



Research report

Males and females show differential brain activation to taste when hungry and sated in gustatory and reward areas[☆]Lori Haase^a, Erin Green^a, Claire Murphy^{a,b,c,*}^a San Diego State University/University of California San Diego, Joint Doctoral Program in Clinical Psychology, San Diego, CA, United States^b Department of Psychology, San Diego State University, San Diego, CA, United States^c Department of Head and Neck Surgery, University of California San Diego School of Medicine, San Diego, CA, United States

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ABSTRACT

Although males and females differ in eating behavior and prevalence rates for eating disorders and obesity, little is known about gender differences in cortical activation to pleasant and unpleasant pure tastes during the physiological states of hunger and satiety. Twenty-one healthy young adults (12 females and 9 males) underwent two functional magnetic resonance imaging scans. Using four pure tastants of differing qualities (i.e., salty, sour, bitter, sweet), the present study examined gender differences in fMRI activation during two motivational states (hunger and satiety). There was greater change in fMRI activation from hunger to satiety in males than females in response to all tastes within the middle frontal gyrus (BA 10), insula, and cerebellum. Males also had greater change in activation from hunger to satiety, relative to females, in limbic regions including dorsal striatum, amygdala, parahippocampal gyrus, and posterior and anterior cingulate; however, activation was stimulus dependent, despite equivalent ratings in perceived pleasantness and intensity. Interestingly, males and females showed significant change from hunger to satiety in response to citric acid, suggesting that in addition to gender and physiological condition, stimulus quality is an important factor in taste fMRI activation. These gender differences may have implications for the pathophysiology of eating disorders and obesity.

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Introduction

Gender differences in eating behavior have been widely documented (Conner, Johnson, & Grogan, 2004; Fagerli & Wandel, 1999; Rolls, Fedoroff, & Guthrie, 1991; Wardle et al., 2004; Zylan, 1996). Clinical manifestations of eating disorders such as bulimia and anorexia nervosa have greater incidence rates among females relative to males (Jacobi, Hayward, de Zwaan, Kraemer, & Agras, 2004; Kjelsas, Bjornstrom, & Gotestam, 2004; Woodside et al., 2001) and prevalence of obesity is greater in females (Flegal, Carroll, & Odgen, 2010). Males and females differ in caloric intake (Basiotis, Thomas, Kelsay, & Mertz, 1989), which may in part, be a result of differential eating styles (Green, 1987; Hill & McCutcheon, 1984; Mori & Pliner, 1987). In addition, differential cultural pressures to achieve ideal body shapes may influence the way males and females

respond to food to a different degree (Ostovich & Rozin, 2004; Rolls et al., 1991; Rozin, Trachtenberg, & Cohen, 2001).

Food consumption and termination are regulated by a complex system of peripheral and central processes that interact with genetics and environmental factors (Lenard & Berthoud, 2008). The gustatory system is one of the first sensory systems involved in food intake. Interestingly, gustatory psychophysical experiments examining gender differences have been inconsistent (Enns, Van Itallie, & Grinker, 1979; Robin, Rousmans, Dittmar, & Vernet-Maury, 2003). Enns et al. (1979) found that while males and females reported identical perceptions of sucrose intensity (using subjective ratings), hedonic evaluations were significantly different. In particular, males perceived higher concentrations of sucrose as more pleasant when compared to females. Conversely, other studies have reported no significant gender differences in the perceived pleasantness of taste stimuli (sweet, sour, salty, bitter; Robin, Rousmans, Dittmar, & Vernet-Maury, 2003) or in the perceived pleasantness and intensity of calcium (Leshem, Katz-Levin, & Schulkin, 2003).

Gender differences in the psychophysical evaluation of taste stimuli are more consistently observed when hunger and satiety are controlled (Laeng, Berridge, & Butter, 1993). Females perceive the sweetness of sucrose as more intense relative to males across physiological condition, and also perceive sucrose as less pleasant

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than males after a meal (Laeng et al., 1993). Additionally, females rate food images as more pleasant than males after a 12-h fast, and less pleasant than males in a non-fasted condition (Stoeckel, Cox, Cook, & Weller, 2007). Although inconclusive, these findings suggest that physiological state may alter the subjective pleasantness of food-related stimuli to a greater extent in females than males.

Although neuroimaging studies have reported significant gender differences in brain activation during the physiological conditions of hunger and satiety in response to flavor (Del Parigi et al., 2002; Smeets et al., 2006) and food pictures (Cornier, Salzberf, Endly, Bessesen, & Tregellas, 2010; Frank et al., 2010; Uher, Treasure, Heining, Brammer, & Campbell, 2006), to date, no study has examined gender differences during hunger and satiety in response to pure tastes.

The perceived valence of a stimulus (e.g., pleasant or unpleasant) modulates patterns of cortical activation. In regard to chemosensory stimuli, valence specific brain activation has been localized within emotion processing regions such as the orbital frontal cortex (OFC) and amygdala (Francis et al., 1999; Kringelbach, O'Doherty, Rolls, & Andrews, 2003; O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001; Small, Zatorre, Dagher, Evans, & Jones-Gotman, 2001; Zald, Hagen, & Pardo, 2002). Findings from research involving other sensory modalities demonstrate that valence-specific activation is further influenced by gender. Specifically, gender differences have been reported in response to stimuli with various affective characteristics including olfaction (Berglunds, Lindstrom, & Savic, 2006; Levy et al., 1997; Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003; Savic, Berglund, & Lindstrom, 2005; Yousem et al., 1999), visual cues (Killgore & Yurgelun-Todd, 2010; Klein et al., 2003; Schienle, Schafer, Stark, Walter, & Vaitl, 2005; Wrase et al., 2003), happiness and sadness (Azim, Mobbs, Jo, Menon, & Reiss, 2005; Schneider, Habel, Kessler, Salloum, & Posse, 2000), and unpleasant words associated with body image (Shirao, Okamoto, Mantani, Okamoto, & Yamawaki, 2005). While the direction of gender effects across experiments vary, consistent differences in activation are observed within the inferior frontal gyrus (IFG), anterior cingulate cortex (ACC), and amygdala.

We have previously shown that the physiological conditions of hunger and satiety influence brain activation in young (Haase, Cerf-Ducastel, & Murphy, 2009) and older adults (Jacobson, Green, & Murphy, 2010) in response to pure taste stimuli. However, gender differences in brain activation during hunger and satiety in response to pure taste stimuli have yet to be examined. Additionally, it is unknown what role gender has in cortical activation in response to pleasant and unpleasant taste stimuli. Therefore, one aim of the present event-related fMRI study was to investigate gender differences in cortical fMRI activation in response to pure taste stimuli when subjects were hungry or satiated. In addition, using this experimental design we have previously reported decreases in fMRI activation in regions implicated in emotion and modulation of eating behavior (e.g., amygdala, hypothalamus, inferior insula, orbitofrontal cortex; Haase et al., 2009), so we also examined gender differences in the change in brain activation from hunger to satiety.

Methods

A more detailed description of the materials and methods used in this study can be found in Haase, Cerf-Ducastel, Buracas, and Murphy (2007), in the *Journal of Neuroscience Methods*.

Participants

Twenty-one healthy young adults, 12 females and 9 males, ranging in age from 19 to 26 years (Males: $M = 20.44$; Females: $M = 21.58$), participated in the study after providing written informed consent. They received monetary compensation for their

participation. The Institutional Review Boards at both San Diego State University and the University of California, San Diego approved the research. Data from these subjects have been previously published (Haase, Cerf-Ducastel, Buracas, & Murphy, 2007; Haase et al., 2009; Jacobson et al., 2010).

Screening session

In the first session, participants completed the chemosensory assessment to screen for ageusia and anosmia with taste and odor threshold measurements (Cain, Gent, Catalanotto, & Goodspeed, 1983; as modified in Murphy, Gilmore, Seery, Salmon, & Lasker, 1990). Exclusionary criteria consisted of ageusia, anosmia, and upper respiratory infection or allergies within the prior two weeks (Harris, Davidson, Murphy, Gilbert, & Chen, 2006). Participants also completed the Three-Factor Eating Questionnaire (Stunkard & Messick, 1985), to screen for restrained eating, and the preliminary fMRI safety screening. With regards to restrained eating, participants were within normal limits (≤ 12), with the exception of one female participant who scored 13 on the cognitive restraint factor.

Experimental procedure

In the second and third sessions, the participants fasted for 12 h prior to arrival and were randomly presented with either a pre-load consisting of 474 ml (700 kcal) of Vanilla flavored Ensure Plus (sated condition) or were not administered a pre-load (hungry condition) and then completed an fMRI session conducted on a 3T GE whole body scanner. Before, after, and during the scans, participants rated the pleasantness of the taste stimuli, using a modified version of the general Labeled Magnitude Scale (gLMS; Bartoshuk et al., 2004; Green, Shaffer, & Gilmore, 1993; Green et al., 1996). Participants also rated their perceived hunger before and after the scans using a modified gLMS.

Stimuli

Participants were administered 6 stimuli while in the scanner, 4 of which represented the basic tastes of bitter, sour, sweet and salty and were the focus of the present manuscript. The taste stimuli were presented dissolved in distilled water: caffeine, 0.04 M; citric acid, 0.01 M; sucrose, 0.64 M; and sodium chloride (NaCl), 0.16 M.

Stimulus presentation

Inside the scanner, the participant lay supine and was fitted with a bite bar, which was positioned comfortably between the lips so that the tubes delivered stimuli to the tip of the tongue (see Fig. 1). The taste stimuli and water were delivered at room temperature each through a unique 25 ft long plastic tube, which was connected to a different computer-programmable syringe pump. The pumps were programmed to present 0.3 ml of solution in 1 s (Haase et al., 2007).

During the functional run, the stimuli were counter-balanced and separated by a 10 s inter-stimulus interval (ISI). Stimulus presentation was followed by two presentations of water; the first presentation of water was used as a rinse and the second presentation of water was used as a baseline comparison for each tastant. Instructions were displayed on a screen through a computer interface.

fMRI scanning paradigm

Experimental design

Scans consisted of a pleasantness run 24 min (1440s) in duration, where each stimulus was presented eight times. Two

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