedonic ratings are shown in Figure 3. Because of the way sweet likers and dislikers were selected, the analysis generated an expected significant Group x Concentration interaction ($F(1,20)=12.3$, $p<.01$). While sweet likers showed no change in hedonic response with metabolic state, dislikers reported that the higher sucrose concentrations tasted less unpleasant when they were

Figure 2: Mean (± SEM) intensity ratings of sucrose concentrations while sated and deprived, for sweet likers (top) and sweet dislikers (bottom). (SEMs not visible fall within the symbol.)


Sweet Likers
INTENSITY RATINGS
200
175
150
125
100
75
50
25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived

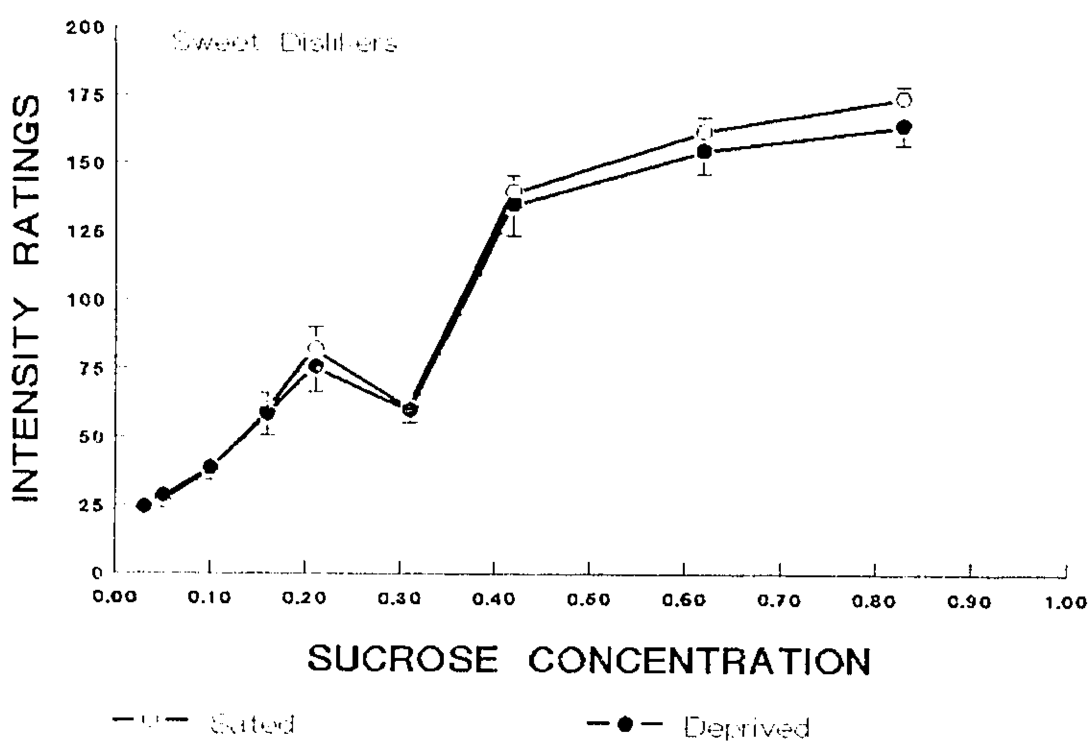
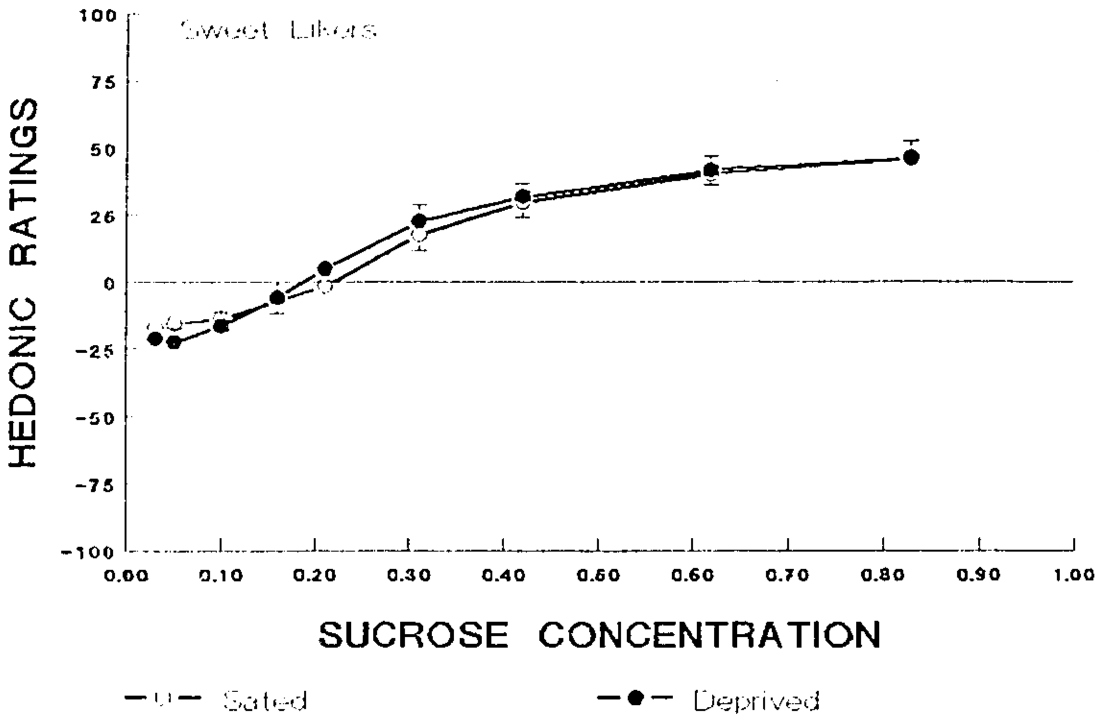
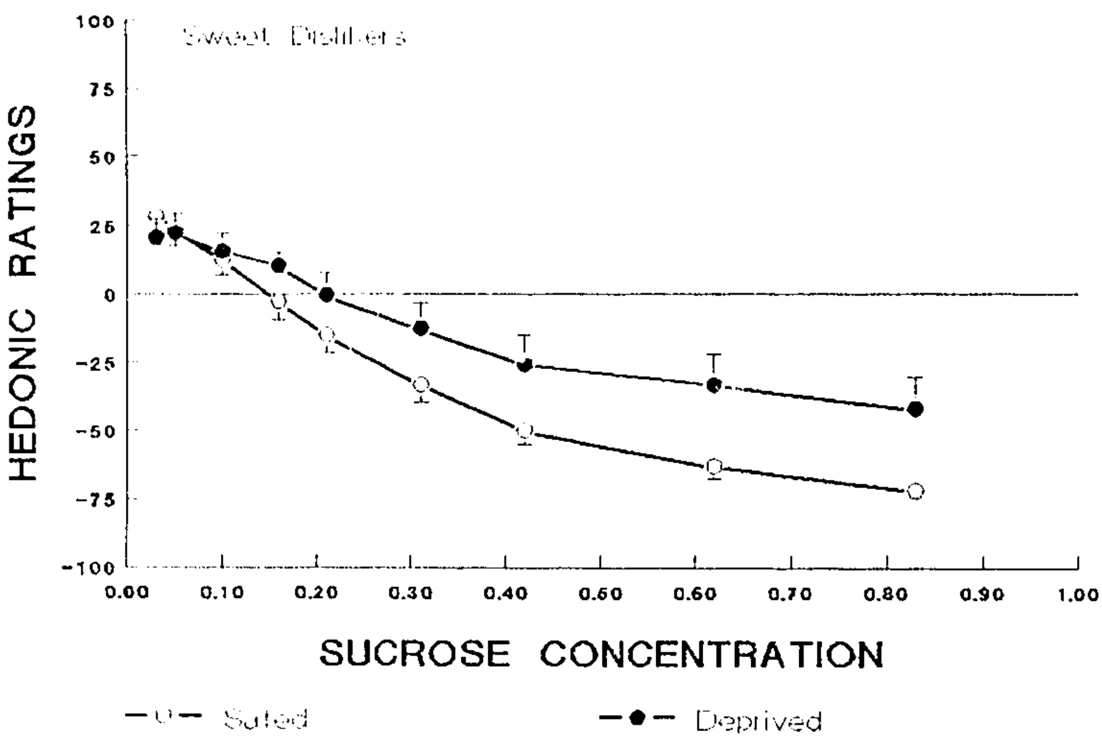

Sweet Dislikers
INTENSITY RATINGS
200
175
150
125
100
75
50
25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived

Figure 3: Mean (± SEM) hedonic ratings of sucrose concentrations while sated and deprived, for sweet likers (top) and sweet dislikers (bottom). (SEMs not visible fall within the symbol.)


Sweet Likers
HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived


Sweet Dislikers
HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived

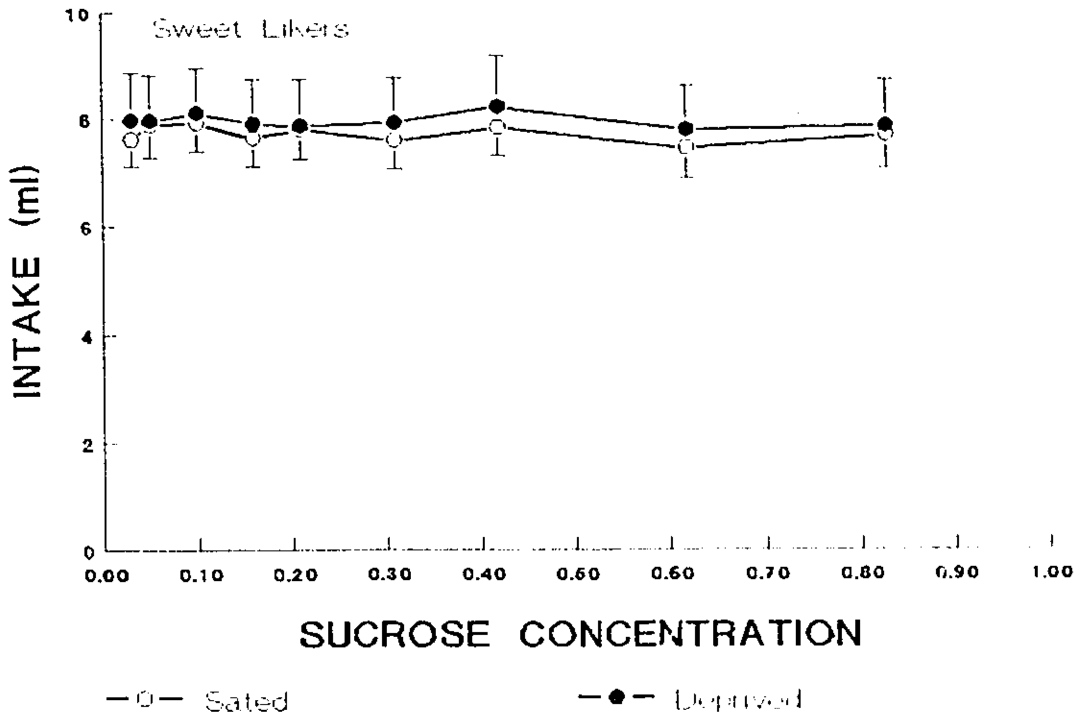
deprived. This differential change of groups with state was reflected in a significant Group x State interaction ($F(1,340)=13.5$, $p<.001$).

Intake measures: The mean intake of sucrose solutions for sweet likers and dislikers across metabolic state is shown in Figure 4. The amount sipped was relatively constant within each group and treatment condition, i.e. intake did not vary significantly with sucrose concentration in either group, nor in either metabolic state. However, a significant Group x State interaction ($F(1,289)=49.3$, $p<.0001$) indicates that the change in the amount sipped between the deprived and sated conditions was different in sweet dislikers and sweet likers. Sweet dislikers showed an increased intake when deprived (Mean=7.0 ml) compared to sated (Mean=5.5 ml). Sweet likers showed no change of intake with metabolic state (Mean=7.7 ml when sated and 7.9 ml when deprived).

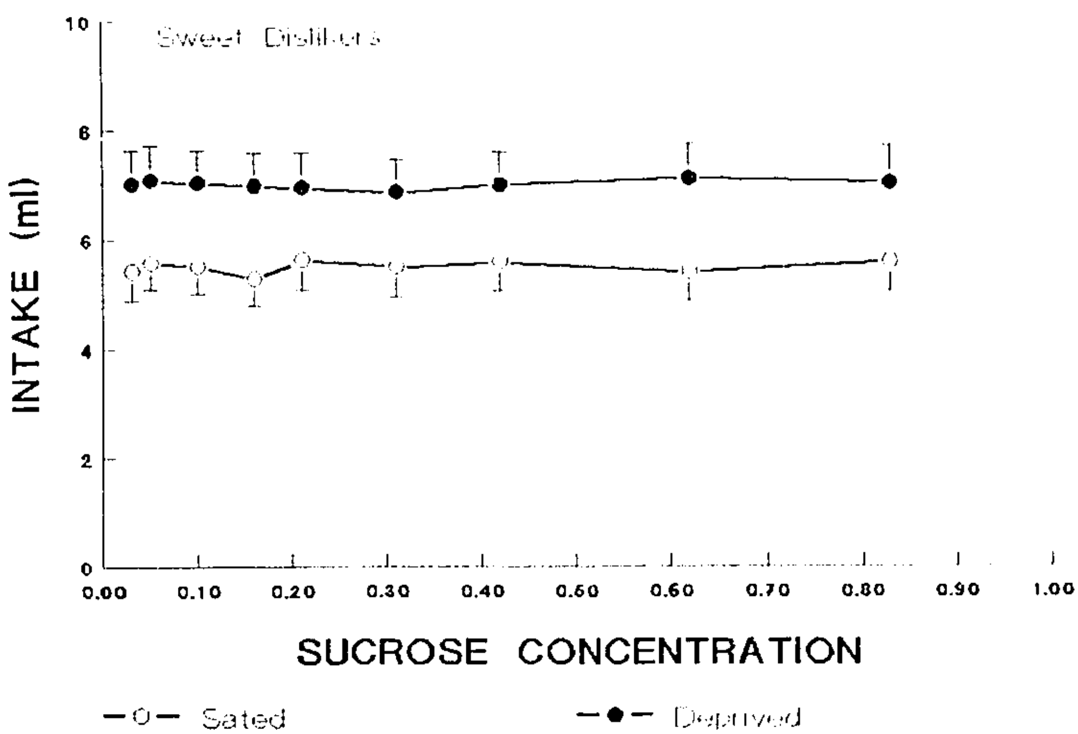
Discussion

The purpose of this study was to explore the interaction between metabolic state and sweet taste reactivity. The study was designed to determine specifically whether any state-induced changes in taste reactivity were mediated by changes in taste intensity or hedonics, and how such changes might be related to measures

Figure 4: Mean (± SEM) intake (amount sipped) of each sucrose concentration while sated and deprived, for sweet likers (top) and sweet dislikers (bottom). (SEMs not visible fall within the symbol.)of intake.



Sweet Likers
INTAKE (ml)
10
8
6
4
2
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived



Sweet Dislikers
INTAKE (ml)
10
8
6
4
2
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sated
Deprived

The results indicate that the effects of metabolic state on sweet reactivity depend upon the individual's underlying pattern of hedonic response to sweet.

Persons whose hedonic response to sweet increased with sucrose concentration ("sweet likers") perceived a small change in sweet intensity, but no change in hedonics with changes in metabolic state. In contrast, persons whose hedonic response decreased with increasing concentration ("sweet dislikers") reported an attenuated dislike for concentrated sweet tastes when deprived. This effect did not depend on changes in perceived intensity. Sweet likers and dislikers also differed in the effects of deprivation on the amount sipped: sweet likers sipped similar amounts when deprived or sated, while sweet dislikers sipped more when deprived than when sated.

Classification of an individual as a sweet liker or disliker was reliable. Subjects showed the same general pattern of hedonic response in both test sessions, despite large differences in metabolic state and feelings of hunger.

The sweet liker/disliker distinction was not related to differences in BMI, or to attitudes toward to eating as measured by the EDI. The gender difference, with females predominating among the sweet dislikers, males among the sweet likers, is intriguing, and will be explored in this thesis with a larger sample size. Rather than reporting the relationship of gender to sweet liker/disliker status for each experiment separately, these data will be summarized and evaluated in the General Discussion (Chapter Nine).

The present study appears to be one of the first to monitor amount sipped in human psychophysical studies of sweet. This measure is relevant because of the argument developed earlier that amount sipped may be the best analogue of measures taken in animal studies of taste reactivity. I found that sweet dislikers sipped less solution, and disliked higher concentrations of sucrose more, when they were sated than when deprived. Sweet likers sipped similar amounts, and demonstrated no change in hedonic evaluation, in both metabolic states. The superficial conclusion that people sip more of a solution they find more pleasant is mitigated by the fact that there was no relationship between liking and intake _within_ groups. That is, while both sweet likers and dislikers reported large changes in hedonic value with concentration, in neither group was there a concomitant change in intake with concentration. Thus, changes in intake, measured by amount sipped, appear to reflect an effect of depletion on intake which is not related to hedonic value. This implies that changes in intake in animal studies may not reflect changes in the palatability of the stimulus. This conclusion reinforces recent findings in the rat sham feeding literature that suggest that changes in hours of deprivation influence intake but do not alter hedonic response to sweet (Weingarten, Duong, Gowans & Elston, 1990).

Different patterns of hedonic response to sweet tastes have been reported previously (Brala & Hagen, 1983; Cabanac, 1979; Enns, VanItallie & Grinker, 1979; Lucas & Bellisle, 1987; Moskowitz, Kumraiah, Sharma, Jacobs & Sharma, 1976; Pangborn, 1970). However, few investigators have explored the relevance of these differences for the dependent measures used in their studies. The present study shows clearly that distinguishing sweet likers from dislikers reveals different response patterns to changes in metabolic state. The responses we observed in sweet dislikers are consistent with Cabanac's alliesthesia (Cabanac, 1971; 1979) and other (Rolls, Rolls & Rowe, 1983; Scherr & King, 1982) work. However, the responses of sweet likers are not consistent with these reports. This suggests the possibility that one factor contributing to contradictory results across studies (e.g. Cabanac, 1971; Moskowitz et al., 1976) may be differences in the relative proportions of sweet likers and dislikers in the subject samples.

The distinction between likers and dislikers is important in understanding individual differences in taste reactivity and the effects of manipulations, such as changes in metabolic state, on taste. Therefore, the nature and possible causes of this distinction need to be explored. The gender difference observed in this study raises one concern: Do sociocultural pressures toward thinness, primarily directed toward females in North American culture (Garner et al., 1980; George & Krondl, 1983), result in females reporting a dislike for sweet solutions simply because the taste is strongly associated with "forbidden", fattening foods? Alternatively, differing hedonic response patterns to sweet may be based on genuine felt experience, and not due to a cognitive assessment of the taste. If so, one might expect the sweet liker/disliker distinction to correlate with other markers of taste, such as facial expressions and the genetically-determined ability to taste 6-n-propylthiouracil (PROP) and the sweet liker/disliker distinction. Finally, the difference between sweet likers and dislikers may also reflect a difference in the perceived taste quality of pure sucrose solutions. These possibilities are explored in the following studies.

Chapter Four

Experiment 2

THE RELATIONSHIP BETWEEN FACIAL REACTIONS AND HEDONIC RESPONSE TO SWEET

The previous study established that an individual's general pattern of hedonic response to sweet tastes predicts the effects of changes in metabolic state on sweet taste reactivity (Experiment 1). Sweet dislikers show an attenuated dislike for concentrated sucrose when food deprived, while sweet likers report no significant change in the hedonic value of sucrose solutions between the sated and deprived states. The predictive value of these hedonic response patterns suggests that the nature of the hedonic response to sweet, and specificially the factors underlying the sweet liker/disliker distinction, need to be explored further. Specifically, do these differing hedonic response patterns to sweet reflect fundamental and qualitative differences in taste reactivity which should be accounted for in any future investigations of the role of taste in the control of eating?

The gender difference observed in the previous study, where females were more likely to be sweet dislikers than males, raises the possibility that hedonic response patterns to sweet tastes are socioculturally determined. That is, perhaps females, in response to sociocultural pressures toward thinness (Garner, Garfinkel, Schwartz & Thompson, 1980; George & Krondl, 1983), are more likely to report a dislike for concentrated sweet tastes simply because the taste is strongly associated with "forbidden", fattening foods. If this were the case, then subjects' self-reported hedonic evaluations may not necessarily reflect their genuine perception of taste stimuli, but rather a more cognitive, perhaps even conscious, decision based on associations between the taste and social acceptability of the foods it represents to them.

To explore this possible source of the sweet liker/disliker distinction, the present experiment correlated subjects' facial responses to the tastes with their hedonic ratings of the sucrose solutions. Research with both humans and animals suggests that there are distinct and reliable reflexive facial responses to taste stimulation (Grill & Norgren, 1978a; Pfaffman, Norgren & Grill, 1977; Steiner, 1979). The reflexive nature of these responses is supported by the observation of these response sequences in decerebrate rats and anencephalic human neonates (Grill & Norgren, 1978b; Steiner, 1979). These stereotyped facial responses have been primarily used to assess the palatability of substances with qualitatively-different tastes (i.e., sweet vs. bitter vs. sour), and reflect hedonic evaluations of the stimuli (Steiner, 1979).

The protocol of the current study was based on this possibility--that subjects would express their genuine hedonic evaluation of the taste of the sucrose solutions through these reflexive facial reactions. These facial responses could then be compared with subjects' hedonic ratings, to obtain a measure of the predictive validity of the hedonic ratings. The strategy employed was simple. Subjects were videotaped while they tasted and rated the sucrose solutions. Raters, blind to the subjects' hedonic ratings, viewed the videotapes and classified the subjects as sweet likers, dislikers, or neutral on the basis of visual cues alone. Consistency between facial responses and hedonic ratings would support the conclusion that subjects report their genuine hedonic reactions on the rating scale. It is unlikely that, over a session involving 40 sucrose solutions, subjects would artificially generate facial responses consistent with their hedonic ratings, in a reliable and systematic manner. Alternatively, inconsistency between the two would suggest that subjects <u>may</u> be basing their hedonic evaluations on more cognitively-assessed, socially-determined aspects or associations of the taste.

A second purpose of this experiment was to replicate the sweet liker/disliker distinction and the gender difference observed in Experiment 1, with a larger subject sample.

Method

Subjects: Sixty-six undergraduate student volunteers participated in the study. There were 38 females and 28 males, age range 18 to 44 years (Mean=20.3, SD=3.5). Subjects were tested over two time periods: from January to March (1990), 46 students (38 females and 8 males) were tested. Because of the small number of males in this initial sample, a further 20 males were tested from September to November (1990).

Stimuli: The test stimuli consisted of five concentrations of sucrose, .05, .10, .21, .42, and .83 M. Eight replications of each concentration were used, for a total of 40 solutions. The 15 PROP solutions were also used, to test for PROP taster/nontaster status.

Procedure:

Evaluating Sucrose Solutions: Subjects were asked to come to the experimental session sated--that is, having eaten within a half-hour of testing. The procedure described in the General Method was followed, with one difference: Directly facing the subject, across the table at which they were seated, was a video camera on a tripod. Subjects were told that the camera was recording the test session, and asked to disregard its presence and proceed with their evaluations of the solutions. The experimenter did not remain in the room while subjects were evaluating the solutions; rather, she left after the first few had been tasted, and then returned every few minutes to check on the subjects' progress. This was done to create a situation in which subjects might relax and respond naturally, rather than controlling their facial expressions because of self-consciousness.

Evaluating Taster/Nontaster Status: Once the sucrose solutions had been tasted, the video camera was turned off, and the subjects were tested for PROP taster/nontaster status. At the end of the session, they were asked complete a brief questionnaire asking for demographic and health information.

Rating the Videotapes: When all subjects had been tested, a videotape was prepared which contained the sequences in which each subject was tasting the highest sucrose concentration only (.83 M). For each subject, three of the eight replications of this solution were chosen, using two criteria: (1) the three occurred within the middle six of the eight replications, to minimize the effects of a possible initial self-consciousness before the camera, and decreasing attention or concentration toward the end; and (2) subjects had reported similar intensities and hedonic values for all three solutions. In almost all cases, any three of middle six replications could be used, as subjects' hedonic ratings were fairly consistent across replications.

Two tapes were prepared: the first contained only females, the second, males. This was necessary because the initial sample tested consisted almost entirely of females, requiring the testing of a later, second sample of males only. Only sweet likers and sweet dislikers were included on the tapes. Subjects reporting a neutral response, those with highly erratic hedonic evaluations, were excluded. As well, a few subjects did their tasting in such a manner that their facial expressions could not been seen clearly on the tapes, and due to this technical difficulty, had to be excluded. In total, there were 27 females on the first videotape, and 21 males on the second.

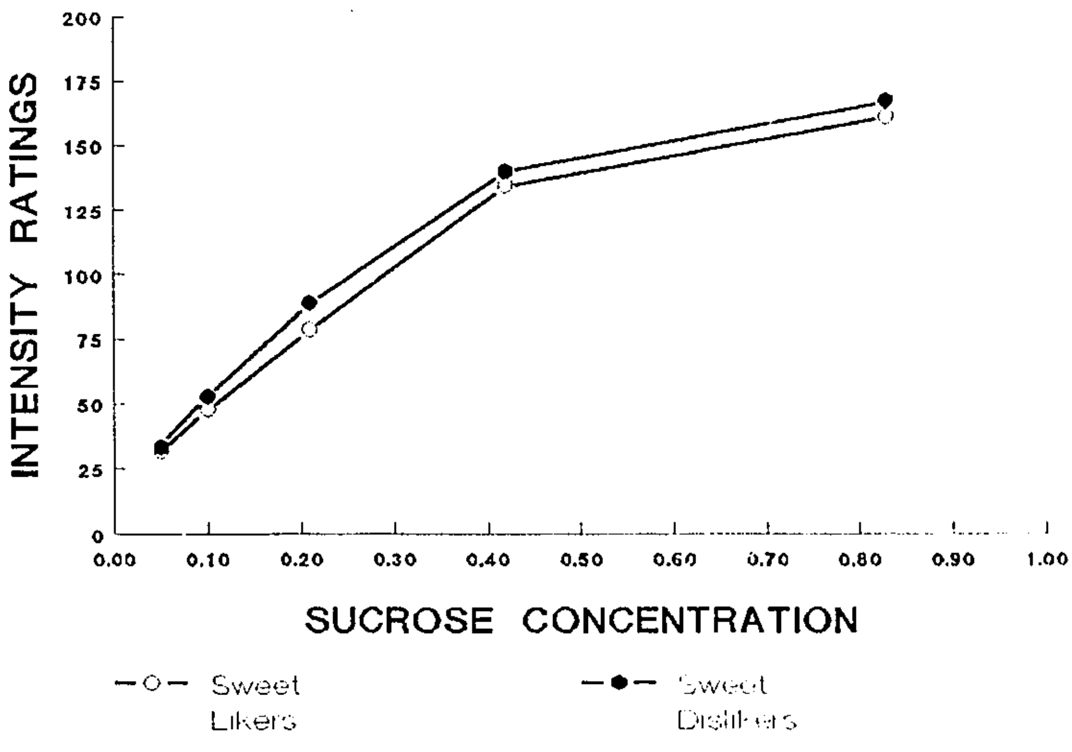
The videotapes were rated by a group of 20 volunteer raters, 10 for each tape, all graduate students or research assistants within the psychology department. The raters viewed the tapes individually. They were instructed to decide whether the subjects liked, were neutral toward, or disliked what they were tasting, on the basis of visual information only. After classifying a subject, they indicated how confident they felt about that classification by circling a number from 1 to 5 ("not confident at all" to "completely confident"). Raters were reminded that "neutral" was to be used as a genuine category (absence of visible affective response), and not simply when the raters felt uncertain of a subject's classification. The raters were permitted to watch the tasting sequences for any subject as often as required to make a classification.

Results

Of the 66 subjects tested, 55 could be classified clearly as sweet likers or dislikers, based on their self-reported hedonic evaluations. The 11 whose data were not used included subjects with neutral hedonic response across concentrations (n=4), and those with erratic responses across concentrations (n=7). Mean ratings of sweetness intensity across concentrations are shown for these sweet likers and dislikers in Figure 5. While the pattern of response in each group is very similar, increasing with increasing concentration ($F(4,216)=1123.15$, $p<.0001$), dislikers did report a significantly greater sweetness intensity across concentrations than did likers (Group $F(1,54)=4.32$, $p<.05$).

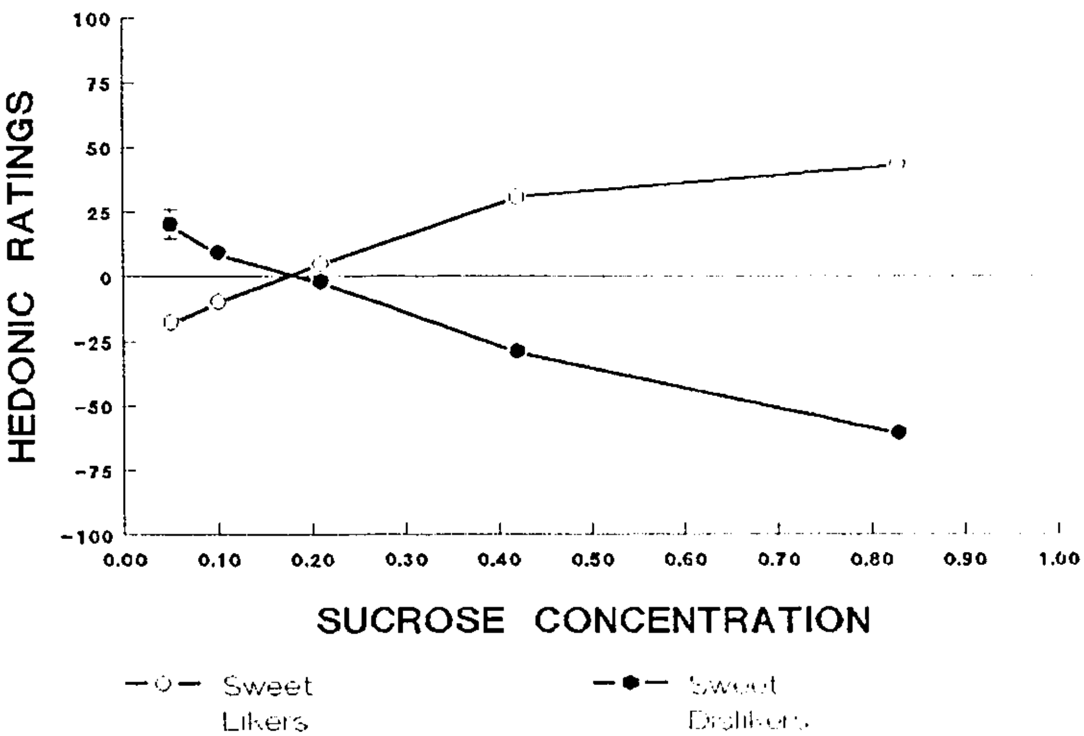
Figure 6 shows the mean hedonic ratings for likers and dislikers across concentrations. By definition, sweet

Figure 5: Mean (± SEM) intensity ratings across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)



INTENSITY RATINGS
200
175
150
125
100
75
50
25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

Figure 6: Mean (± SEM) hedonic ratings across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)


HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet
Likers

likers showed an increasingly positive response with increasing sucrose concentrations, while dislikers reported an increasingly negative reaction. These differences were confirmed by ANOVA, with an expected Group x Concentration interaction ($F(4,216)=143.93$, $p<.0001$), and main effects of Group ($F(1,54)=61.75$, $p<.0001$) and Concentration ($F(4,216)=2.99$, $p<.05$).

The raters' accuracy and confidence in classifying the videotaped subjects are summarized in Table II. Accuracy was calculated as the percentage of correct (that is consistent with self-reports) judgements across all raters.

The raters found the classification of sweet likers to be difficult. This difficulty was not a confusion between the liking and disliking responses, however, as sweet likers who were not classified as such were classified as neutral, not as dislikers. In fact, when classifications of likers as likers <u>or</u> neutral were combined, raters' accuracy increased to the level seen for dislikers. In contrast, the raters were able to classify most sweet dislikers accurately.

Half of the raters were asked directly, after they had evaluated the videotape, what visual cues they had used to make their classifications. (Many other raters spontaneously mentioned the cues they had used.) For

Table II: Raters' Classifications of Likers & Dislikers from Videotapes

RATERS' CLASSIFICATIONS:	Female Tape n	Female Tape accuracy	Male Tape n	Male Tape accuracy
Likers classified as Likers:	9	41.1 %	12	41.7 %
Likers classified as Likers <u>or</u> Neutral:	9	90.0 %	12	84.2 %
Dislikers classified as Dislikers:	18	83.9 %	9	88.7 %

RATERS' CONFIDENCE: (Mean value out of a maximum of 5)	Female Tape	Male Tape
(1) Likers:	2.94	3.23
(2) Dislikers:	4.13	3.88

classification as a disliker, raters mentioned: frowning, tongue thrusting, whole-face grimacing, closing, widening, or rolling of the eyes, nostrils flaring, head rearing back, and a down-turned or open mouth. All raters reported that dislike was very easy to detect. Representative photographs of individuals classified as sweet dislikers are shown in Figure 7. For likers, the cues mentioned were: raised eyebrows, licking of the lips, nodding, smiling. However, these cues were considered subtle, inconsistent, and difficult to interpret. The neutral category was used when raters could see no evidence of affect in either direction, as raters had been instructed. The confidence scores (see Table II) are consistent with these verbal reports: raters were significantly more confident in their classification of sweet dislikers than they were for sweet likers (for females, $t(25)=-3.902$, $p<.001$; for males, $t(19)=-2.293$, $p<.05$).

The results of the assessment of PROP taster/nontaster status will be discussed separately in Chapter Five, in combination with the PROP data from the other subjects in this thesis.

Discussion

Consistent with the results of Experiment 1, two main hedonic response patterns to the sucrose solutions

Figure 7: Representative photographs, taken from the videotapes, of sweet dislikers tasting .83 M sucrose. These subjects gave informed written consent for the use of their photographs.




emerged in the present sample, allowing classification of subjects as sweet likers or dislikers. Only 11 of the 66 subjects could not be classified into one of these two groups. This confirms the existence and reliability of the sweet liker/disliker distinction.

Independent raters, blind to subjects' hedonic evaluations, were remarkably accurate and confident in classifying sweet dislikers as dislikers. They were somewhat less accurate and confident in classifying sweet likers; however, sweet likers not classified as likers were classified as neutral, not as dislikers. The visual cues which raters reported using to make their classifications are consistent with those suggested by Grill and Norgren (1978) and Steiner (1979) as reflecting a reflexive facial reaction to the hedonic value of taste stimuli. (Although Gilbert, Fridlund and Sabini (1987) suggest caution in interpreting these reactions as reflexive: they may instead be <u>ritualistic</u> behaviours which occur for the purpose of social communication.) The present results imply that the cues interpreted as dislike or unpleasantness are reliable indicators of what the subject is experiencing and reporting; however, the cues which signal liking or pleasantness could not be reliably used to determine the subjects' self-reported responses.

The accuracy of the raters' classifications of the sweet dislikers in this study lends weight to the argument that this hedonic response pattern is indeed a reflection of the subjects' actual experience when tasting the solutions. It is highly unlikely that subjects not only gave what they perceived to be socially-desirable ratings (i.e., reporting that they dislike the taste of sucrose because of its association with fattening foods even when they in fact experience it as pleasant), but consistently modified their facial expressions to be consistent with such a response, when the experimenter was not present with them. It remains possible that these genuine hedonic responses have been learned over years of dietary experience and socialization. These data do not imply that hedonic responses must be innate. However, the concern that subjects' self-reports of the hedonic value of the sucrose solutions might not reflect their genuine felt experience is mitigated by these results.

These results therefore support the possibility that hedonic response patterns to sucrose solutions reflect genuine differences in percept, and provide further justification for exploring the nature of the sweet liker/disliker distinction at the level of taste perception.

Chapter Five

GENETIC ABILITY TO TASTE 6-N-PROPYLTHIOURACIL PREDICTS HEDONIC RESPONSE TO SWEET

The previous experiment confirmed the prevalence of the sweet liker and disliker hedonic response patterns to sucrose, and provided evidence that these self-reported hedonic evaluations are based on subjects' genuine reactions to the taste, rather than a more consciously cognitive, or socially-desirable, assessment. We turn now to an exploration of possible differences in the structure or function of the gustatory system which might underlie the sweet liker/disliker distinction.

One possibility, discussed in Experiment 1 and the General Introduction, is that the genetically-determined sensitivity to the bitter taste of PROP is related to these hedonic response patterns to sweet. The genetics of PROP sensitivity may encode structural or functional modifications of the gustatory system which alter the percept of various gustatory stimuli; these alterations in perceptual experience may directly or indirectly translate into very different hedonic evaluations of those stimuli affected.

It is known that PROP sensitivity predicts an individual's perception of a number of other taste stimuli. For example, PROP tasters find other bitter-tasting compounds more intensely bitter than do nontasters (Bartoshuk, 1979; Marks et al., 1988). As well, sucrose and saccharin taste more intensely sweet to tasters than to nontasters (Gent & Bartoshuk, 1983; Marks et al., 1988).

While the studies cited above have focused on the relationship between PROP sensitivity and perceptions of taste <u>intensity</u>, it is not clear whether there is any link between PROP sensitivity and <u>hedonic</u> evaluations of a taste. Indirect evidence for this latter possibility comes from research which suggests that PROP sensitivity can predict food likes and dislikes, particularly for those foods containing bitter components (Drewnowski, 1990; Fischer et al., 1961; Glanville & Kaplan, 1965; Krondl, Coleman, Wade & Milner, 1983). However, a clear link between palatability or food acceptance and PROP sensitivity has yet to be established. The research relating PROP sensitivity to food preferences is complicated by the fact that "real" foods are extremely complex taste and flavour mixtures, with strong cultural and experiential associations. Exploration of a relationship between PROP sensitivity and hedonic response patterns may be studied best initially by using relevant but simple tastes; in this case, pure sucrose solutions.

Sweet liker/disliker and PROP taster/nontaster status were assessed for most subjects who participated in the experiments reported throughout this thesis. The present chapter summarizes this accumulated data for all the adult subjects tested.

A total of 144 university undergraduate volunteers were tested and clearly classified as sweet likers or dislikers, PROP tasters or nontasters. There were 51 males and 93 females, ranging in age from 18 to 45 years (mean=20.7 years). Sweet likers and dislikers only from Experiment 1 were recalled to determine their PROP sensitivity. All other subjects were tested for taster/nontaster status as a part of a larger experimental protocol (see the experiments described in other chapters).

Overall, of the 144 subjects, 34 (23.6%) were PROP nontasters, while 110 (76.4%) were PROP tasters. This proportion of tasters and nontasters lies within the range observed across numerous populations (Whissell-Buechy, 1990b), and is consistent with the predicted frequency based on a single-gene model of PROP sensitivity (Whissell-Buechy, 1990a).

Figure 8 shows the distributions of PROP detection thresholds for sweet likers and for dislikers, and Table III summarizes the relationship between PROP taster/nontaster status and the sweet liker/disliker patterns.

Figure 8: Frequency distributions of PROP detection thresholds for sweet likers (top) and sweet dislikers (bottom).

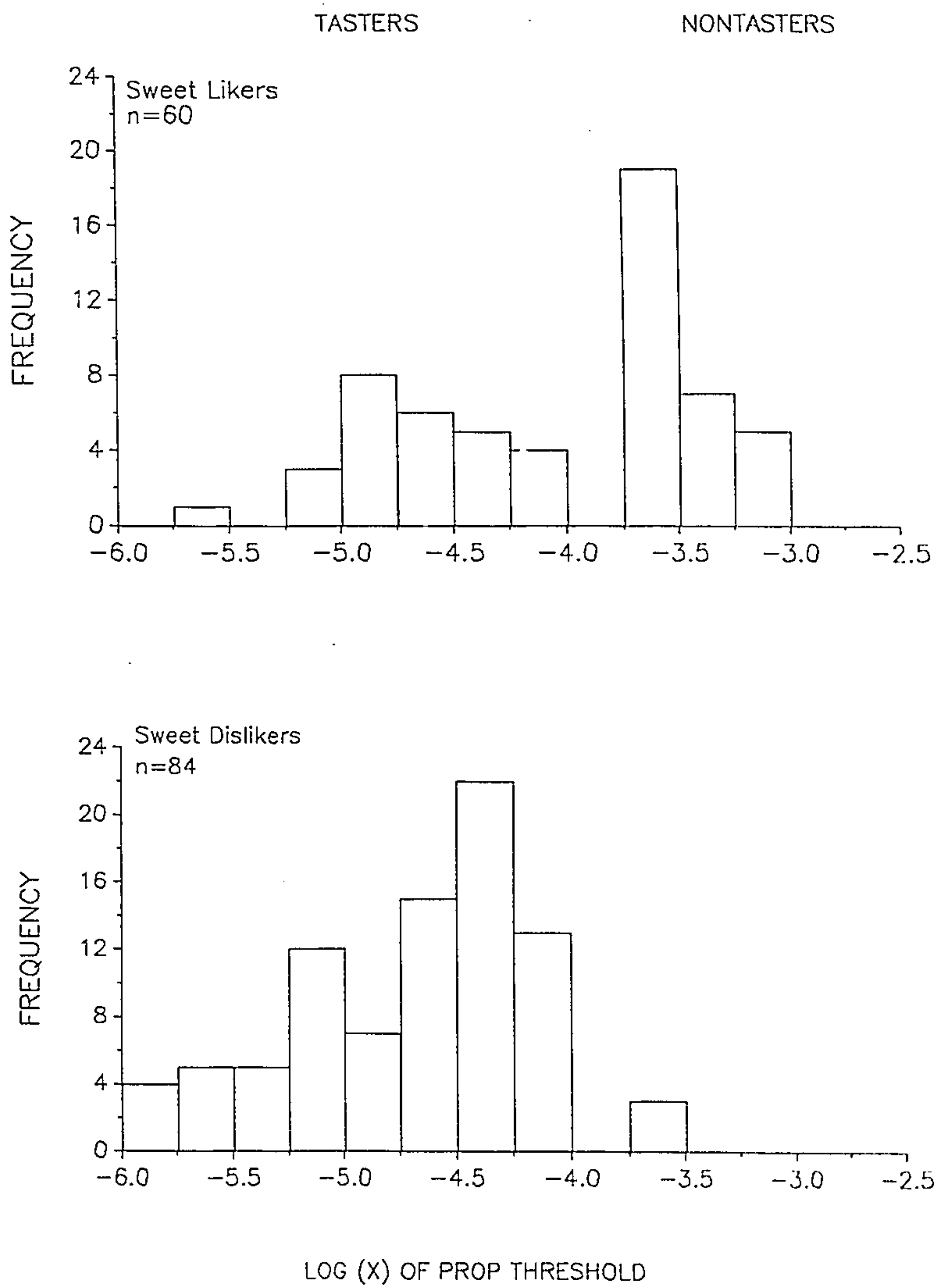

TASTERS
NONTASTERS
Sweet Likers
n=60
FREQUENCY
24
20
16
12
8
4
0
−6.0
−5.5
−5.0
−4.5
−4.0
−3.5
−3.0
−2.5
Sweet Dislikers
n=84
FREQUENCY
LOG (X) OF PROP THRESHOLD

Table III: Relationship Between PROP Sensitivity and Sweet Liker/Disliker Status Among Adults

	Sweet Liker	Sweet Disliker	
PROP Taster	29	81	110
PROP Nontaster	31	3	34
	60	84	144

There is a highly significant, asymmetrical relationship between PROP sensitivity and hedonic response pattern to sweet (X^2 = 44.89, p<.0001). The combination of PROP nontaster/sweet disliker almost never occurs. Therefore, sweet dislikers are almost always PROP tasters, while PROP nontasters are almost always sweet likers. The reverse is not true. This is the first report of a link between the predominant marker of genetic taste differences and hedonic response to a simple taste stimulus.

Although this relationship is striking, it does not in itself indicate any mechanisms by which sensitivity to PROP influences hedonic response to sweet. There are several possibilities. First, PROP tasters and nontasters may differ in their perceptions of the <u>intensity</u> of sweetness, as reported by Gent and Bartoshuk (1983) and Marks et al. (1988). Whether the small magnitude of the differences in perceived intensity, when observed, underlie the almost completely opposing patterns of hedonic response observed in sweet likers and dislikers, needs to be investigated further.

A second possibility is that PROP tasters and nontasters may differ in the perceived <u>quality</u> of the taste sensation arising from sucrose stimulation. It is not known what structural or functional effects the presence or absence of the taster gene has on the gustatory system.

However, one study has suggested that PROP tasters have a type of receptor for bitter tastes which PROP nontasters do not have, bitter tastes being mediated by more than one receptor type (Hall, Bartoshuk, Cain & Stevens, 1974). Another study provides preliminary evidence for a reduction in taste bud density among PROP nontasters which is related to reduced perceptions of taste intensity (taste quality was not measured; Miller & Reedy, 1990). The absence of certain receptor types, or a reduced number of receptors, among nontasters could well result in altered perceptions of the quality of a particular taste stimulus. Changes in perceived quality could in turn contribute to a modified assessment of the hedonic value of that stimulus.

Determination of a mechanism by which PROP sensitivity predisposes an individual toward a particular hedonic response pattern to sweet will require further research. The possibility that quality differences may be involved in this relationship is explored in Chapter Seven.

Chapter Six

Experiment 3

ASSESSMENT OF THE SWEET LIKER/DISLIKER DISTINCTION AND ITS RELATIONSHIP TO PROP SENSITIVITY AMONG CHILDREN

The previous experiments have established that in an adult population, most individuals can be classified as either a sweet liker or disliker. These hedonic response categories are reliable: subjects will show similar patterns over two test sessions, separated by a number of days (see Experiment 1), and their facial responses reliably reflect their self-reported ratings, especially in the case of sweet dislikers (see Experiment 2). There is also a strong relationship between PROP taster/nontaster status and the sweet liker/disliker distinction, suggesting a genetic component underlying the hedonic response to sucrose (see Chapter Five).

Taken together, these data suggest that hedonic response to sucrose is a stable characteristic of the individual which may reflect individual differences in the structure or function of the taste sense. However, the relationship between innate aspects of the gustatory system and hedonic response is imperfect and indirect. For example, PROP taster/nontaster status cannot perfectly predict hedonic response pattern to sucrose. Previous research has also shown that preferences for sweet tasting substances can be modified. Compared with adults, children on average prefer higher sucrose concentrations, and longitudinal research suggests that the preferred amount of sucrose decreases over time (Cowart, 1981; Desor & Beauchamp, 1987; Desor, Greene & Maller, 1975; but see Enns et al., 1979). Dietary exposure to sweetened water in early infancy seems to be necessary to maintain an inborn preference for sweet, at least up to two years of age (Beauchamp & Cowart, 1985; Beauchamp & Moran, 1982; 1984).

Therefore, although the sweet liker/disliker distinction appears to be stable within individuals over the short term, it is unclear how plastic these hedonic response patterns are over the long term. Is this distinction, and its relationship to PROP taster/nontaster status, evident only during adulthood, or is it a robust phenomenon which can be observed at other stages in the lifespan?

This question was addressed in a cross-sectional manner in the present study by asking seven-to-ten-year-old children to evaluate the intensity and hedonic value of sucrose solutions, and assessing their PROP taster/nontaster status. This age group was chosen for two reasons. First, while children in this age range have already had considerable dietary experience, previous research has shown that on average, they do prefer higher sucrose concentrations than adults (Desor et al., 1975). Second, children younger than seven years of age might have difficulty comprehending the experimental task.

Method

Subjects: A total of 72 children were tested, from two different elementary schools. There were 31 females and 29 males, ranging in age from 7 to 10 years (mean=9.03 years, SD=.73). Permission to test the children was obtained from the principals and the teachers involved. The children were volunteers, and their parents gave informed consent for their child's participation prior to the study. The children were rewarded with a sticker for their participation. At the completion of testing, the teachers and parents were sent a letter explaining the research in detail and summarizing the results of the study.

Stimuli: Three sucrose concentrations were used: .05, .21, and .83 M. Six replications of each concentration were used, for a total of 18 solutions. The PROP solutions, described in the General Method, were also used to assess taster/nontaster status.

Rating Scales: The rating scales for the sucrose solutions were similar to the 200 mm visual analogue scales used for the adult samples (see General Method). However, some modifications were made to simplify the task. First, the wording was simplified. The intensity question read: "How <u>sweet</u> was the taste?", and the anchors labelled "not sweet at all" and "<u>very</u> sweet". The hedonic value question read: "How much did you <u>like</u> the taste?", and the anchors were labelled "did not like at all", beneath which was a sketch of a grimacing face with its tongue protruding, and "liked a lot", beneath which was a sketch of a happy face licking its lips.

<u>Procedure</u>: Each child was tested individually, during the school day. They were instructed in the sip and spit and evaluation procedures, which were identical to those followed by the adults. Prior to tasting the test solutions, each child was given two practice trials to ensure that they understood the tasting procedure, and how to use the rating scales. Once they began with the test solutions, the experimenter no longer provided verbal step-by-step instructions; however, she continued to observe the subjects, and supplied additional instructions and encouragement as required. Most children grasped the experimental task with little difficulty.

Once all the sucrose solutions had been evaluated, the subjects were tested for PROP taster/nontaster status.

The detection threshold procedure described in the General Method was followed, with some minor modifications. First, the task was presented to the children as a game: "One of these cups has a taste and one does not. Can you tell me which one has the taste?" In order to retain their interest, subjects were given feedback about the correctness of their response each time. The procedure was not continued for the seven "turn-around" points required to establish a precise PROP detection threshold, as this would have made the test session too long for the children. Instead, the "game" was continued only for as long as required to clearly establish whether the child was a PROP taster or nontaster. Ability to discriminate solution 7 or weaker from water reflects presence of the taster trait; if the subject could not discriminate until solution 5 or stronger, they were classified as a nontaster.

Results

Of the original 72 subjects tested, 60 could be clearly classified as sweet likers or dislikers. The other twelve either showed no affect across concentrations, very erratic responses, or did not understand the experimental task.

The mean intensity and hedonic ratings for the sweet likers and dislikers across concentrations are shown in

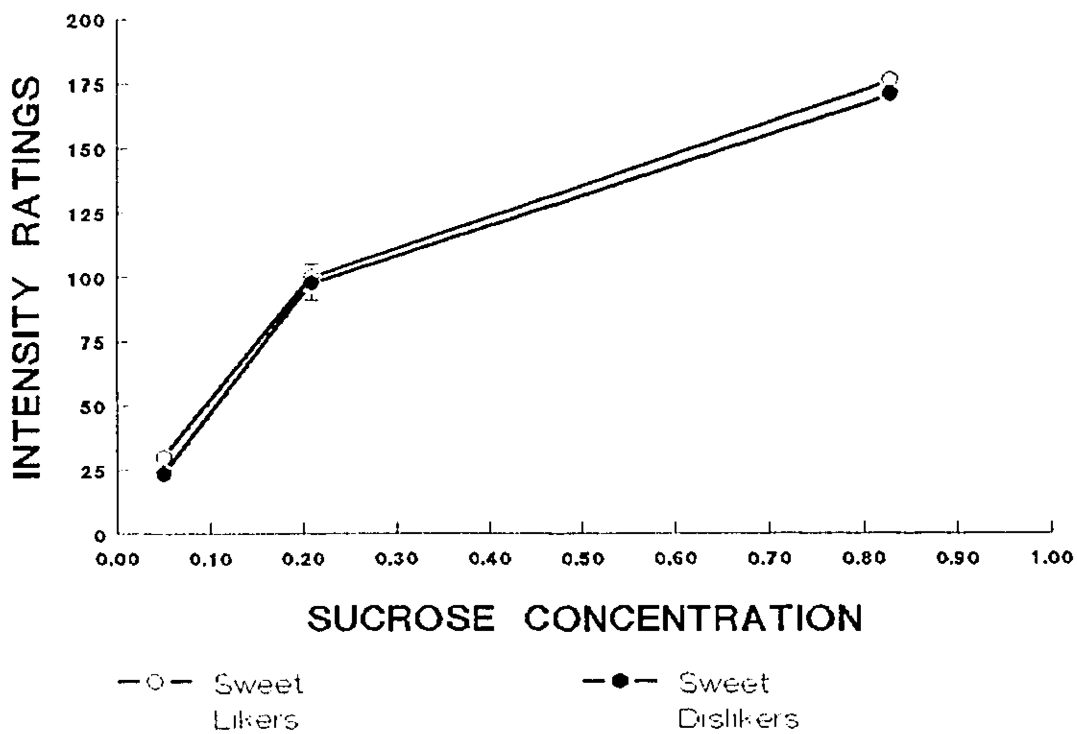
Figures 9 and 10, respectively. As expected, intensity ratings increased with increasing concentration ($F(2,116)=805.69$. $p<.0001$), but there were no significant differences in intensity ratings between sweet likers and dislikers. Analysis of the hedonic ratings showed the expected Group x Concentration interaction ($F(2,116)=234.92$, $p<.0001$), as well as a main effect of Group ($F(1,58)=7.24$, $p<.01$).

Table IV summarizes the relationship between PROP sensitivity and hedonic response to sucrose. There is clearly a strong relationship between PROP taster/nontaster status and hedonic response to sucrose: sweet dislikers are PROP tasters, while PROP nontasters are sweet likers, and again this relationship is asymmetrical ($X^2 = 13.73$, $p<.0005$).

Discussion

The results of the present study reveal that the majority of children can be classified on the basis of their hedonic response patterns to sucrose as sweet likers and dislikers, as could the adults in previous studies. The presence of sweet dislikers among the children is interesting in light of the widespread assumption in North American culture that children like sweet tastes, and the sweeter the better.

Figure 9: Mean (± SEM) intensity ratings across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)



INTENSITY RATINGS
200
175
150
125
100
75
50
25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

<u>Figure 10</u>: Mean (± SEM) hedonic ratings across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)

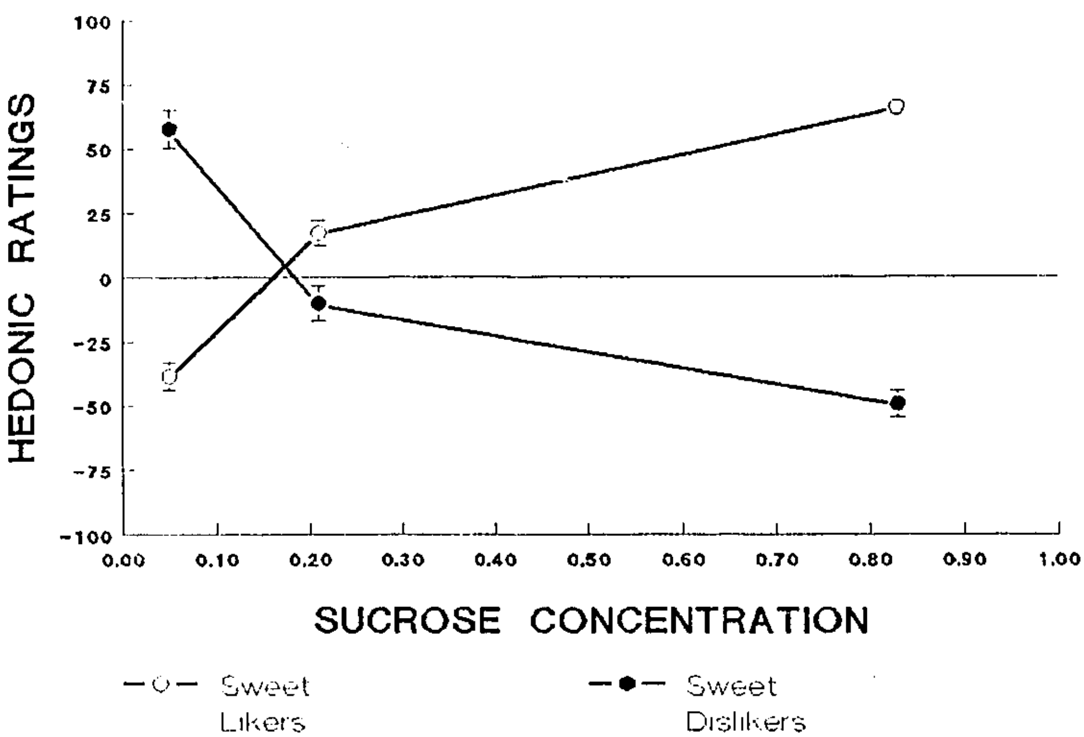

HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

Table IV: Relationship of PROP Sensitivity to Sweet Liker/Disliker Status Among Children

	Sweet Liker	Sweet Disliker	
Taster	21	22	43
Nontaster	17	0	17
	38	22	60

Among the children, there were more sweet likers than dislikers (38 versus 22). This contrasts with the proportions of sweet likers and dislikers observed in the adult samples (9 vs. 13 in Exp. 1; 22 vs. 33 in Exp. 2). The observation that there were proportionally more sweet likers among children than adults is consistent with the research demonstrating that children on average prefer higher concentrations of sucrose than adults (Cowart, 1981; Desor & Beauchamp, 1987; Desor et al., 1975). It also implies that hedonic response patterns to sucrose must be changeable over time, for the proportion of sweet likers to shift with the age of the subject sample.

However, despite the greater proportion of sweet likers among the children, the relationship of hedonic response pattern to PROP taster/nontaster status was identical with that seen among adults. That is, all sweet dislikers were PROP tasters, while all PROP nontasters were sweet likers. Taken together, these observations imply that, since in both the adult and child samples PROP nontasters are almost always sweet likers, only childhood sweet likers who are also PROP tasters make the shift to the sweet disliker pattern by adulthood.

In summary, the results of this study indicate that, while in some cases hedonic response to sweet can be altered over development, the liker/disliker patterns are robust and for many individuals may be "set" relatively early in life. The conclusion that hedonic response to sweet may be established early (at least by age seven), and is consistently tied to PROP sensitivity, provides further indirect support for the possibility that likers and dislikers actually perceive something different when tasting sucrose. In Experiment 4, this hypothesis is addressed directly.

Chapter Seven

Experiment 4

THE RELATIONSHIP BETWEEN PERCEPTIONS OF SUCROSE TASTE QUALITY AND HEDONIC RESPONSE PATTERN TO SWEET

In the previous two chapters, a strong relationship between PROP taster/nontaster status and hedonic response pattern to sucrose (sweet liker versus disliker) was reported for both adults (Chapter Five) and children (Chapter Six). Sweet dislikers are almost always PROP tasters, while PROP nontasters are almost always sweet likers. However, the mechanism by which PROP sensitivity might mediate hedonic response to sucrose has yet to be determined.

One possibility is that the gene coding for PROP sensitivity modifies the taste system in such a manner that the perceived taste quality of certain substances, including sucrose, is altered. Other research has suggested that PROP taster/nontaster status may be related to structural modifications such as a missing receptor population or a reduced number of receptors among PROP nontasters (Hall et al., 1974; Miller & Reedy, 1990). Such modifications could underlie differences in the perception of many gustatory stimuli apart from PROP and its relatives.

As well, even simple stimuli, such as sucrose, do not necessarily evoke a pure, singular quality of sensation (Erickson & Covey, 1980). If subjects were asked to analyze the quality of the taste sensation they experienced from sucrose solutions, they would not necessarily report only a sensation of sweetness. The sucrose itself might evoke a more complex taste (Erickson & Covey, 1980), and the distilled water in which the sucrose is dissolved may also contribute to the quality of sensation (McBurney & Bartoshuk, 1973).

Therefore, since even pure sucrose solutions can potentially evoke a complex taste sensation, and the PROP gene may modify the way in which taste stimuli are encoded, it is possible that PROP sensitivity mediates hedonic responses to sucrose by altering the perceived quality of the taste of sucrose. This hypothesis was evaluated in the present experiment by asking sweet likers and dislikers to evaluate the taste quality of sucrose solutions.

Method

<u>Subjects</u>: Subjects were 48 undergraduate psychology students. There were 34 females and 14 males in the age range 18 to 45 years (mean=20.9 years, SD=5.4).

Stimuli: Five sucrose concentrations, .05, .10, .21, .42 and .83 M, were used. There were five replications of each concentration, for a total of 25 solutions. The same solutions, in a different random order within blocks, were presented in both experimental sessions.

Rating Scales: To assess the taste quality of the solutions, a procedure developed by McBurney (McBurney & Bartoshuk, 1973; Smith & McBurney, 1969) was employed. Subjects were asked to provide a numerical magnitude estimate of the total taste intensity (disregarding taste quality) of each solution. The subjects were then instructed to indicate what proportion of that total taste intensity was due to a bitter, sweet, sour and/or salty quality. They could do this either by dividing their numerical magnitude estimate appropriately across qualities, or by giving the percent of the taste that was bitter, sweet, sour or salty. (This latter strategy was preferred by most subjects; the experimenter simply converted these percentages into proportions of the magnitude estimate.) A separate rating sheet was provided for each solution.

Procedure: Subjects participated in two sessions, each 20 to 30 minutes long, with no more than seven days between sessions. They were asked to ensure that they were not feeling hungry when tested, by eating within an hour prior to the test session.

In one session, the intensity and hedonic value of the sucrose solutions, and PROP taster/nontaster status, were determined.

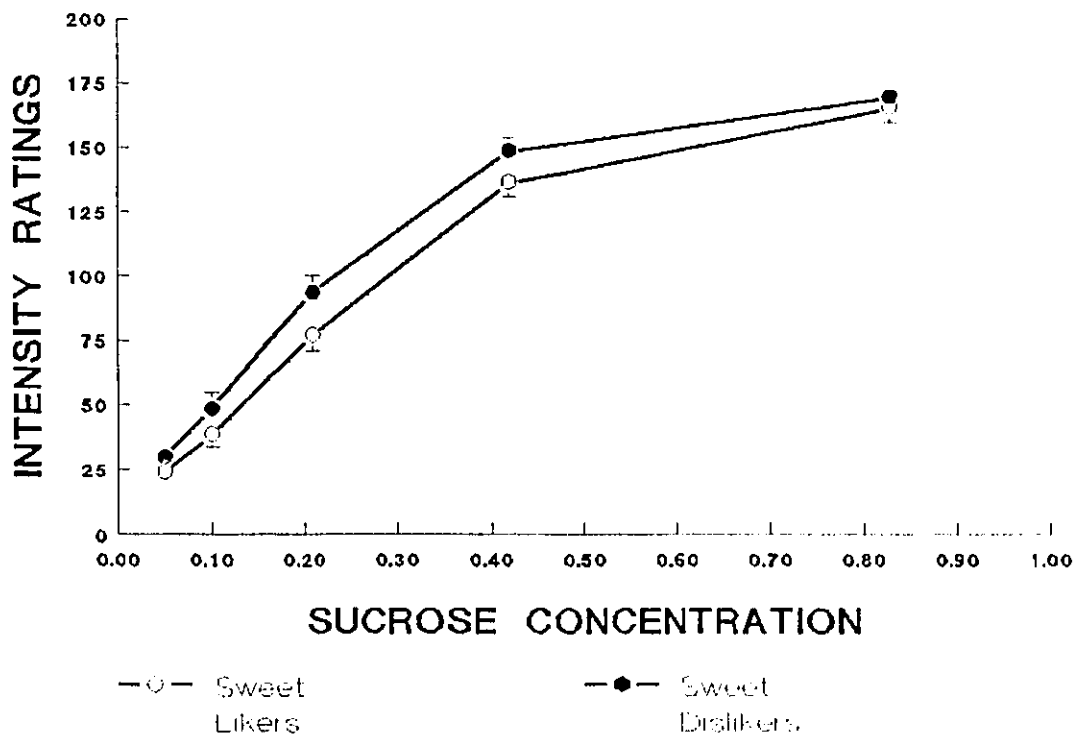
In the other session, subjects were instructed to sip-and-spit the solutions, and follow the method for assessing their taste quality, as described above. They were given two practice trials to ensure that they understood the magnitude estimation/quality assessment procedure. The experimenter was careful to give no indication of the actual contents of the solutions, to avoid biasing subjects' expectations about what the solutions ought to taste like. To further reduce the demand characteristics of the procedure, subjects were assured that there was no "correct" taste, that they were to simply report what they really perceived.

The order of the two sessions was counterbalanced across subjects.

Results

Of the 48 subjects tested, 42 could be unambiguously classified as sweet likers or dislikers. The mean intensity ratings for these sweet likers and dislikers across sucrose concentrations are shown in Figure 11. Although for each group perceived intensity increases with increasing concentration (Concentration $F(4,160)=433.03$, $p<.0001$),

Figure 11: Mean (± SEM) intensity ratings, using the visual analogue scales, across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)



INTENSITY RATINGS
200
175
150
125
100
75
50
25
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

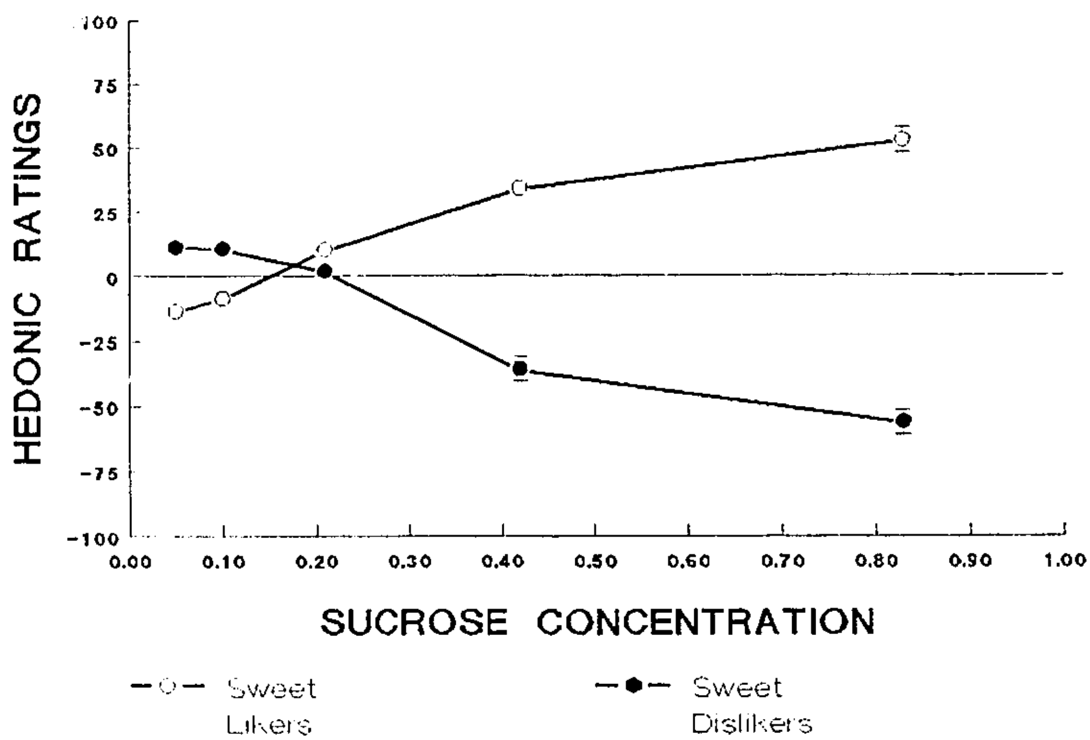
dislikers reported a significantly greater perceived intensity over all concentrations (Group $F(1,40)=4.73$, $p<.05$).

Figure 12 shows the mean hedonic ratings across concentrations for sweet likers and dislikers. Not surprisingly, ANOVA revealed a Group x Concentration interaction ($F(4,168)=129.04$, $p<.0001$), and a main effect of Group ($F(1,42)=68.58$, $p<.0001$).

Because subjects use different absolute numbers when making numerical magnitude estimates, these scales must be normalized or equated prior to averaging across subjects (Bartoshuk, 1978). This was accomplished using the following procedure (Bartoshuk, 1978; McBurney & Bartoshuk, 1973; Marks, 1974): Each subject's responses to the five sucrose concentrations were averaged. The averages for all subjects were then equated to a value of 10 by multiplying by the appropriate constant. The constant used for each subject was then applied to all the magnitude estimates for every concentration for that subject. These adjusted data were averaged arithmetically across subjects, as usual. This procedure reduces variability introduced by the absolute size of the magnitude estimates without affecting the ratios between the estimates (Bartoshuk, 1978).

The mean numerical estimates of total taste intensity across concentrations for sweet likers and

Figure 12: Mean (± SEM) hedonic ratings across sucrose concentrations for sweet likers and dislikers. (SEMs not visible fall within the symbol.)

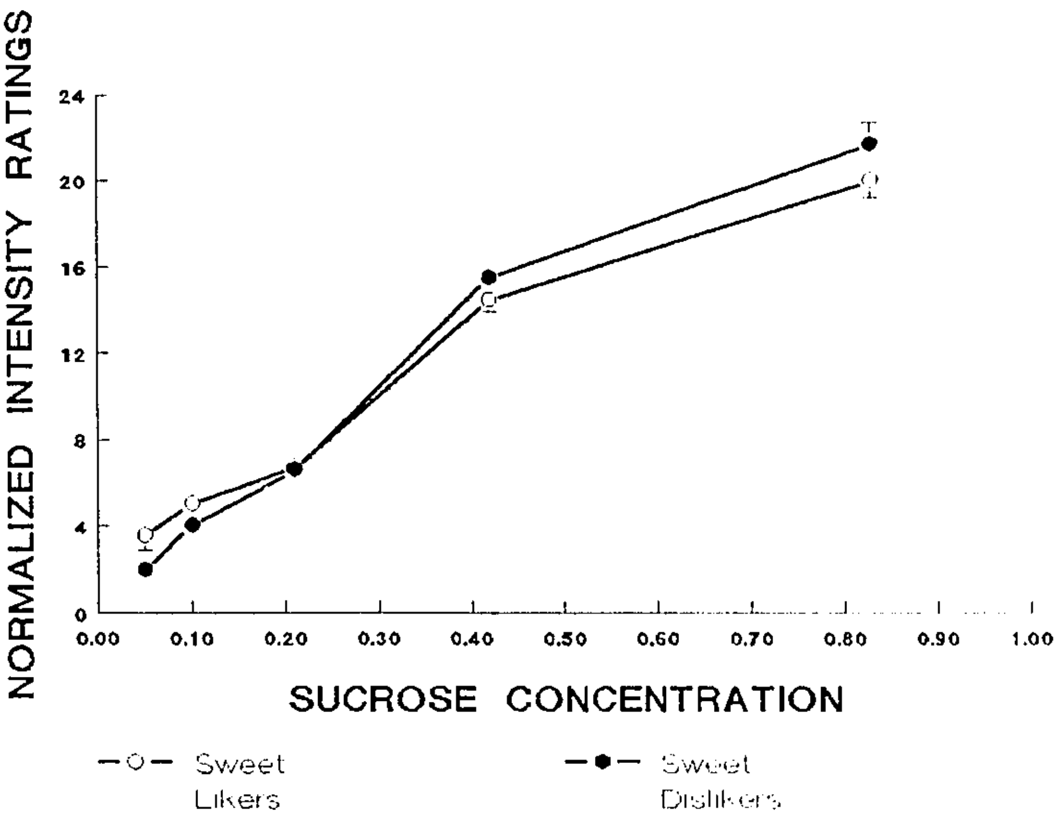

HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

dislikers are shown in Figure 13. For both groups perceived intensity increases with increasing concentration (Concentration $F(4,160)=271.05$, $p<.0001$).

Figure 14 shows the average intensity of the sweet component of the taste of the sucrose solutions for sweet likers and dislikers. ANOVA revealed a significant Group x Concentration interaction ($F(4,156)=2.99$, $p<.05$), as well as significant main effects of Group ($F(1,40)=19.03$, $p<.0005$) and Concentration ($F(4,156)=256.02$, $p<.0001$). That is, sweet dislikers perceived a significantly greater sweet component in the sucrose solutions, particularly at higher concentrations, than did sweet likers.

Because the contribution of any one of the other three quality components (bitter, sour and salty) to the taste was quite small, these were combined into a total "nonsweet" component. The average intensities of this nonsweet component for sweet likers and dislikers are shown in Figure 15. ANOVA revealed only a significant Group effect ($F(1,40)=21.03$, $p<.0001$). These results indicate that sweet likers consistently reported the presence of a small nonsweet component to the taste of the sucrose solutions, while sweet dislikers perceived virtually nothing apart from sweet.

Figure 13: Mean (± SEM) normalized magnitude estimates of the total intensity of sucrose solutions for sweet likers and dislikers. (SEMs not visible fall within the symbol.)



NORMALIZED INTENSITY RATINGS
24
20
16
12
8
4
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

Figure 14: Average (± SEM) intensity of the sweet component of the taste of sucrose solutions for sweet likers and dislikers. (SEMs not visible fall within the symbol.)

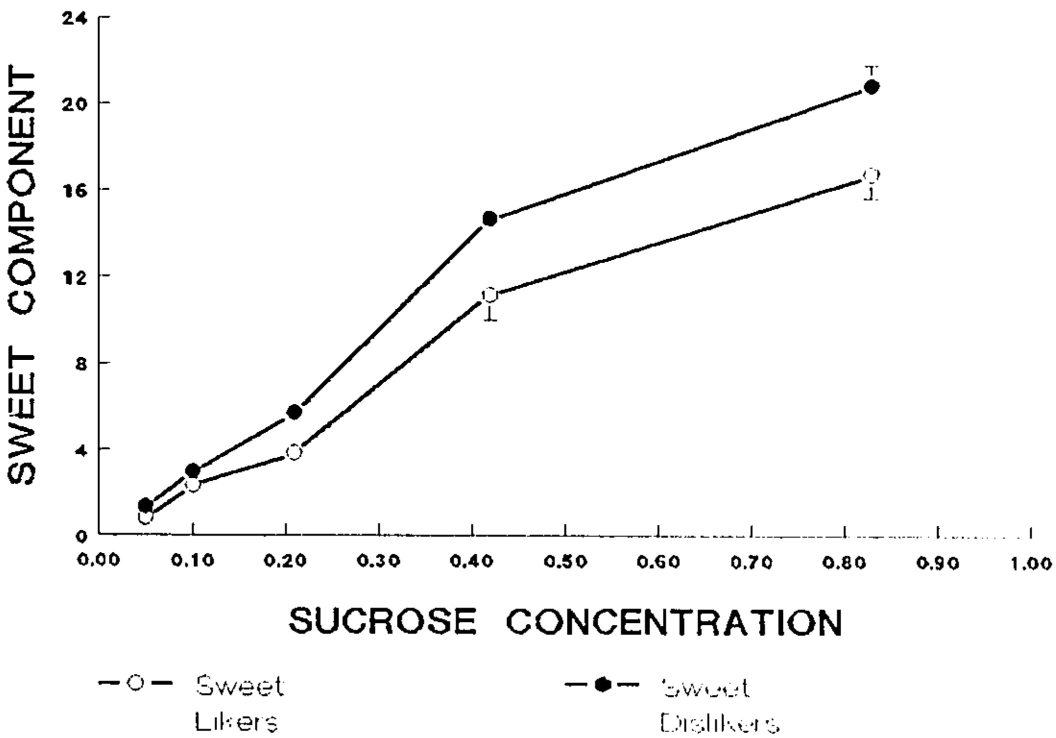
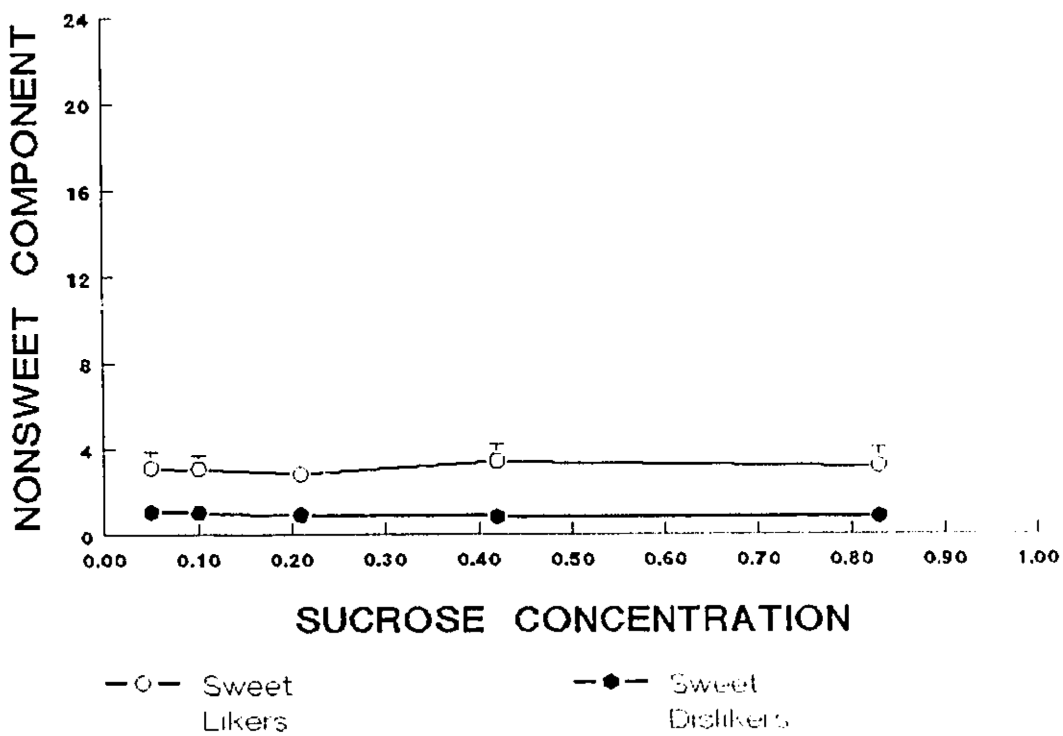

SWEET COMPONENT
24
20
16
12
8
4
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

Figure 15: Average (± SEM) intensity of the nonsweet component (bitter, salty and sour, summed) of the taste of sucrose solutions for sweet likers and dislikers. (SEMs not visible fall within the symbol.)



NONSWEET COMPONENT
24
20
16
12
8
4
0
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sweet Likers
Sweet Dislikers

Discussion

As in previous experiments, the present study confirms the existence and prevalence of the sweet liker and disliker hedonic response patterns to sucrose solutions.

The results of the taste quality assessment are interesting and somewhat surprising. Humans tend to report a greater preference for sweet relative to bitter, sour, or salty tastes. On this basis, we might predict that sweet dislikers dislike concentrated sucrose because they taste some bitterness, or other unpleasant quality, in the solution. And, the prediction might be that sweet likers perceive only sweetness, and therefore find even concentrated sucrose pleasant. The present results are consistent with an opposite hypothesis. The sweet likers reported the presence of qualities other than sweet (such as bitter, salty or sour) in the sucrose solutions, while the sweet dislikers perceived an almost pure sweet taste.

It is possible that either the less intense sweetness, the greater overall complexity of the taste, or both, rendered the sucrose solutions more pleasant for the sweet likers than for the dislikers. This hypothesis that a less intense sweet taste and/or a complex versus a "pure" taste is hedonically more positive, <u>and</u> is of sufficient magnitude to underlie the sweet liker/disliker distinction, needs to be investigated.

One approach would be to ask sweet dislikers to evaluate both pure sucrose solutions, and sucrose solutions with the addition of small amounts of citric acid or NaCl to evoke the slightly more complex tastes which sweet likers reported. If the mixtures are perceived as more pleasant than the pure solutions, and in fact if the hedonic response to these mixtures begins to look like a sweet liker-type pattern, then we would have stronger evidence to suggest that the quality differences observed in the present study underlie the sweet liker/disliker hedonic response patterns. However, this experiment would not reveal <u>why</u> sweet likers perceive a qualitatively-different taste than sweet dislikers when assessing identical sucrose solutions.

This second question may be related to the issue of PROP sensitivity. Since the hedonic responses to sucrose are also strongly related to PROP taster/nontaster status, the difference in the perceived taste quality of sucrose may be the result of whatever structural or functional modifications in the taste system underlie PROP sensitivity. What those modifications are, and how they mediate the more complex taste experience of the sweet likers (who comprise almost all of the PROP nontasters), is another topic for further research.

The conclusions that differences in the perceived quality of sucrose solutions underlie the sweet liker/disliker hedonic response patterns, and that these quality differences represent the mechanism by which PROP sensitivity mediates these hedonic responses, cannot be made solely on the basis of the present data. Further research, as suggested in the previous paragraphs, is required before conclusions can be made.

Chapter Eight

Experiment 5

DO HEDONIC RESPONSE PATTERNS TO SUCROSE SOLUTIONS TRANSFER TO A MODIFIED SWEET STIMULUS?

The previous chapters have outlined an extensive investigation into the nature and possible sources of the sweet liker and disliker hedonic response patterns to sucrose solutions. We have established that these hedonic response patterns represent important individual differences in taste reactivity. But are these individual differences relevant when investigating the role of taste reactivity in food preferences and intake, or are they only important within the constrained parameters of the experiments conducted here? That is, do these hedonic patterns predict preferences and responses when we move from pure sucrose solutions toward the complex stimuli which constitute the types of substances we normally consume?

Because "real foods" are so complex, and because eating behaviour is governed by factors other than taste reactivity, such as learning, context, and experience (Warwick, 1990; Weingarten, 1985), it is difficult to isolate the role of taste reactivity. Therefore, rather than move directly from using simple sucrose solutions to complex "real foods", we took a more moderate first step. In the present experiment we examined whether the sweet liker/disliker distinction would be maintained if a colour and strong, pleasant odour were added to the sucrose solutions. This is a small step toward examining "real foods", but in psychophysical terms, constitutes a fairly large change in the test stimuli. Should the patterns and relationships observed in the previous studies be maintained with this change in stimulus, this would provide justification for examining the relevance of individual differences such as hedonic response pattern and PROP taster/nontaster status for real food preferences and intake. If the altered stimulus radically changes the patterns previously observed, then those previous data, while relevant for understanding the mechanics of taste perception, are unlikely to be useful in furthering our understanding of eating behaviour.

Method

Subjects: Thirty-eight undergraduate student volunteers participated in the study. There were 27 females and 11 males, ranging in age from 19 to 39 years (mean=20.9 years, SD=4.9).

Stimuli: There were five sucrose concentrations, .05, .10, .21, .42 and .83 M. Five replications of each concentration were used, for a total of 25 solutions. The modified stimuli (hereafter known as strawberry solutions) were identical to the sucrose solutions in composition, concentration, and number, with one change: about 3.0 ml of a liquid (obtained at a local health food store) which primarily imparts a strawberry odour without altering the taste, plus 4.0 ml of red food colouring, were added to each litre of solution. This resulted in a bright red colour and a strong strawberry odour.

Procedure: There were two test sessions: one in which subjects evaluated the intensity and hedonic value of the pure sucrose solutions, and one in which they evaluated the intensity and hedonic value of the strawberry solutions. The order of these sessions were counterbalanced across subjects. Testing for PROP taster/nontaster status occurred at the end of the first session, regardless of which sweet solution had been evaluated immediately prior. Subjects were asked to come to the two test sessions sated; that is, having eating within an hour of testing.

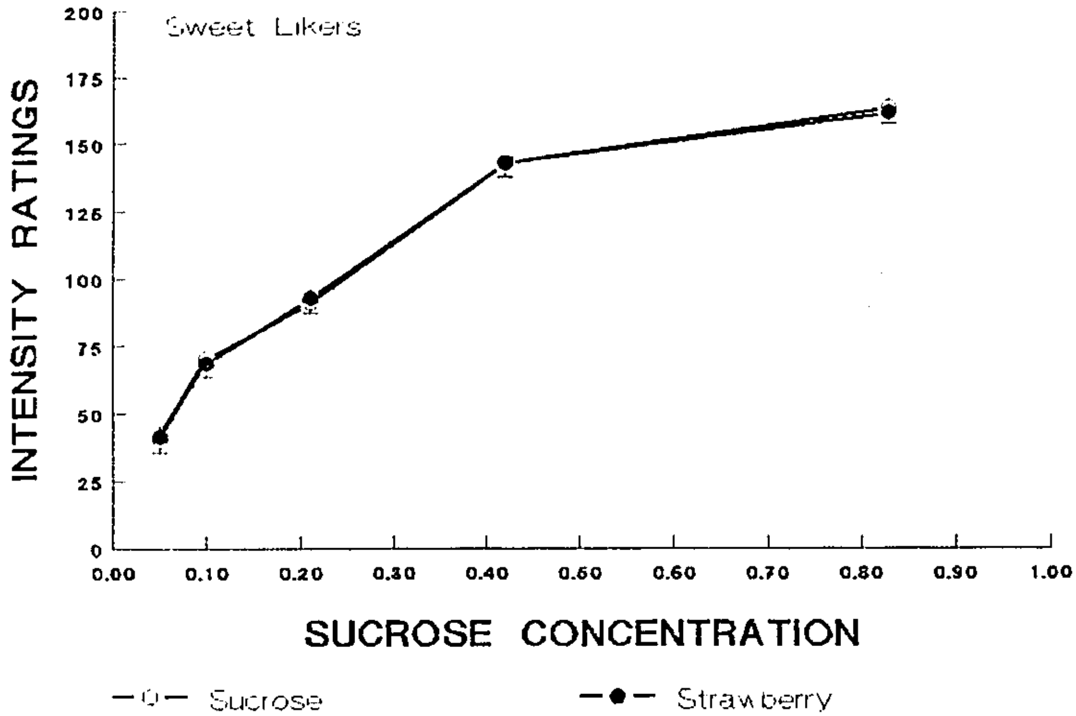
Results

The classification of subjects into sweet likers and dislikers was done on the basis of their hedonic response pattern to the pure sucrose solutions, ignoring responses to the strawberry solutions, since this was how all subjects in previous experiments had been classified. Of the 38 subjects tested, 27 could be clearly classified as sweet likers or dislikers. The others showed either flat affect across concentrations, erratic responses, or a symmetrical inverted-U shaped function.

The mean intensity ratings across concentrations of both sucrose and strawberry solutions for sweet likers and dislikers are shown in Figure 16. A mixed ANOVA, with Group (liker/disliker) as the between factor, and Solution (sucrose/strawberry) and Concentration as the within factors, confirmed that intensity ratings increased with increasing concentration for both groups tasting both solutions (Concentration $F(4,100)=361.47$, $p<.0001$). There were no significant differences between groups for either of the two types of solution (i.e., no Group x Solution interaction).

Mean hedonic responses across concentrations for the sucrose and strawberry solutions for sweet likers and dislikers are shown in Figure 17. A mixed ANOVA showed the expected Group x Concentration interaction ($F(4,100)=81.59$, $p<.0001$), plus main effects of Group ($F(1,25)=31.37$, $p<.0001$) and Concentration ($F(4,100)=3.55$, $p<.01$). From Figure 17, it appears that sweet likers reported no

Figure 16: Mean (± SEM) intensity ratings across concentrations for sucrose and strawberry solutions, for sweet likers (top) and sweet dislikers (bottom). (SEMs not visible fall within the symbol.)


Sweet Likers
INTENSITY RATINGS
0
25
50
75
100
125
150
175
200
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sucrose
Strawberry

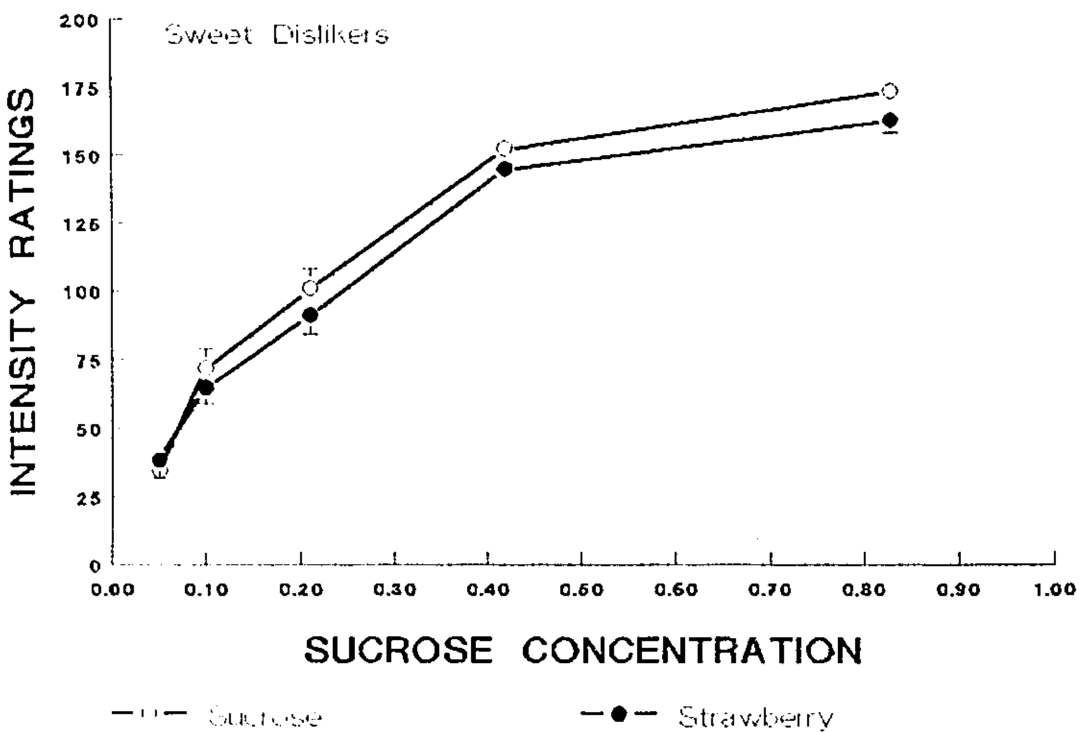
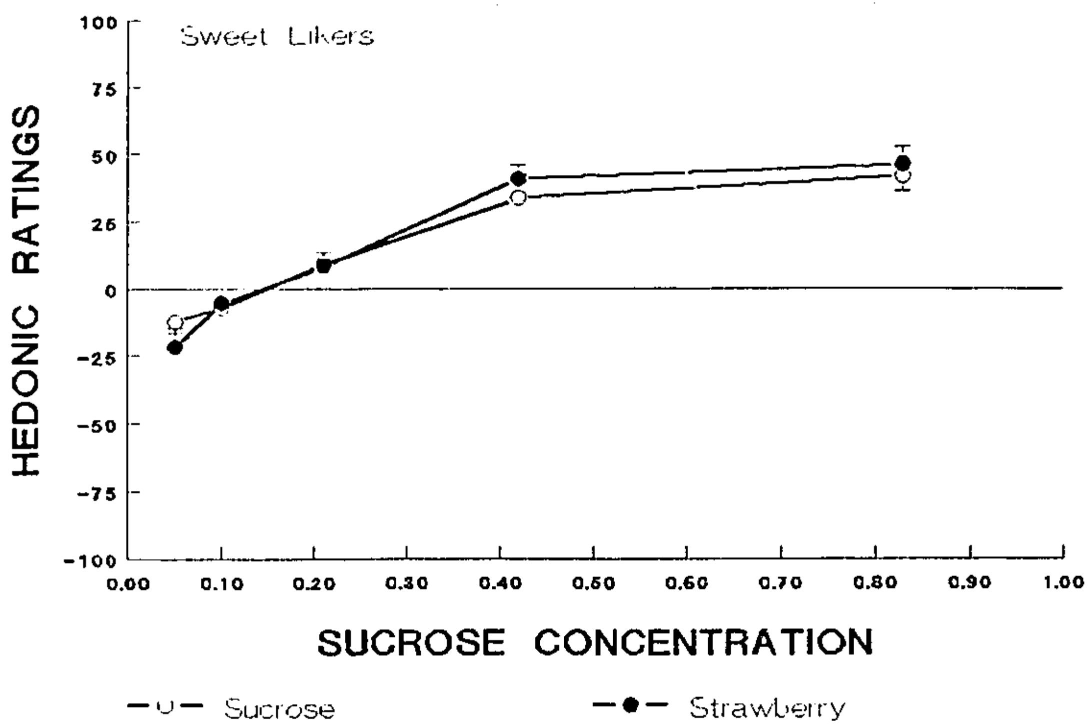
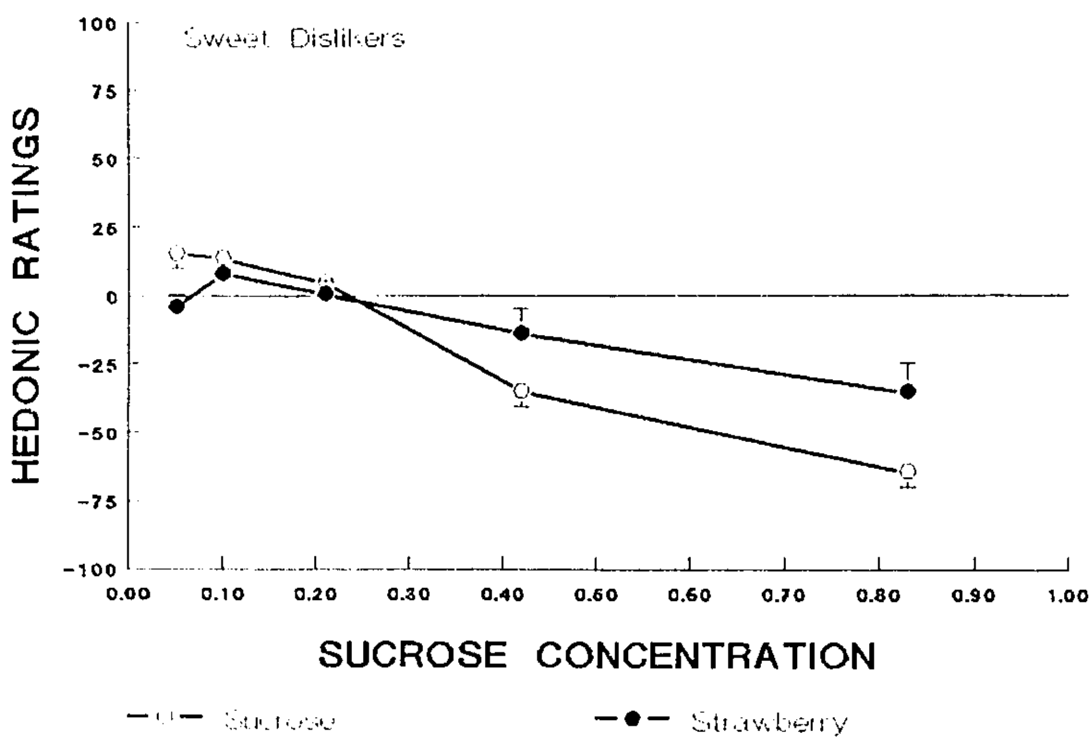

Sweet Dislikers
INTENSITY RATINGS
0
25
50
75
100
125
150
175
200
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
SUCROSE CONCENTRATION
Sucrose
Strawberry

Figure 17: Mean (± SEM) hedonic ratings across concentrations for the sucrose and strawberry solutions, for sweet likers (top) and sweet dislikers (bottom). (SEMs not visible fall within the symbol.)


Sweet Likers
HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00 0.10 0.20 0.30 0.40 0.50 0.60 0.70 0.80 0.90 1.00
SUCROSE CONCENTRATION
Sucrose
Strawberry


Sweet Dislikers
HEDONIC RATINGS
100
75
50
25
0
-25
-50
-75
-100
0.00 0.10 0.20 0.30 0.40 0.50 0.60 0.70 0.80 0.90 1.00
SUCROSE CONCENTRATION
Strawberry

difference in hedonic value for the sucrose and strawberry solutions. In contrast, sweet dislikers reported that the strawberry solutions were less unpleasant than the sucrose solutions, particularly at the higher concentrations. These observations are confirmed by the significant interactions of Solution x Concentration ($F(4,100)=14.60$, $p<.0001$) and Group x Solution x Concentration ($F(4,100)=5.09$, $p<.005$).

Since the classification of subjects as sweet likers and dislikers was based on their hedonic responses to the sucrose solutions, and since the primary question of this experiment was whether these patterns are robust when the stimulus is altered, subjects were also classified as likers or dislikers based on their hedonic responses to the strawberry solutions. Table V summarizes the comparison between classification based on sucrose and on strawberry solutions. In almost every case, a subject would have been classified similarly whether that classification was based on their hedonic responses to the sucrose or to the strawberry solutions. Note that this does not mean that subjects gave identical hedonic values to both sets of solutions. It only means that the direction of their responses across concentrations were similar.

Discussion

As in the previous studies, the sweet liker/disliker

Table V: Comparison of Sweet Liker/Disliker Classifications Based on Responses to Sucrose and Strawberry Solutions

	Sucrose Liker	Sucrose Disliker	
Strawberry Liker	12	1	13
Disliker	1	13	14
	13	14	27

distinction accounted for the majority of subjects' hedonic response patterns to the sucrose solutions.

The central question of this experiment was whether the sweet liker/disliker distinction was unique to pure sucrose solutions, or whether these hedonic response patterns would generalize to another, different sweet stimulus which was more similar to "real foods" than the sucrose solutions. From Table V, the answer is clear: these hedonic response patterns are maintained even when, in psychophysical terms, the sweet stimulus is changed significantly. The addition of a strong strawberry odour and a vivid colour to the sweet solutions did not affect subjects' general hedonic response pattern, except in the case of two subjects. That is, almost every subject would have been classified in the same hedonic response category regardless which type of solution was used as the basis for this classification.

However, although the broad classification is robust, the presence of the odour and colour did significantly attenuate the unpleasantness of the higher sucrose concentrations for the sweet dislikers. The odour and colour were not irrelevant additions to the stimuli, and these data suggest that on a preference test, sweet dislikers may well prefer a greater intensity of sweetness if the sweetness is associated with an odour and/or colour than if it is not.

The results reported suggest that attempts to generalize the conclusions from the series of experiments reported in this thesis to preferences for the even more complex "real foods" should be done with caution. As well, experiments designed to establish the predictive value of the sweet liker/disliker distinction (or PROP taster/nontaster status) for food preferences and intake (e.g., Drewnowski, 1990) should take into account the fact that increasing the sensory complexity of a food stimulus may significantly affect the results. Nevertheless, the robustness of the hedonic response pattern observed in the present study provides sufficient justification to explore further the implications of this important individual difference for eating behaviour.

Chapter Nine

GENERAL DISCUSSION

This thesis addressed the general question of the role of sweet taste reactivity in eating behaviour. The results of the first experiment suggested that individual differences in taste reactivity--specifically, hedonic response to sweet--may be relevant for understanding the relationship between taste reactivity and food intake. Subsequent experiments examined the nature and possible sources of these individual differences in hedonic response pattern to sweet. They established that the sweet liker/disliker patterns are robust phenomena which are related to genetic and possibly sensory differences in the taste system, yet show some plasticity over time. These data imply that a more complete understanding of individual differences in taste reactivity is needed before predictions can be made regarding the role of sweetness in food preferences and intake.

Overall, the results of these experiments suggest that most individuals, 80% of adults (144/180) and 83% of children (60/72), can be classified as either a sweet liker or disliker based simply upon their self-reports of the hedonic value of sucrose within the concentration ranges used. Of the 36 adults who could not be clearly classified as a sweet liker or disliker, 17 showed minimal affective response across concentrations ("neutrals"), while the remainder showed erratic or symmetrical inverted-U shaped functions. Of the 17 neutrals, 8 were male, 9 were female, 16 were PROP tasters, and 1 was a PROP nontaster.

Two issues that emerge repeatedly in this series of experiments are the questions of perceived intensity and the relationship of gender to sweet liker/disliker status. These will be addressed in turn.

Perceived intensity, as measured using a visual analogue scale, was assessed in all the experiments reported in this thesis. In some experiments (Experiments 1, 2 and 4), but not others (Experiments 3 and 5), statistically significant differences in intensity were observed, with sweet dislikers reporting the higher intensity of taste. The results of the taste quality experiment (Experiment 4) provide a possible explanation for the difference in perceived sweet intensity when it is apparent. Differences in intensity between likers and dislikers may be due to mixture suppression, which refers to the weakening of the perceived intensity of components in a mixture, relative to the intensity of those components tasted separately (Bartoshuk, 1975; Kroeze, 1979). Because sweet likers perceive other qualities apart from sweet in sucrose solutions (see Experiment 4), the intensity of the sweet component may have been reduced relative to sweet dislikers who perceive no accompanying additional nonsweet taste components. Based on this argument, differences in perceived intensity _per se_ do not underlie the sweet liker/disliker distinction, but rather are the result of differences in sensory quality experienced by sweet likers and dislikers.

Whatever differences in perceived intensity might exist between sweet likers and dislikers, and regardless of the basis of these differences, it is unlikely that intensity differences underlie the radically different hedonic response patterns characteristic of likers and dislikers. For example, from Figure 14, it can been seen that sweet likers report the same intensity of the sweet quality for 0.83 M sucrose as the sweet dislikers report for 0.42 M sucrose. Yet sweet dislikers find 0.42 M sucrose unpleasant, while likers report that 0.83 M sucrose (and 0.42 M, of course) tastes pleasant! It is important to note that the sucrose concentrations used in these studies range from just about threshold to intensely sweet and, for almost any level of perceived intensity, likers and dislikers assign different hedonic values.

The relationship of gender to sweet liker/disliker status is summarized in Table VI for all the adult subjects tested, and in Table VII for the children.

Among the adults, females were more likely to be sweet dislikers than were males ($X^2 = 5.69$, $p<.05$). A similar relationship was observed among the children ($X^2 = 3.79$, $p<.05$). This relationship of gender to sweet liker/disliker status is intriguing. It may be that some of the observed trend arises because sociocultural pressures towards thinness are directed primarily toward females (Garner et al., 1980; George & Krondl, 1983), and, therefore, females may report a dislike for sweet tastes because these tastes are associated with forbidden, fattening foods. This argument is not consistent, however, with the results of the facial expression study (Experiment 2), which suggest that hedonic ratings are a genuine reflection of the taste percept. It remains possible that females are more likely to be sweet dislikers because sociocultural pressures to treat sweetness as "bad" have, over many years of socialization, caused some females to develop a genuinely negative reaction to sweet tastes. Another possibility is that genetic or physiological factors associated with gende[illegible] an impact on taste perception,

Table VI: Relationship Between Sweet Liker/Disliker Status and Gender Among Adults

	Sweet Liker	Sweet Disliker	
Male	28	23	51
Female	32	61	93
	60	84	144

Table VII: Relationship Between Sweet Liker/Disliker Status and Gender Among Children

	Sweet Liker	Sweet Disliker	
Male	22	7	29
Female	16	15	31
	38	22	60

or at least on the affective value of taste stimuli. Given the evidence presented in the present experiments for genetic correlates and sensory differences among sweet likers and dislikers, the possibility of gender-related physiological differences in taste perception seems reasonable. Previous research has indicated that there may be gender and hormonal correlates of both taste sensitivity and preference (Aaron, 1975; Dippel & Elias, 1980; Enns et al., 1979; Gandelman, 1983; Velle, 1987; Weizenbaum, Benson, Solomon & Brehony, 1980; Wright & Crow, 1973). However, further research is needed to understand fully the relevance of gender for the hedonic evaluation of sweet tastes.

Experiment 1 examined the effects of short-term changes in metabolic state (hunger and satiety) on the perceived intensity, hedonic value, and intake of sweet solutions. The results of this experiment suggest that baseline individual differences in taste reactivity predict the effect of metabolic state changes on taste reactivity. Specifically, individuals who are sweet dislikers show an attenuation of the unpleasantness of concentrated sweet solutions when they are food-deprived. They also take more solution into their mouths in the deprived, relative to the sated, state. Sweet likers, in contrast, report no change in hedonic value, and show no change in intake, across metabolic states. That is, sweet tastes better when you're hungry only if you are a sweet disliker to begin with.

These individual differences in hedonic response to sucrose may account for the inconsistent observation in previous research of Cabanac's (1979) alliesthesia for sweet tastes. Cabanac (1979) predicts that the pleasantness of a taste is tied to internal signals. States of energy depletion should cause an increase in the pleasantness of the taste, while satiation would cause a decrease. Some studies (Cabanac, 1971; Rolls et al., 1983; Scherr & King, 1982) have confirmed the alliesthesia hypothesis, while others (Cabanac & Duclaux, 1970; Moskowitz et al., 1976) have not observed it. The results of Experiment 1 suggest that alliesthesia may not occur for all individuals; specifically, sweet likers do not show this effect. Therefore, differences in the proportion of sweet likers in the subject samples may underlie the conflicting results of previous studies. It should also be noted that the sweet liker and disliker patterns were observed for a particular range of sucrose concentrations. While most studies of sweet taste reactivity employ similar concentrations, some caution should be maintained in comparing across studies. The present data do not predict the hedonic ratings which sweet likers and dislikers would give to sucrose solutions more concentrated than those employed in the present studies. However, since the motivation of this research is to explore the role of taste in eating behaviour, higher concentrations than the ones employed here are probably irrelevant, as "real foods" are rarely, if ever, more intensely sweet. Indeed, the sucrose concentration of Koolaid is about 0.38 M, while pop has a sweetness intensity equivalent to about 0.38 to 0.46 M sucrose. Both concentrations are well within the range employed in the present experiments.

As well, the absence of an alliesthesia effect among sweet likers sheds some doubt on the generality of the alliesthesia hypothesis. Cabanac (1979) argues that the pleasantness of a stimulus is directly related to the current needs of the organism and the usefulness of that stimulus to meet those needs. Sweet tastes usually signal safe and nutritionally valuable foods which the organism needs, while bitter tastes are primarily associated with toxic substances which the organism should avoid. Consistent with Cabanac's hypothesis, sweet tastes are generally perceived as more pleasant than bitter tastes (Schiffman & Erickson, 1971).

However, Cabanac's theory goes further and says that the hedonic value of a food stimulus should change for each <u>individual</u> depending upon their current state of need. The results of Experiment 1 appear to contradict this prediction. Not all subjects reported an increase in the pleasantness of the sweet stimuli when hungry--the sweet likers showed no change at all. To reconcile this observation with Cabanac's hypothesis, we would have to argue that the sweet likers differ physiologically from the sweet dislikers in such a manner that they constantly "need" stimuli associated with sweet tastes, whether sated or deprived. To support this argument, we would have to find a relevant internal signal for gustatory alliesthesia which behaves differently in sweet likers and dislikers. In the absence of such a difference, however, it becomes difficult to apply the alliesthesia hypothesis at the individual level.

Where do the sweet liker and disliker hedonic response patterns come from? Experiment 2 addressed the concern that some individuals, in response to sociocultural pressures toward thinness, are more likely to report a dislike for sweet tastes simply because the taste is strongly associated with forbidden, fattening foods. If this were true, then the stability of the sweet liker/disliker distinction would be called into question. To investigate the validity of the hedonic ratings, therefore, we used facial responses to the taste as a concurrent measure of hedonic response. Naive, independent raters were indeed able to "correctly" identify the sweet likers and in particular, the dislikers, using only the subjects' facial responses to the tastes. Since the facial responses were so consistent with the subjects' self-reported hedonic ratings of the stimuli, it is unlikely that these hedonic response patterns reflect a desire on the part of some subjects to give socially-desirable, rather than honest, responses. This does not mean that the sociocultural context is irrelevant in the development of hedonic responses to sweet over time, but simply that the self-reported hedonic ratings are probably a valid and reliable reflection of the subjects' actual perceptual experience.

If the sweet liker and disliker hedonic response patterns reflect the individuals' taste experience, then that experience must logically be different for likers versus dislikers. This difference could be purely cognitive; that is, sweet likers evaluate the pleasantness of the taste as high, while dislikers evaluate the identical taste as unpleasant. However, the difference could also be truly perceptual; that is, based on some sort of functional or structural alteration of the taste system.

Experimentally, it is difficult to distinguish between these two possibilities. In Chapter Five, the hypothesis that the sweet liker/disliker distinction is based on structural or functional differences in the taste system was indirectly explored by correlating the genetically-determined sensitivity to the bitter taste of PROP with hedonic response to sweet. A powerful relationship emerged. Sweet dislikers are almost always PROP tasters, while PROP nontasters are almost always sweet likers. This is true for both adults and children (Experiment 3). While this observation is correlational, it does permit the possibility that sweet likers and dislikers differ in the manner in which they encode the taste of the sucrose solutions. However, further research is needed before any conclusions regarding a causal relationship between PROP sensitivity and hedonic response to sweet can be made.

If PROP taster/nontaster status can affect (or at least predict) hedonic responses to simple sweet tastes, then this genetic trait may be a reasonable predictor of more complex taste or food preferences. While previous research has focused on the predictive value of PROP sensitivity for bitter- or sharp-tasting foods which presumably share some taste qualities with PROP (Drewnowski, 1990; Fischer et al., 1961; Glanville & Kaplan, 1965; Krondl et al., 1983; Marino et al., 1991), no one has examined whether preferences for "real foods" with other qualities, particularly sweet, could also be related to PROP taster/nontaster status.

However, the correlation between hedonic response to sucrose and PROP sensitivity is not perfect. Only the combination sweet disliker/PROP nontaster rarely occurs. Therefore, given the information that an individual is a sweet disliker, we can accurately predict that they must also be a PROP taster. If we know an individual is a PROP nontaster, they are almost certain to be a sweet liker. In contrast, we cannot make any predictions if we only know that the individual is a PROP taster or a sweet liker. This implies that, even if PROP sensitivity (or the alterations in the taste system of which this sensitivity is a reflection) is causally related to hedonic response to sweet, there must be intervening, mitigating factors which also play a role in hedonic response. Thus, it may be more relevant to use hedonic response pattern to sweet, rather than PROP sensitivity, to predict food preferences, especially when examining foods with a sweet-tasting component.

While hedonic response patterns to sweet appear to be stable within an individual over the short term (see Experiments 1 and 4), Experiment 3 addressed the question of whether the sweet liker/disliker distinction is unique to adults, or present earlier in the developmental process. The results support the idea that hedonic response to sweet, and its relationship to PROP sensitivity, is established by the age of seven. That is, seven-to-ten-year-old children show the sweet liker and disliker hedonic response patterns, and these patterns are related to PROP sensitivity, in a manner which directly parallels that seen in adults. However, the results also point to some plasticity in the hedonic response. Consistent with previous research (Desor & Beauchamp, 1987; Desor et al., 1975), there were proportionally more sweet likers among the children than among the adults. During development, some individuals must reverse their hedonic response pattern to sucrose from that of a sweet liker to that of a disliker. The fact that the relation between PROP sensitivity and hedonic response was identical for adults and children implies that this reversal only occurs for those individuals who are childhood sweet likers and PROP tasters.

Whether in fact such reversals of hedonic response pattern do occur during development, the maturational and/or experiential factors which influence this change, and the relevance of genetic "predispositions" for this process, are important questions for future, longitudinal studies. Nevertheless, Experiment 3 does suggest that in general, the hedonic response to sweet is established early. That, and the consistency of the relationship with PROP taster/nontaster status, are indirect support for the argument that sweet likers and dislikers differ in their perceptual experience of sucrose.

Another approach to the possibility that sweet likers and dislikers differ in the perceived taste of the sucrose solutions is to examine directly the quality of that perceived taste. The finding of a strong relationship between a genetically-determined taste trait and hedonic response to sucrose provides further justification for suggesting that such a difference in percept might exist. When sweet likers and dislikers were asked to describe the taste quality of the sucrose solutions (Experiment 4), the sweet likers reported a less intense sweet component, and the presence of more nonsweet qualities (bitter, sour and salty) to the taste than did the sweet dislikers. That is, the sweet likers tasted a mixture of taste qualities, while the sweet dislikers perceived the solutions to be almost purely sweet.

This result could be interpreted to mean that the sucrose solutions are differentially encoded by the taste system such that, for sweet likers, the resulting sensory experience is pleasant, while for sweet dislikers it is unpleasant. That is, a strong pure sweet taste may be experienced as unpleasant while a mixture which includes a strong sweet component is pleasant. This can be tested by presenting sweet dislikers with a mixture designed to mimic the relative strengths of the taste qualities reported by sweet likers, and see whether this mixture can transform a sweet disliker into a "liker".

However, these results could also simply mean that sweet dislikers find the sweet component of the taste to be so unpleasant that they are unable to focus their attention on any other taste qualities present, while sweet likers are able to do so. This latter explanation would imply that the actual perceptual experience is identical for both groups, and that for some (probably cognitive) reason, sweet dislikers find it unpleasant. If this latter explanation is correct, it further implies that PROP sensitivity is not causally related to the hedonic response. (It is possible that the gene which codes for PROP sensitivity has multiple effects, and alters some neural structure outside of the peripheral taste system controlling hedonic response. However, this would be difficult to test, since the neural bases of hedonic response are not known at present.)

Further exploration of the factors which influence hedonic response to sucrose will be more interesting and important if it can be demonstrated that these hedonic response patterns are indeed relevant for taste and food preferences and intake behaviour. While there are a number of ways to approach this question, the first step is to determine whether the sweet liker and disliker patterns predict hedonic response to other sweet stimuli. In Experiment 5, subjects' hedonic responses to sucrose solutions altered by the addition of a strong strawberry odour and vivid red colour were compared with responses to the standard pure sucrose solutions. In almost every case, subjects' classifications as sweet likers or dislikers based on their hedonic evaluations of pure sucrose were identical with their classifications based on their evaluations of the strawberry solutions. However, the addition of the odour and colour did result in a significant attenuation of the unpleasantness of the strong sucrose concentrations for the sweet dislikers. These results are encouraging in that the hedonic response classification is robust even when, in psychophysical terms, the stimulus is substantially altered. However, future investigations of the relevance of hedonic responses to sweetness for food preferences and intake must also take into account the significant attenuation of the sweet disliker response as a result of increasing the complexity of the taste stimuli. Whether sweet dislikers will in general prefer less intensely sweet tastes in food than sweet likers may well depend upon the relative intensity of the sweet taste and upon other sensory aspects, including odour and possibly colour, of the food stimulus.

Future Research

The current set of experiments suggest that individual differences in sweet taste reactivity must be taken into account in future investigations of the role of taste in eating behaviour. These individual differences may also provide an excellent tool for further explorations of the mechanisms of peripheral taste encoding. Specifically, differences in the hedonic response pattern to sucrose may be of great predictive value (see Experiment 1). PROP taster/nontaster status may also be a relevant individual difference, either directly, or through its relationship with hedonic response pattern to sweet.

Encoding of Gustatory Stimuli: While sensitivity to the bitter taste of PROP has long been known to have a genetic basis (Fischer, 1967), the precise structural or functional elements of the taste system which this gene affects have not been determined. At present, there are two related hypotheses. Hall et al. (1974) suggest the absence of a particular family of bitter receptors among PROP nontasters, while Miller and Reedy (1990) point to a possible reduction in taste receptor number for nontasters.

Once it was discovered that PROP sensitivity was related to alterations in the perception of other gustatory stimuli (Bartoshuk, 1979; Marks et al., 1988), the possibility emerged of using PROP sensitivity as a tool for examining mechanisms of gustatory encoding.

At first it was assumed that PROP sensitivity could only help us explore the processes involved in encoding bitter-tasting substances, but recently PROP sensitivity has been reported to predict perception of non-bitter stimuli, such as sweet- and salty-tasting substances (Bartoshuk & Marks, 1986; Gent & Bartoshuk, 1983; Marks et al., 1988). Suddenly a specific, genetically-determined sensitivity to the taste of a group of rather obscure compounds appears to be related to some important alterations in the taste system which affect gustatory perception more generally than was thought.

The present research extends the predictive power of the PROP marker not only to differences in gustatory encoding, but also to the hedonic value placed on a sweet-tasting stimulus. These results further support the hypothesis that the PROP gene affects encoding of sweet stimuli, and that individual differences in gustatory encoding affect the hedonic value of a sweet taste.

Future studies need to examine this hypothesis further. Differences between PROP tasters and nontasters in the way a variety of gustatory stimuli are encoded and therefore perceived need to be more clearly established. For example, does PROP sensitivity predict perception and hedonic response to other sugars apart from sucrose? Detailed comparisons of receptor populations in tasters and nontasters should be made, using both psychophysical and electrophysiological techniques. This research will clarify the manner in which individuals differ in the structure and function of the gustatory system, and clarify questions of gustatory encoding by relating those individual differences to differences in perceptual experience.

Finally, there must be studies to shed light on the relationship between perceptual experience and hedonic evaluation. Is hedonic value an aspect of gustatory stimuli which is encoded directly (that is, an inseparable part of the percept), is it correlated with particular information encoded from gustatory stimuli, or is it primarily a cognitive evaluation of the sensation which occurs after the encoding process in complete and is, in theory, separable from the actual perceptual experience? One study which could begin to address these questions would examine the effect of altering the taste quality and complexity of the sweet stimulus to determine whether hedonic response patterns could be altered. For example, would adding a small sour component to a primarily sweet solution change a sweet disliker into a liker? And would somehow increasing the intensity or "purity" of the sweet taste change a liker into a disliker (see Experiment 5, Chapter Seven)?

<u>Taste and Internal Signals</u>: Since the gustatory system lies at the interface between the internal and external environments (Scott, 1991), the relationship between individual differences in the taste system for the impact of internal signals on taste reactivity needs to explored. Experiment 1 (Chapter Three) showed that hedonic response to sucrose could predict whether taste reactivity changes with changes in metabolic state. This effect should be examined further. As well, other internal signals related to meal initiation and termination should be studied with regard to individual differences in taste. It is even possible that sweet likers and dislikers show differences in the nature and function of these internal signals. For example, sweet likers may show an abnormal pattern of plasma glucose fluctuations, or an altered metabolic rate, relative to sweet dislikers, which might be related to their heightened preference for sweet tastes and their lack of responsiveness to general changes in metabolic state. This is purely speculation, but these possibilities are worth investigating.

Taste and Eating Behaviour: Although in this thesis there has been much focus on the sweet liker and disliker hedonic response patterns, the relationship between these patterns and eating behaviour has not been addressed at all. We do know that the sweet liker/disliker distinction predicts whether a change in taste reactivity occurs with changes in metabolic state (see Experiment 1, Chapter Three). However, we do not know whether changes in taste reactivity would occur with normal fluctuations in metabolic state--that is, under more ecologically valid circumstances, such as between and within normal meals. Nor do we know whether the liker/disliker distinction would predict the nature of such changes under these circumstances. We also do not know whether any such changes in taste reactivity have an impact on food preference and intake. The research by Rolls and colleagues (Rolls et al., 1981; 1982; 1983) on sensory-specific satiety suggests that there are indeed changes in the hedonic value of food stimuli between and throughout meals, and that these changes can affect choice and amount ingested.

The present research implies that individual differences in taste reactivity, especially the sweet liker/disliker distinction, should be taken into account when investigating these questions, something which has not been done in previous studies. Thus future investigations of taste reactivity and food intake using "real foods" under more normal eating conditions should also measure individual differences in hedonic evaluation of sweet, and possibly PROP taster/nontaster status as well, and determine whether these individual differences can predict responses and clarify the interpretation of the results.

Another question which arises in relating hedonic response patterns to sweet to eating behaviour is whether the sweet liker/disliker distinction is specific to sweet tastes, or whether it generalizes to other gustatory classes. That is, are sweet likers also salt likers, sour likers, perhaps even bitter likers? Do they seek intense stimulation of the gustatory system? Might this generalize even further, to preferences for spicy, astringent, or burning flavours, which stimulate the trigeminal system? The answer to this question will not only have relevance for the encoding issues discussed above, but will also help direct investigations into the relationship between hedonic response and food preferences.

While laboratory studies exploring individual differences in taste reactivity and their relationship to food choice and intake are necessary and important, information about these relationships can also be obtained through surveys of food preferences or through the use of food diaries, using a population for whom hedonic response category and PROP sensitivity have been established. This latter method, while fraught with problems of validity, has the advantage over laboratory studies in that the range of foods available is not severely limited. People may report, quite honestly, very different food preferences if selecting from a limited set in the laboratory, describing the foods they normally eat, or ranking preferences from a sample including foods they would like to eat if they could or if they were available.

If hedonic response to sweet, and/or PROP sensitivity, are shown to predict with some degree of accuracy food preferences and even food intake, there will be important implications both for the food industry and for a theoretical understanding of the factors involved in human eating behaviour.

REFERENCES

Aaron, M. (1975). Effect of the menstrual cycle on subjective ratings of sweetness. Perceptual and Motor Skills, 40, 974.

Akey, L.R., Chen, S.C., Rosen, S., Paulson, G., Travers, S.P. & Travers, J.B. (1991). Taste preference in Parkinson's Disease patients. Abstract presented at the Association for Chemoreception Sciences Annual Meeting, Sarasota, 1991.

Arvidson, K. & Friberg, U. (1980). Human taste: Response and taste bud number in fungiform papillae. Science, 209, 807-808.

Bartoshuk, L.M. (1974). Taste illusions: Some demonstrations. Annals of the New York Academy of Sciences, 237, 279-285.

Bartoshuk, L.M. (1975). Taste mixtures: Is mixture suppression related to compression? Physiology and Behavior, 14, 643-649.

Bartoshuk, L.M. (1978). The psychophysics of taste. The American Journal of Clinical Nutrition, 31, 1068-1077.

Bartoshuk, L.M. (1979). Bitter taste of saccharin related to the genetic ability to taste the bitter substance 6-n-propylthiouracil. Science, 205, 934-935.

Bartoshuk, L.M. (1988). Taste. In R.C. Atkinson, R.J. Herrnstein, G. Lindzey & R.D. Luce (Eds.), Steven's Handbook of Experimental Psychology, 2nd Ed.. New York: Wiley. pp. 461-499.

Bealer, S.L. & Smith, D.V. (1975). Multiple sensitivity to chemical stimuli in single human taste papillae. Physiology and Behavior, 14, 795-799.

Beauchamp, G.K. & Moran, M. (1982). Dietary experience and sweet taste preference in human infants. Appetite, 3, 139-152.

Beauchamp, G.K. & Moran, M. (1984). Acceptance of sweet and salty tastes in 2-year-old children. Appetite, 5, 291-305.

Beauchamp, G.K. & Cowart, B.J. (1985). Congenital and experiential factors in the development of human flavor preferences. Appetite, 6, 357-372.

Bédard, M. & Weingarten, H.P. (1989). Postabsorptive glucose decreases excitatory effects of taste on ingestion. American Journal of Physiology, 256, R1142-R1147.

Blundell, J.E., Rogers, P.J. & Hill, A.J. (1988). Uncoupling sweetness and calories: Methodological aspects of laboratory studies on appetite control. Appetite, 11(Suppl), 54-61.

Boudreau, J.C. (1984). A peripheral neural correlate of the human fungiform papillae salty, insipid sensations. Chemical Senses, 9, 341-353.

Boudreau, J.C., Sivakumar, L., Do, L.T., White, T.D., Oravec, J. & Hoang, N.K. (1985). Neurophysiology of geniculate ganglion (facial nerve) taste systems: species comparisons. Chemical Senses, 10, 89-127.

Brala, P.M. & Hagen, R.L. (1983). Effects of sweetness perception and caloric value of a preload on short term intake. Physiology and Behavior, 30, 1-9.

Cabanac, M. (1971). Physiological role of pleasure. Science, 173, 1103-1107.

Cabanac, M. (1979). Sensory pleasure. The Quarterly Review of Biology, 54, 1-22.

Cabanac, M. & Duclaux, R. (1970). Obesity: Absence of satiety aversion to sucrose. Science, 168, 496-497.

Cabanac, M. & Fantino, M. (1977). Origin of olfacto-gustatory alliesthesia: Intestinal sensitivity to carbohydrate concentration? Physiology and Behavior, 18, 1039-1045.

Cabanac, M. & LaFrance, L. (1990). Postingestive alliesthesia: The rat tells the same story. Physiology and Behavior, 47, 539-543.

Cowart, B.J. (1981). Development of taste perception in humans: Sensitivity and preference throughout the life span. Psychological Bulletin, 90, 43-73.

Crook, C.K. (1978). Taste perception in the newborn infant. Infant Behavior and Development, 1, 52-69.

Davis, J.D. (1973). The effectiveness of some sugars in stimulating licking behavior in the rat. Physiology and Behavior, 11, 39-45.

Davis, J.D. & Smith, G.P. (1988). Analysis of lick rate measures the positive and negative feedback effects of carbohydrates on eating. Appetite, 11, 229-238.

Desor, J.A. & Beauchamp, G.K. (1987). Longitudinal changes in sweet preferences in humans. Physiology and Behavior, 39, 639-641.

Desor, J.A., Greene, L.S. & Maller, O. (1975). Preferences for sweet and salty in 9- to 15-year-old and adult humans. Science, 190, 686-687.

Diamant, H., Oakley, B., Ström, L., Wells, C. & Zotterman, Y. (1965). A comparison of neural and psychophysical responses to taste stimuli in man. Acta Physiologia Scandinavica, 64, 67-74.

DiLorenzo, P.M. & Schwartzbaum, J.S. (1982a). Coding of gustatory information in the pontine parabrachial nuclei of the rabbit: Magnitude of neural response. Brain Research, 251, 229-244.

DiLorenzo, P.M. & Schwartzbaum, J.S. (1982b). Coding of gustatory information in the pontine parabrachial nuclei of the rabbit: Temporal patterns of neural response. Brain Research, 251, 245-257.

Dippel, R.L. & Elias, J.W. (1980). Preferences for sweet in relationship to use of oral contraceptives and pregnancy. Hormones and Behavior, 14, 1-6.

Drewnowski, A. (1990). Genetics of taste and smell. World Review of Nutrition and Dietetics, 63, 194-208.

Drewnowski, A., Brunzell, J.D., Sande, K., Iverius, P.H. & Greenwood, M.R.C. (1985). Sweet tooth reconsidered. Physiology and Behavior, 35.

Duncan, G.H., Bushnell, M.C., Lavigne, G.J. (1989). Comparison of verbal and visual analogue scales for measuring the intensity and unpleasantness of experimental pain. Pain, 37, 295-303.

Enns, M.P., VanItallie, T.B. & Grinker, J.A. (1979). Contributions of age, sex and degree of fatness on preferences and magnitude estimations for sucrose in humans. Physiology and Behavior, 22, 999-1003.

Erickson, R.P. (1963). Sensory neural patterns and gustation. In Y.Zotterman (Ed.), Olfaction and Taste: I (pp.205-213). New York: Pergamon Press.

Erickson, R.P. (1982). Studies on the perception of taste: Do primaries exist? Physiology and Behavior, 28, 57-62.

Erickson, R.P. (1985). Grouping in the chemical senses. Chemical Senses, 10, 333-340.

Erickson, R.P. & Covey, E. (1980). On the singularity of taste sensations: What is a taste primary? Physiology and Behavior, 25, 527-233.

Fischer, R. (1967). Genetics and gustatory chemoreception in man and other primates. In Kare, M.R. and Maller, O. (Eds.), The Chemical Senses and Nutrition (pp.61-81). Baltimore: Johns Hopkins Press.

Fischer, R., Griffin, F., England, S., et al. (1961). Taste thresholds and food dislikes. Nature, 191, 1328.

Frank, M. (1974). The classification of mammalian afferent taste nerve fibres. Chemical Senses and Flavor, 1, 53-60.

Gandelman, R. (1983). Gonadal hormones and sensory function. Neuroscience and Biobehavioral Reviews, 7, 1-17.

Garner, D.M., Garfinkel, P.E., Schwartz, D. & Thompson, M. (1980). Cultural expectations of thinness in women. Psychological Reports, 47, 483-491.

Garner, D.M., Polivy, J. & Olmstead, M.P. (1983). Development and validation of a multidimensional eating disorder: Inventory for anorexia nervosa and bulimia. International Journal of Eating Disorders, 2, 15-34.

Gent, J.F. & Bartoshuk, L.M. (1983). Sweetness of sucrose, neohesperidin dihydrochalcone, and saccharin is related to genetic ability to taste the bitter substance 6-n-propylthiouracil. Chemical Senses, 7, 265-272.

George, R.S. & Krondl, M. (1983). Perceptions and food use of adolescent boys and girls. Nutrition and Behavior, 1, 115-125.

Gilbert, A.N., Fridlund, A.J. & Sabini, J. (1987). Hedonic and social determinants of facial displays to odors. Chemical Senses, 12, 355-363.

Giza, B.K. & Scott, T.R. (1983). Blood glucose selectively affects taste-evoked activity in the rat nucleus tractus solitarius. Physiology and Behavior, 31, 643-650.

Giza, B.K. & Scott, T.R. (1987a). Blood glucose level affects perceived sweetness intensity in rats. Physiology and Behavior, 41, 459-464.

Giza, B.K. & Scott, T.R. (1987b). Intravenous insulin infusions in rats decrease gustatory-evoked responses to sugars. American Journal of Physiology, 252, R994-R1002.

Glanville, E.V. & Kaplan, A.R. (1965). Food preference and sensitivity of taste for bitter compounds. Nature, 205, 851-852.

Goetzl, F.R., Ahokas, A.J. & Payne, J.G. (1950). Occurrence in normal individuals of diurnal variations in acuity of the sense of taste for sucrose. Journal of Applied Physiology, 2, 619-626.

Greene, L.J., Desor, J.A. & Maller, O. (1975). Heredity and experience: Their relative importance in the development of taste preference in man. Journal of Comparative and Physiological Psychology, 89, 279-284.

Grill, H.J. & Norgren, R. (1978a). The taste reactivity test. I. Mimetic responses to gustatory stimuli in neurologically normal rats. Brain Research, 143, 263-279.

Grill, H.J. & Norgren, R. (1978b). The taste reactivity test. II. Mimetic responses to gustatory stimuli in chronic thalamic and chronic decerebrate rats. Brain Research, 143, 281-297.

Hall, M.J., Bartoshuk, L.M., Cain, W.S. & Stevens, J.C. (1975). PTC taste blindness and the taste of caffeine. Nature, 253, 442-443.

Hellekant, G., Ninomiya, Y. & Dubois, G. (1991). On the question of basic tastes (qualities). Abstract presented at the Association for Chemoreception Sciences Annual Meeting, Sarasota, 1991.

Henning, H. (1916). The quality range of taste. Zeitschrift für Psychologie, 74, 203-219. (National Research Council of Canada, Technical Translation 1736, translated by E. Staub).

Hill, A.J., Magson, L.D. & Blundell, J.E. (1984). Hunger and palatability: Tracking ratings of subjective experience before, during and after the consumption of preferred and less preferred food. Appetite, 5, 361-371.

Janowitz, H.D. & Grossman, M.I. (1949). Gusto-olfactory thresholds in relation to appetite and hunger sensations. Journal of Applied Physiology, 2, 217-222.

Jensen, M.P., Karoly, P. & Braver, S. (1986). The measurement of clinical pain intensity: A comparison of six methods. Pain, 27, 117-126.

Kroeze, J.H.A. (1979). Masking and adaptation of sugar sweetness intensity. Physiology and Behavior, 22, 347-351.

Krondl, M. & Coleman, P. (1986). Social and biocultural determinants of food selection. Progress in Food and Nutrition Science, 10, 179-203.

Krondl, M., Coleman, P., Wade, J. & Milner, J. (1983). A twin study examining the genetic influence on food selection. Human Nutrition: Applied Nutrition, 37A, 189-198.

Kuznicki, J.T. & Ashbaugh, N. (1982). Space and time separation of taste mixture components. Chemical Senses, 7, 39-53.

Lucas, F. & Bellisle, F. (1987). The measurement of food preferences in humans: Do taste-and-spit tests predict consumption? Physiology and Behavior, 39, 739-743.

Lundgren, B., Jonsson, B., Pangborn, R.M., et al. (1978). Taste discrimination versus hedonic response to sucrose in coffee beverage. An interlaboratory study. Chemical Senses, 3, 249-265.

Marino, S., Bartoshuk, L.M., Monaco, J., Anliker, J.A., Reed, D. & Desnoyers, S. (1991). PTC/PROP and the tastes of milk products. Abstract presented at the Association for Chemoreception Sciences Annual Meeting, Sarasota, 1991.

Marks, L.E. (1974). Sensory Processes: The New Psychophysics. New York: Academic Press.

Marks, L.E., Stevens, J.C., Bartoshuk, L.M., Gent, J.F., Rifkin, B. & Stone, V.K. (1988). Magnitude-matching: The measurement of taste and smell. Chemical Senses, 13, 63-87.

Mattes, R.D. & Mela, D.J. (1986). Relationships between and among selected measures of sweet-taste preference and dietary intake. Chemical Senses, 11, 523-539.

McBride, R.L. (1985). Stimulus range influences intensity and hedonic ratings of flavour. Appetite, 6, 125-131.

McBurney, D.H. (1972). Gustatory cross-adaptation between sweet tasting compounds. Perception and Psychophysics, 11, 225-227.

McBurney, D.H. (1979). Are there primary tastes for man? Chemical Senses, 1, 17-28.

McBurney, D.H. & Bartoshuk, L.M. (1973). Interactions between stimuli with different taste qualities. Physiology and Behavior, 10, 1101-1106.

McBurney, D.H. & Collings, V.B. (1984). Introduction to Sensation/Perception (2nd Ed.). Englewood Cliffs: Prentice Hall.

McBurney, D.H. & Gent, J.F. (1979). Taste of methyl-α-D-mannopyranoside: Effects of cross adaptation and Gymnema sylvestre. Chemical Senses, 4, 45-50.

McBurney, D.H. & Gent, J.F. (1981). On the nature of taste qualities. Psychological Bulletin, 86, 151-167.

McBurney, D.H., Smith, D.V. & Schick, T.R. (1972). Gustatory cross adaptation: Sourness and bitterness. Perception and Psychophysics, 11, 228-232.

Meyer, D.R. (1952). The stability of human gustatory sensitivity during changes in time of food deprivation. Journal of Comparative and Physiological Psychology, 45, 373-376.

Miller, I.J. Jr., & Reedy, F.E. Jr. (1990). Variations in human taste bud density and taste intensity perception. Physiology and Behavior, 47, 1213-1219.

Moskowitz, H.R., Kluter, R.A., Westerling, J. & Jacobs, H.L (1974). Sugar sweetness and pleasantness: Evidence for different psychological laws. Science, 172, 583-585.

Moskowitz, H.R., Kumraiah, V., Sharma, K.N., Jacobs, H.L. & Sharma, S.D. (1976). Effects of hunger, satiety and glucose load upon taste intensity and taste hedonics. Physiology and Behavior, 16, 471-475.

Oakley, B. (1985). Taste responses of human chorda tympani nerve. Chemical Senses, 10, 469-481.

Öhrwall, cited in Erickson, R.P. (1985). Grouping in the chemical senses. Chemical Senses, 10, 333-340.

Pangborn, R.M. (1970). Individual variation in affective responses to taste stimuli. Psychonomic Science, 21, 125-126.

Pfaffman, C. (1941). Gustatory afferent impulses. Journal of Cellular and Comparative Physiology, 17, 243-258.

Pfaffman, C. (1951). Taste and smell. In S.S. Stevens (Ed.), Handbook of Experimental Psychology. New York: Wiley. pp.1143-1171.

Pfaffman, C., Frank, M. & Norgren, R. (1979). Neural mechanisms and behavioral aspects of taste. Annual Review of Psychology, 30, 283-325.

Pfaffman, C., Norgren, R. & Grill, H.J. (1977). Sensory affect and motivation. Annals of the New York Academy of Sciences, 290, 18-34.

Piggott, J.R. & Harper, R. (1975). Ratio scales and category scales of odor intensity. Chemical Senses, 1, 307-316.

Price, D.D., McGrath, P.A., Rafii, A. & Buckingham, B. (1983). The validation of visual analogue scales as ratio scale measures for chronic and experimental pain. Pain, 17, 45-56.

Rolls, B.J. (1986). Sensory specific satiety. Nutrition Review, 44, 93-101.

Rolls, B.J., Hetherington, M. & Laster, L.J. (1988). Comparison of the effects of aspartame and sucrose on appetite and food intake. Appetite, 11(Suppl), 62-67.

Rolls, E.T., Rolls, B.J. & Rowe, E.A. (1983). Sensory-specific and motivation-specific satiety for the sight and taste of food and water in man. Physiology and Behavior, 30, 185-192.

Rolls, B.J., Rolls, E.T., Rowe, E.A. and Sweeney, K. (1981). Sensory specific satiety in man. Physiology and Behavior, 27, 137-142.

Rolls, B.J., Rowe, E.A. and Rolls, E.T. (1982). How sensory properties of foods affect human feeding behavior. Physiology and Behavior, 29, 409-417.

Sandick, B. & Cardello, A.V. (1981). Taste profiles from single circumvallate papillae: comparison with fungiform profiles. Chemical Senses, 6, 197-214.

Scherr, S. & King, K.R. (1982). Sensory and metabolic feedback in the modulation of taste hedonics. Physiology and Behavior, 29, 827-832.

Schiffman, S.S., Cahn, H. & Lindley, M.G. (1981). Multiple receptor sites mediate sweetness: Evidence from cross-adaptation. Pharmacology, Biochemistry, and Behavior, 15, 377-388.

Schiffman, S.S. & Erickson, R.P. (1971). A psychophysical model for gustatory quality. Physiology and Behavior, 7, 617-633.

Schiffman, S.S., McElroy, A.E. & Erickson, R.P. (1980). The range of taste quality of sodium salts. Physiology and Behavior, 24, 217-224.

Sclafani, A. (1987). Carbohydrate taste, appetite, and obesity: An overview. Neuroscience and Biobehavioral Reviews, 11, 131-153.

Sclafani, A. (1988). Carbohydrate appetite in rats: Taste and postingestive factors. Appetite, 11, 20-25.

Sclafani, A. & Nissenbaum, J.W. (1985). Is gastric sham feeding really sham feeding? American Journal of Physiology, 248, R387-R390.

Scott, T.R. (1991). Gustatory control of food selection. In E.M. Stricker (Ed.), Handbook of Behavioral Neurobiology: Vol. 10. Neurobiology of Food and Fluid Intake (pp.243-263). New York: Plenum Press.

Smith, D.V. & McBurney, D.H. (1969). Gustatory cross-adaptation: Does a single mechanism code the salty taste? Journal of Experimental Psychology, 80, 101-105.

Smith, V.V. & Halpern, B.P. (1983). Selective suppression of judged sweetness by ziziphins. Physiology and Behavior, 30, 867-874.

Smith, D.V., VanBuskirk, R.L., Travers, J.B. & Bieber, S.L. (1983a). Gustatory neuron types in hamster brain stem. Journal of Neurophysiology, 50, 522-540.

Smith, D.V., VanBuskirk, R.L., Travers, J.B. & Bieber, S.L. (1983b). Coding of taste stimuli by hamster brain stem neurons. Journal of Neurophysiology, 50, 541-558.

Steiner, J.E. (1979). Human facial expressions in response to taste and smell stimulation. Advances in Child Development and Behavior, 13, 257-295.

Stevens, S.S. (1961). To honor Fechner and repeal his law. Science, 133, 80-86.

Stone, H. & Sidel, J.L. (1985). Sensory Evaluation Practices. Orlando: Academic Press.

Thompson, D.A., Moskowitz, H.R. & Campbell, R.G. (1977). Taste and olfaction in human obesity. Physiology and Behavior, 19, 335-337.

Tonosaki, K. & Funakoshi, M. (1988). Voltage- and current-clamp recordings of the receptor potential in mouse taste cell. Brain Research, 445, 363-366.

Travers, J.B., Travers, S.P. & Norgren, R. (1987). Gustatory neural processing in the hindbrain. Annual Review of Neuroscience, 10, 595-632.

Velle, W. (1987). Sex differences in sensory functions. Perspectives in Biology and Medicine, 30, 490-522.

Warwick, Z.S. (1990). Development of taste preferences: Implications for nutrition and health. Nutrition Today, 15-18.

Weingarten, H.P. (1985). Stimulus control of eating: Implications for a two-factor theory of hunger. Appetite, 6, 387-401.

Weingarten, H.P. & Bedard, M. (1991). Diet palatability: Its definition, measurement, and experimental analysis. In S.J. Cooper & J.M. Liebman (Eds.), The Neuropharmacology of Appetite. Oxford University Press.

Weingarten, H.P., Duong, A., Gowans, S. & Elston, D. (1990). The interpretation of sham feeding data: Curve shift. Abstract #376.17, presented at the Society for Neuroscience Annual Conference, St. Louis, November 1990.

Weingarten, H.P. & Watson, S.D. (1982). Sham feeding as a procedure for assessing the influence of diet palatability on food intake. Physiology and Behavior, 28, 401-407.

Weizenbaum, F., Benson, B., Solomon, L. & Brehony, K. (1980). Relationship among reproductive variables, sucrose taste reactivity and feeding behavior in humans. Physiology and Behavior, 24, 1053-1056.

Westermann, R. (1982). Empirical test of scale type resulting from the Power Law for heaviness. Perceptual and Motor Skills, 55, 1167-1173.

Wetherill, G.B. & Levitt, H. (1965). Sequential estimation of points on a psychometric function. British Journal of Mathematical and Statistical Psychology, 18, 1-10.

Whissell-Buechy, D. (1990). Genetic basis of the phenylthiocarbamide polymorphism. Chemical Senses, 15, 27-37.

Whissell-Buechy, D. (1990b). Effects of age and sex on taste sensitivity to phenylthiocarbamide (PTC) in the Berkeley Guidance sample. Chemical Senses, 15, 39-57.

Witherly, S.A., Pangborn, R.M. & Stern, J.S. (1980). Gustatory responses and eating duration of obese and lean adults. Appetite, 1, 53-63.

Wright, P. & Crow, R.A. (1973). Menstrual cycle: Effect on sweetness preferences in women. Hormones and Behavior, 4, 387-391.

Yensen, R. (1959). Some factors affecting taste sensitivity in man. I. Food intake and time of day. Quarterly Journal of Experimental Psychology, II, 221-229.

Young, P.T. & Greene, J.T. (1953). Quantity of food ingested as a measure of relative acceptability. Journal of Comparative and Physiological Psychology, 46, 288-294.

Zellner, D.A., Berridge, K.C., Grill, H.J. & Ternes, J. (1985). Rats learn to like the taste of morphine. Behavioral Neuroscience, 99, 290-300.

Zwislocki, J.J. & Goodman, D.A. (1980). Absolute scaling of sensory magnitudes: A validation. _Perception and Psychophysics_, _28_, 28-38.