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Cortical activation in response to pure taste stimuli during the physiological states of hunger and satiety

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ABSTRACT

This event-related functional magnetic resonance imaging (er-fMRI) study investigated BOLD signal change in response to a series of pure gustatory stimuli that varied in stimulus quality when subjects were hungry and sated with a nutritional pre-load. Group analyses showed significant differences in activation in the hunger minus satiety condition in response to sucrose, caffeine, saccharin, and citric acid within the thalamus, hippocampus, and parahippocampus. When examining the hunger and satiety conditions, activation varied as a function of stimulus, with the majority of the stimuli exhibiting significantly greater activation in the hunger state within the insula, thalamus, and substantia nigra, in contrast to decreased activation in the satiated state within the parahippocampus, hippocampus, amygdala, and anterior cingulate. Region of interest (ROI) analysis revealed two significant interactions, ROI by physiology and ROI by physiology by stimulus. In the satiety condition, the primary (inferior and superior insulae) and secondary (OFC 11 and OFC 47) taste regions exhibited significantly greater brain activation in response to all stimuli than regions involved in processing eating behavior (hypothalamus), affect (amygdala), and memory (hippocampus, parahippocampus and entorhinal cortex). These same regions demonstrated significantly greater activation within the hunger condition than the satiety condition, with the exception of the superior insula. Furthermore, the patterns of activation differed as a function taste stimulus, with greater activation in response to sucrose than to the other stimuli. These differential patterns of activation suggest that the physiological states of hunger and satiety produce divergent activation in multiple brain areas in response to different pure gustatory stimuli.

Introduction

Taste influences caloric intake and warns against ingestion of harmful substances (Scott et al., 1995). Behaviorally, caloric intake is modulated by physiological and psychophysical changes associated with hunger and satiety. Specifically, there is a positive association between physiological states of hunger and perceived taste pleasantness, a phenomenon termed "allesthesia" (Cabanac, 1971). Moreover, Cabanac and Duclaux (1970) demonstrated that the modulation of perceived pleasantness by physiological state occurs 45 min after food consumption, suggesting that post digestive signals influence pleasantness and subsequent food consumption. Eating behavior can also be modified by changes in the perceived pleasantness of the sensory qualities associated with food recently consumed, termed sensory specific satiety (Rolls et al., 1981). Sensory-specific satiety can occur as early as 2 min after ingestion of food, and results in decreased pleasantness and subsequent termination of intake of the food previously consumed (Rolls et al., 1981).

Single neuron recordings from the non-human primate provide anatomical and functional foundations on which to base hypotheses regarding cortical taste regions in humans. Electrophysiological studies investigating the sight and taste of food have demonstrated that regions within the primary and secondary taste cortices are differentially modulated by satiety. Specifically, satiety did not alter neuronal signaling in response to taste stimuli in the nucleus of the solitary tract (Rolls, 1989; Yaxley et al., 1985), frontal opercular cortex (Rolls et al., 1988), or the insular cortex (Yaxley et al., 1985). However, satiety modulated the signaling of individual neurons within the amygdala, by as little as 1% and as much as 100%, with a mean suppression rate of 58%. Interestingly, single neuronal signaling in the caudolateral orbitofrontal cortex [OFC; (Rolls et al., 1989)], and hypothalamus (Burton et al., 1976), decreased to zero when the monkey became satiated. However, when presented with a novel stimulus, signaling within these regions returned. It has been suggested that the amygdala's functional and anatomical location between the primary gustatory cortex, which shows no effect of satiety, and the OFC and hypothalamus, which show complete

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suppression after satiety, may be indicative of the amygdala's involvement in processing affective information that is partially modulated by physiological state (Yan and Scott, 1996).

Human neuroimaging studies provide further information regarding neuroanatomical correlates involved in the physiological states of hunger and satiety. Several neuroimaging studies examining the effects of hunger and satiety on activation to chemosensory stimuli have reported consistent activation within the insular cortex (Tataranni et al., 1999; Del Parigi et al., 2002b; Kringelbach et al., 2003; Uher et al., 2006), OFC; (Small et al., 2001; Del Parigi et al., 2002a; Kringelbach et al., 2003; Gottfried et al., 2003), hippocampal formation (Tataranni et al., 1999; Gautier et al., 1999), dorsolateral prefrontal cortices (Tataranni et al., 1999; Uher et al., 2006), and the striatum (Tataranni et al., 1999; Kringelbach et al., 2003). However, inconsistencies remain in the literature regarding global patterns of activation. These inconsistencies in brain regions modulated by hunger and satiety may be a result of the type of chemosensory stimuli employed. To address this concern, the current study investigated brain response to a series of pure gustatory stimuli that varied in stimulus quality, using an event-related fMRI design to investigate modulation of response to pure gustatory stimuli by hunger and satiety.

Flavor stimuli elicit the involvement of taste and olfactory systems. Behaviorally, for the participant, this often results in taste–smell confusions; in which an odor stimulus presented in the oral cavity is attributed to taste and not olfaction (Cerf-Ducastel and Murphy, 2001; Frank and Byram, 1988; Murphy and Cain, 1980; Murphy et al., 1977; Rozin, 1982; Stevenson et al., 1999).

At the central level, non-human primate studies using single neuron recordings provide a neuroanatomical basis for taste/smell confusion. Previous research has shown that there is close proximity within the OFC of unimodal neurons involved in taste, olfaction, and vision and bimodal and multi-modal neurons (Tanabe et al., 1975; Thorpe et al., 1983; Rolls et al., 1990; Rolls and Baylis, 1994). Moreover, in functional magnetic resonance imaging (fMRI) experiments, Cerf-Ducastel and Murphy (2001) showed that olfactory stimuli delivered in the mouth activated areas typically associated with taste response, e.g., OFC, insula and Rolandic operculum; and de Araujo and colleagues demonstrated that delivering taste and olfactory stimuli independently elicited activation that overlapped within the caudal OFC, amygdala, insula, and frontal operculum (de Araujo et al., 2003c).

Recent fMRI experiments examining the response to complex flavor stimuli during hunger and satiety suggest that sensory qualities of the stimuli may differentially activate regions involved in flavor perception (Uher et al., 2006; Kringelbach et al., 2003). Discriminating between brain regions involved in gustatory processing from regions involved in olfactory processing during hunger and satiety is an important component in understanding regions involved in flavor perception, as well as the effect of physiological condition on eating behavior.

The present study used event-related fMRI (er-fMRI) to investigate differential brain activation in response to six pure taste stimuli in two physiological states: hunger and satiety. The purpose of the current study is to elucidate the central processes involved in taste perception and the modulation by hunger and satiety of activation in these regions. Thus, a series of stimuli representing different taste qualities were employed in order to extract commonalities associated with taste stimulation and examine differences associated with quality. In addition, understanding how taste is modulated by hunger and satiety is critical for determining the neural substrates of eating disorders and the nutritional deficits that occur in the aging population.

Method

A more detailed description of the development of the materials and methods used in this study can be found in Haase et al., 2007, in the Journal of Neuroscience Methods.

Participants

Eighteen healthy young adults, nine females and nine males, ranging in age from 19 to 22 years (M=20.7, SD=0.99) participated in the study after giving informed consent. Subjects received monetary compensation for participating in the study. The Institutional Review Boards at both San Diego State University and the University of California, San Diego approved the research.

Screening session

In the first session subjects completed the chemosensory assessment to screen for ageusia and anosmia with taste and odor threshold measurements (Cain et al., 1983; as modified in Murphy et al., 1990). Exclusionary criteria consisted of ageusia, anosmia, and upper respiratory infection or allergies within the prior 2 weeks. Subjects completed preliminary fMRI safety screening and the Three Factor Eating Questionnaire (Stunkard and Messick, 1985) was administered to screen for restrained eating. Participants were within normal limits.

Experimental procedure

In the second and third sessions, the participants fasted for 12 h prior to arrival and were randomly presented either with pre-load consisting of 474 ml (two bottles) of Vanilla flavored Ensure Plus or without pre-load and then completed an fMRI session conducted on a 3T GE whole body scanner.

Immediately before, after, and during the scan, participants rated their hunger and the pleasantness and intensity of the six stimuli. Participants used the general Labeled Magnitude Scale (gLMS) to rate intensity and a modified gLMS scale to rate pleasantness and hunger (Fig. 1; Green et al., 1993; Green et al., 1996; Bartoshuk et al., 2004). Data analysis involving the evaluation of intensity and pleasantness during the scan is not described here but is the subject of another manuscript.

Stimuli

The following pure taste stimuli were presented dissolved in distilled water: caffeine, 0.04 M; citric acid, 0.01 M; guanosine 5′-

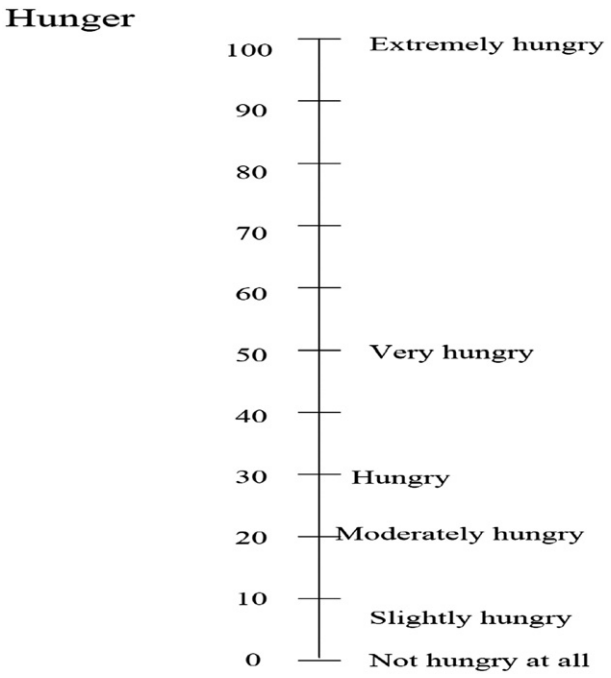

Fig. 1. Labeled magnitude scale (LMS) for hunger.