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Age differences in the brain mechanisms of good taste

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ABSTRACT

There is strong evidence demonstrating age-related differences in the acceptability of foods and beverages. To examine the neural foundations underlying these age-related differences in the acceptability of different flavors and foods, we performed an fMRI study to investigate brain and hedonic responses to orange juice, orange soda, and vegetable juice in three different age groups: Young (22), Middle (40) and Elderly (60 years). Orange juice and orange soda were found to be liked by all age groups, while vegetable juice was disliked by the Young, but liked by the Elderly. In the insular primary taste cortex, the activations to these stimuli were similar in the 3 age groups, indicating that the differences in liking for these stimuli between the 3 groups were not represented in this first stage of cortical taste processing. In the agranular insula (anterior to the insular primary taste cortex) where flavor is represented, the activations to the stimuli were similar in the Elderly, but in the Young the activations were larger to the vegetable juice than to the orange drinks; and the activations here were correlated with the unpleasantness of the stimuli. In the anterior midcingulate cortex, investigated as a site where the activations were correlated with the unpleasantness of the stimuli, there was again a greater activation to the vegetable than to the orange stimuli in the Young but not in the Elderly. In the amygdala (and orbitofrontal cortex), investigated as sites where the activations were correlated with the pleasantness of the stimuli, there was a smaller activation to the vegetable than to the orange stimuli in the Young but not in the Elderly. The Middle group was intermediate with respect to the separation of their activations to the stimuli in the brain areas that represent the pleasantness or unpleasantness of flavors. Thus age differences in the activations to different flavors can in some brain areas be related to, and probably cause, the differences in pleasantness of foods as they differ for people of different ages. This novel work provides a foundation for understanding the underlying neural bases for differences in food acceptability between age groups.

Introduction

There are age-related differences in the acceptability of different foods. For example children may not take readily to a wide range of vegetables, yet find sweet foods palatable (Birch, 1999; Hetherington et al., 2011). Adults may find a wide range of foods pleasant. As people age, smell and even taste may become less sensitive (for example when tested with stimuli close to threshold) (Jacobson et al., 2010; Murphy, 1993; Murphy et al., 2002; Stevens et al., 1995), and this may contribute to the changes in eating that can occur in aging (Green et al., 2011; Murphy, 1989; Rolls, 1999). However, age-related changes in the ability to discriminate foods at the sensory threshold – the point at which we can just detect tastes – may not be the main factor that accounts for why people's propensity to different foods is different at different ages, because most foods have ingredients that are far above the detection threshold. Therefore we did not attempt to measure effects close to threshold in the different age groups, but instead used the real foods and beverages described. In order to examine the neural mechanisms underlying the age-related differences in the acceptability of different flavors and foods, we performed the fMRI study described here with three different age groups (termed Young, mean age 22 years; Middle, mean age 40; and Elderly, mean age 60) and used foods, that is stimuli that include different taste, olfactory, and texture components, rather than pure tastes (such as sweet or bitter) which have been used in some previous studies (Green et al., 2013; Jacobson et al., 2010), because we are interested in responses to real, ecologically valid, foods. Indeed, in previous studies we have shown that the convergence of taste and odor to produce flavor occurs anterior to the insular taste cortex in the agranular insular cortex and areas that receive from it including the orbitofrontal cortex and anterior cingulate cortex (de Araujo et al., 2003c; Rolls, 2015c,e); and that the flavor formed by convergence of a taste such as monosodium glutamate and an odor such as vegetable odor can produce a flavor much more pleasant than the components, which is reflected in activations in the orbitofrontal and anterior cingulate cortex (McCabe and Rolls, 2007). Further, we were interested in how cognitive descriptions of foods, such as "no

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added calories", and "nutritionally relevant for the elderly" might influence the responses of different brain regions to foods in the different age groups, given that we have shown that there are strong effects of cognitive descriptions on the responses of some brain regions to odor (de Araujo et al., 2005), and to taste and flavor (Grabenhorst et al., 2008).

A further important aim of this investigation was to measure the extent to which responses of brain systems involved in the identification and intensity processing of a food differ from those involved in determining the pleasantness in people of different age groups, for it is likely to be the processing in pleasantness (hedonic or affective) systems that drives food intake (Rolls, 2012b, 2014a, 2015d,e). Indeed, in the primate including human brain, there are two partly independent systems for analyzing taste, olfaction, and flavor. One system is for the intensity and identity of taste (the insular primary taste cortex in the anterior dorsal granular insula and adjoining frontal operculum) and odor (pyriform primary olfactory cortex), where activations correlate with intensity and not pleasantness ratings, and where feeding to satiety does not reduce neural activity (Grabenhorst and Rolls, 2008; Rolls, 2012b, 2014a; Rolls et al., 1988, 2008; Yaxley et al., 1988). These areas project into the agranular insular cortex just anterior to the primary taste cortex to produce flavor representations (de Araujo et al., 2003c). The second main system (which receives input from the agranular insula, and the insular primary taste cortex and the pyriform primary olfactory cortex) is the orbitofrontal cortex, which then projects onto the anterior cingulate cortex. Activations in both the orbitofrontal cortex and anterior (pregenual) cingulate cortex are linearly correlated with the subjective pleasantness of the taste, odor, or flavor (Grabenhorst and Rolls, 2011; Rolls, 2005, 2012b; Rolls and Grabenhorst, 2008). These taste, olfactory, and flavor processing pathways are illustrated in diagrams available elsewhere (Grabenhorst and Rolls, 2011; Rolls, 2012b, 2014a, b, 2015c, e; Rolls and Grabenhorst, 2008).

Given these aims, the research questions and associated hypotheses to be tested included the following: H1. For sweet and savory whole food stimuli (that include taste, olfactory, and texture components), are there age-related differences in activations in the insular primary taste cortex that are related to the liking (measured by subjective pleasantness) of the different foods? H2. For sweet and savory whole food stimuli, are there age-related differences in activations in the agranular insula, orbitofrontal cortex, amygdala, and anterior cingulate cortex that are related to the liking (measured by subjective pleasantness) of the different foods? H3. How do differences in different age groups in brain processing that are related to pleasantness separate from any differences in the processing of the intensity of the stimuli? H4. Do cognitive descriptions of foods influence differently in different age groups the responses of different brain systems to foods? To test H4 we compared responses to the identical flavor (Fanta®) when it was labeled as the regular energy Fanta® and as the low energy orange flavor drink (Fanta® Zero) that was labeled "no added calories". It was hypothesized that this might have an effect especially in the Young group. We also tested H4 by comparing responses to identical vegetable juice, but in one case providing a cognitive description claiming that it contained ingredients useful for healthy aging. It was hypothesized that this might have different effects in the Elderly vs the Young group.

We had prior hypotheses about the locations in the brain where different types of flavor-related activation would be found, as follows (Grabenhorst and Rolls, 2011; Rolls, 2012b, 2014a, 2015c,e; Rolls and Grabenhorst, 2008). Activations to taste, flavor, and texture stimuli are found in the primary taste cortex in the anterior dorsal granular insula and adjoining frontal opercular cortex (de Araujo et al., 2003a; de Araujo and Rolls, 2004; Small, 2010), and these activations reflect the subjective intensity of the stimuli (Grabenhorst and Rolls, 2008) and can be influenced by top-down processing (Bender et al., 2009; Ge et al., 2012; Grabenhorst and Rolls, 2008; Luo et al., 2013; Nitschke et al., 2006). Activations to taste, odor, and their combination to produce flavor, are found in the agranular insular cortex (de Araujo et al., 2003c; Small and Prescott, 2005). Activations to the hedonic value of taste, flavor, and texture stimuli are found in the orbitofrontal cortex, with activations medially related to the pleasantness of the stimuli, and more laterally to the unpleasantness of the stimuli (Grabenhorst and Rolls, 2011). Activations to taste and flavor stimuli are found in the amygdala (which receives inputs from the primary taste and olfactory cortices (Rolls, 2014a)), with activations that are produced by pleasant and by unpleasant stimuli (Kadohisa et al., 2005a; Karadi et al., 1998; O'Doherty et al., 2001). Activations to the hedonic value of taste, flavor, and texture stimuli are found in the anterior cingulate cortex, with activations in the pregenual cingulate cortex related to the pleasantness of the stimuli, and in the anterodorsal cingulate cortex to the unpleasantness of the stimuli (Grabenhorst and Rolls, 2011; Rolls, 2015a).

We note that as commonly used, "taste" applied to foods includes at least gustatory components as defined by taste receptors sensitive to sweet, salt, bitter, sour, and umami; olfactory components sensed by the olfactory receptors in the nose; and texture components, including oral viscosity, fat texture, and grittiness (Rolls, 2012b, 2015c,e). Together, these components, with further contributions of the sight of the food and cognitive effects such as the verbal description of the food, produce what is often termed flavor. The stimuli used in this investigation were real foods and beverages, so included these components, and it is the neural bases of these flavor effects that are being investigated. For simplicity and consistent with natural language usage, we sometimes refer to the stimuli as taste stimuli, but for the stimuli used in this investigation, note that flavor as defined above is a more technical term that applies to these stimuli.

Methods

Design of the investigation

Volunteers in three age groups were scanned using fMRI while different drinks were delivered with different picture and label descriptions to investigate whether the representations of the reward value of these beverages in the brain changes as a function of age.

The three age groups recruited were: 18–26 (Young, Y); 34–46 (Middle, M); and 53–67 (Elderly, E) years of age, with further description under Participants. One of the beverages used was the soft drink Fanta®, which is highly acceptable to the Young group, but consumed less by the older groups. It was provided in two forms which have the same flavor but different labels which may influence different groups differently, Fanta® and Fanta® Zero. The third Fanta stimulus was the flavor without a labeled picture, and was incorporated in case it helped to reveal cognitive effects. Brain activations to these were compared to orange juice (which is pleasant and is known to be consumed by most age groups so forms a useful reference stimulus). Comparisons were also made to a savory drink, a tomato flavor vegetable drink, V8®, because this is more likely to appeal to the Elderly group and is potentially suitable for incorporating health-promoting ingredients with labels designed to appeal to the Elderly group. The V8 was provided in two forms, one with a cognitive label emphasizing attributes that might be of especial interest to the elderly, and the other with the same picture of V8 but without the same cognitive label.

The design was to recruit for each group 20 participants, 10 males and 10 females, to allow between-group statistical comparisons. The subjects were recruited from Reading, UK. All stimuli were purchased in the UK, and were as follows, with the images displayed during the delivery of the beverages as described.

T1. Fanta® with a picture label of a can of Fanta® designed to ensure that we are measuring brain responses in this condition to a beverage identified as Fanta®.

T2. Fanta® with a picture label of a can of Fanta® zero and the words "No added sugar" designed to appeal to those concerned with their energy intake.